35937

National Library of Canada / Bibliothèque nationale du Canada

CANADIAN THESES ON MICROFICHE / *THÈSES CANADIENNES SUR MICROFICHE*

NAME OF AUTHOR/*NOM DE L'AUTEUR* LOBBAN, CHRISTOPHER SIMON

TITLE OF THESIS/*TITRE DE LA THÈSE* TRANSLOCATION OF ^{14}C IN THE GIANT KELPS MACROCYSTIS INTEGRIFOLIA AND M. PYRIFERA.

UNIVERSITY/*UNIVERSITÉ* SIMON FRASER

DEGREE FOR WHICH THESIS WAS PRESENTED/*GRADE POUR LEQUEL CETTE THÈSE FUT PRÉSENTÉE* Ph.D.

YEAR THIS DEGREE CONFERRED/*ANNÉE D'OBTENTION DE CE GRADE* 1977

NAME OF SUPERVISOR/*NOM DU DIRECTEUR DE THÈSE* DR. LOUIS D. DRUEHL

Permission is hereby granted to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

L'autorisation est, par la présente, accordée à la BIBLIOTHÈQUE NATIONALE DU CANADA de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans l'autorisation écrite de l'auteur.

DATED/*DATÉ* Feb 22 1977 SIGNED/*SIGNÉ* [redacted]

PERMANENT ADDRESS/*RÉSIDENCE FIXE* [redacted]

NL-91 (3-74)

National Library of Canada

Cataloguing Branch
Canadian Theses Division

Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada

Direction du catalogage
Division des thèses canadiennes

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us a poor photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de mauvaise qualité.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE

TRANSLOCATION OF ^{14}C IN THE GIANT KELPS *MACROCYSTIS INTEGRIFOLIA* AND *M. PYRIFERA*

by

CHRISTOPHER SIMON LOBBAN

B.Sc., Dalhousie University, 1971

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE

REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in the Department

of

Biological Sciences

SIMON FRASER UNIVERSITY

DECEMBER 1976

APPROVAL

Name: Christopher Simon Lobban

Degree: Doctor of Philosophy

Title of Thesis: Translocation of ^{14}C in the Giant Kelps Macrocystis Integrifolia and M. Pyrifera

Examining Committee:

Chairman: R.M.F.S. Sadleir

L.D. Druehl
Senior Supervisor

G.H. Geen

C.R. Lister

R.F. Scagel
Chairman, Botany Dept.
University of B.C.

L. Srivastava

PARTIAL COPYRIGHT LICENSE

I hereby grant to Simon Fraser University the right to lend my thesis or dissertation (the title of which is shown below) to users of the Simon Fraser University Library, and to make partial or single copies only for such users or in response to a request from the library of any other university, or other educational institution, on its own behalf or for one of its users. I further agree that permission for multiple copying of this thesis for scholarly purposes may be granted by me or the Dean of Graduate Studies. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Title of Thesis/Dissertation:

TRANSLOCATION OF ^{14}C IN THE GIANT KELPS MACROCYSTIS INTEGRIFOLIA AND M. PYRIFERA

Author:

(signature)

CHRISTOPHER S. LOBBAN

(name)

Feb 22 1977

(date)

ABSTRACT

The pattern of import and export of ^{14}C-labeled assimilates in Macrocystis integrifolia Bory (in British Columbia) and in M. pyrifera (L.) C.A. Agardh (in southern California) was studied by labeling single blades on fronds. A system of naming the fronds was devised to show their ontogenetic relationships, as a basis for understanding the translocation pattern.

A lag period of about 4 h before translocation could be detected was found in both species. Most experiments were of 24 h duration to allow accumulation of ^{14}C in weak sinks, while minimizing enclosure stresses on the labeled blade.

The pattern of import and export was similar to that of dicotyledons: actively growing tissue imported and did not export. As a blade reached maturity it began to export, at first only to the apex above it, later also down the frond to sporophylls and frond initials at the base of the frond, and into the apical regions of juvenile fronds; finally there was a phase, late in the life of the blade, when transport was only downwards. Young fronds imported from older fronds until they were approximately 1.5-2 m long in the case of M. integrifolia, and 3 m long in M. pyrifera, by which they had developed mature, upward-exporting blades. The distances of a blade from the apex at which export began and at which downward translocation began differed with the final length of adult fronds. This length

is a function of the depth of water in which the plant grows. Thus there were differences between the two species and also between different depth populations of M. pyrifera. In M. pyrifera at Arch Rock (8-10 m below low water) export began at approximately 1 m from the apex and downward transport 3.5 m from the apex. In M. integrifolia (1-2 m below low water) export began at about 0.3 from the apex, while downward transport began about 1.2 m from the apex in spring, and 0.5 m in fall. The seasonal changes in translocation pattern in M. integrifolia could be correlated with growth rate changes.

The translocation pattern was studied at various stages of the development of young M. integrifolia. The first few blades which are formed in the primary fronds -- which become frond initials and sporophylls -- begin export at about the time they are freed from the apical scimitar, but cease export when mature sterile laminae have been formed above them.

No translocation was found from a younger frond to an older frond, nor was there translocation upwards from a blade on a frond lacking the apical region. Removal of the apical scimitar and immature blades led to an increase in downward export. The apical scimitar and the immature free blades were found to be two sinks each capable of sustaining upward translocation . The cutting experiments suggest that there is apical dominance in Macrocystis.

ACKNOWLEDGEMENTS

First and foremost I must attempt to express my gratitude to my principal adviser, Dr. Louis D. Druehl. This is a difficult task, for at every stage of my research, and in so many ways, he provided guidance and counsel, while still leaving me ample room to think the project through myself. Not only that, he provided encouragement and recommendations for my studies abroad, which besides improving my thesis, were invaluable experiences that enriched my life and are appreciated more and more as time goes by.

I am thankful to Dr. Geoffry R. Lister for providing a plant physiologist's experience in guiding my research and evaluation of the results, as well as to the third member of my advisory committee, Dr. Glen H. Geen.

My fellow graduate students Dan Pace and Glyn Sharp were helpful on a day-to-day basis, often shivering beside me while I set up the experiments underwater, and often providing the first advice and criticism of my work. They were also good companions in the wilds of Bamfield (and the sometime wilds of the Marine Station!).

The list of other people who at times have provided a sounding board for my ideas, or comments on my research, is a longer one than I could copy down, but certainly I would be remiss to omit Hugo Barrales, Michael Coon, Glenn Cota, Mary Jo Duncan, Bruce Leaman and Wheeler North.

My studies on *M. integrifolia* were carried out at the Marine

Station, Bamfield, B.C. during the years in which it was becoming "established". The research station was set up through the efforts of many people at the five Western Canadian Universities, notably Drs. N.J. Wilimovsky (UBC) and D.M. Ross (U of A).

My studies of M. pyrifera were made possible through the cooperation and/or support of Dr. Wheeler J. North at Kerckhoff Marine Laboratory, and of Dr. David A. Coon at University of California, Santa Barbara. Dr. North gave me full use of the facilities in his lab, and an apartment at K.M.L.; Dr. Coon provided immediate assistance for four frantic days, tolerating my railroading with kindness and aplomb.

My attempt to study translocation with M. pyrifera in Argentina was thwarted despite the strenuous efforts of Dr. Hugo L. Barrales. Nevertheless, the ecological study which we were able to carry out was of great benefit to me, and the experience with M. pyrifera which it gave me is incorporated into this dissertation in many subtle ways.

On the technical side, I must first thank very much Dave Morley, radiation technician in Biological Sciences at Simon Fraser U. I sent him for counting far more scintillation vials than either of us cares to think about. He obtained the counts, and did the computer conversions of the great majority of the samples I prepared. In so doing he saved me not only the work itself, but also the innumerable trips to Vancouver that would have been necessary for me to do it.

During summer 1975 I had the capable assistance of Barbara Craig and Heather Washburn, whom the Provincial Government hired as

diver-technicians for me. Very many people, including Barb and Heather, have been persuaded to buddy for me in diving, sometimes for the fun of it, sometimes for reciprocity, and often as a favour. To all of them I express my thanks and appreciation.

The research was funded principally through National Research Council of Canada research grants to Dr. Druehl. The B.C. Dept. Recreation and Conservation, Marine Resources Branch provided a grant for the project, "Growth, translocation and harvesting interactions in Macrocystis integrifolia" -- thanks to L. Michael Coon of M.R.B. for his part in obtaining those funds. At S.F.U. the Faculty of Graduate Studies, through Dean Jon Wheatley, and the Biological Sciences Dept., chaired by Dr. Geen and later by Dr. John M. Webster, provided bursaries for my trip to Argentina in 1974, and for a course at the Marine Biological Laboratory, Wood Hole, in 1976.

I was supported by scholarships first from N.R.C., and then from S.F.U.; my hearty thanks to these organizations for P.B.J. to hold body and soul together.

Finally, my thanks to the scientists who have given critical reviews of the dissertation itself: my advisory committee, of course: Drs Druehl, Geen, and Lister; my external examiner, Dr. R.F. Scagel; and Dr. L.M. Srivastava.

TABLE OF CONTENTS

	Page
ABSTRACT	iii
ACKNOWLEDGEMENTS	v
TABLE OF CONTENTS	viii
LIST OF TABLES	x
LIST OF FIGURES	xii
INTRODUCTION	1
METHODS	5
I. Field procedures	5
II. Laboratory techniques	7
III. The study sites and species investigated	9
1. Macrocystis integrifolia Bory	9
2. Macrocystis pyrifera (L.) C.A. Agardh	11
MORPHOLOGY AND DEVELOPMENT OF MACROCYSTIS	25
RESULTS	25
I. Translocation in M. integrifolia	25
1. Bamfield Inlet, 1973	30
2. Ross Islets, 1975	35
3. Experiments on deep M. integrifolia	41
4. Development of translocation in young plants	41
5. Harvesting and translocation	51

Page

II. Translocation in Macrocystis pyrifera 51

1. Macrocystis pyrifera at Arch Rock 52
2. Macrocystis pyrifera at Kerckhoff Marine Laboratory 63
3. Macrocystis at Santa Barbara 70
4. Translocation in 1° fronds of M. pyrifera 70
5. Translocation in fronds lacking the apex 70

DISCUSSION 71

I. Translocation pattern in Macrocystis 71

II. Translocation and the environments of M. integrifolia and M. pyrifera 75

III. Harvesting, and apical dominance 78

IV. Translocation in Macrocystis and in vascular plants 80

REFERENCES 85

APPENDIX: Tables 1-6 + 9-11 94

LIST OF TABLES

Page

Table 1. Translocation experiments on M. integrifolia at Bamfield Inlet, May-June 1973 31

Appendix Table 1 97

Table 2. Translocation experiments on M. integrifolia at Bamfield Inlet, August-October 32

Appendix Table 2 101

Table 3. Translocation experiments on M. integrifolia at Ross Islets, February and March 1975 37

Appendix Table 3 107

Table 4. Translocation experiments on M. integrifolia at Ross Islets, August-November 1975 38

Appendix Table 4 109

Table 5. Translocation results on deep M. integrifolia at San José Islets 40

Appendix Table 5 113

Table 6. Translocation experiments on young M. integrifolia 44

Appendix Table 6 116

Table 7. Experiments on the effect of harvesting on translocation, M. integrifolia 47

Table 8. Short-term translocation experiments on M. pyrifera 53

Table 9. Translocation experiments on M. pyrifera at Arch Rock 56

Appendix Table 9 119

Page

Table 10. Translocation experiments on M. pyrifera at Kerckhoff Marine Laboratory 64

Appendix Table 10 124

Table 11. Translocation experiments on Macrocystis at Santa Barbara 66

Appendix Table 11 127

Table 12. Translocation from blades on primary fronds of M. pyrifera 67

LIST OF FIGURES

		Page
Figure 1.	Map of study sites in Barkley Sound	10
Figure 2.	Map of study sites in southern California	12
Figure 3.	Development of Macrocystis fronds	16
Figure 4.	Drawing of a M. integrifolia frond	17
Figure 5.	Diagram of a young Macrocystis plant	18
Figure 6.	Two stages in the later development of M. pyrifera ..	19
Figure 7.	Developmental sequence of M. pyrifera	20
Figure 8.	(a) drawing, and (b) diagram of the base of a small M. pyrifera plant	22
Figure 9.	Drawing of the younger part of a M. integrifolia plant to show relations between fronds	23
Figure 10.	Standard growth rates of M. integrifolia at Bamfield Inlet (1973) and Ross Islets (1975)	26
Figure 11.	M. integrifolia: results of 3 h, 4 h, 5.2 h, and 7.5 h translocation experiments	27
Figure 12.	M. integrifolia: accumulation of ^{14}C in immature blades with time	28
Figure 13.	Autoradiograph of an apical scimitar of M. integrifolia	29

Page

Figure 14. M. integrifolia: example of translocation in the fall 34

Figure 15. Diagramatic summary of the spring and fall patterns of translocation in M. integrifolia 42

Figure 16. M. integrifolia: translocation in a young plant 45

Figure 17. M. integrifolia: translocation in young 2° fronds 46

Figure 18. M. pyrifera: autoradiographs of (a) mature frond, and (b) juvenile frond apices 54

Figure 19. M. pyrifera: graph of ^{14}C in single samples as a function of blade distance from the apex 55

Figure 20. M. pyrifera: example of translocation only upwards 59

Figure 21. M. pyrifera: two experiments showing the change from only-upwards to upward and downward transport .. 60

Figure 22. Diagramatic summary of translocation pattern in M. pyrifera 61

Figure 23. Diagramatic summary of export from source blades on mature fronds of M. pyrifera 62

Figure 24. M. pyrifera: three examples of experiments at Kerckhoff Marine Laboratory 65

Figure 25. M. pyrifera: two examples of translocation from blades on 1° fronds 68

Page

Figure 26. M. pyrifera: effect of apex loss on translocation to the juvenile frond 69

INTRODUCTION

It has long been supposed that brown algae of the Order Laminariales are able to translocate photoassimilated carbon compounds within their thalli. Reinke (1876) first reported filaments of elongated cells with perforated end-walls, in Laminaria saccharina (L.) Lam. and Alaria esculenta (L.) Grev. The first report of filaments in Macrocystis was Will's (1884) description from M. luxurians Hook. fil. et Harv., now referred to M. pyrifera (L.) C.A. Ag. Since then various authors have elaborated these descriptions, both at the light microscope level (summarized by Esau 1969), and at the ultrastructural level (Ziegler & Ruck 1967; Parker & Philpott 1961; Parker & Huber 1965). In recent years Schmitz & Srivastava (1974, 1975, 1976) have conducted elegant electron microscope studies of the development of sieve elements in various kelps.

Investigations into the functioning of the sieve elements of kelps was at first deductive: exudation was found at the cut ends of stipes (Crafts 1939); then Sargent & Lantrip (1952) showed that growth of Macrocystis pyrifera apices could not be accounted for by their own photosynthesis, whereas in mature regions of the thallus carbon fixation was considerably in excess of growth, and concluded that translocation redistributed photoassimilates. Direct evidence of translocation was first provided by Parker (1963, 1965), who demonstrated movement of ^{14}C and fluorescein dye both upwards and downwards in the stipe of M. pyrifera from the source blade, and into other blades, including the apical blade.

It has now been shown for Nereocystis leutkeana (Mert.) P.&R. (Nicholson & Briggs 1972), and for Laminaria hyperborea (Gunn.) Fosl. (Steinbiss & Schmitz 1973), that the sieve elements are indeed the conduits for for translocation.

The picture of the sieve element system that has emerged from the works of the various authors cited, and especially from those of Schmitz & Srivastava, is one of a reticulum of sieve elements, each cell having a full complement of mitochondria, Golgi bodies, endoplasmic reticulm, etc., and in some species retaining the nucleus throughout their functional lifetime. The sieve elements form an interconnected network in the medulla of stipe and blades, and originate from cells of the inner cortex.

Although the translocation pattern had not been demonstrated experimentally at the time I began my experiments, the accepted concept of translocation in Macrocystis was one of mature sources supplying photoassimilates to immature, meristematic sinks. This was a logical extrapolation from vascular plant studies, and had been made even before Sargent & Lantrip's work (1952). In higher plants this concept has been well worked out using radiotracers (cf. Esau 1969; Aronoff et al. 1975). It can be briefly summarized as follows: The plant body can be divided into two regions: those in which photosynthetic carbon fixation accounts for or exceeds the needs for their own growth, and those in which it does not. The first category includes only mature leaves. The second category (the sinks) includes non-green stems, roots, and most meristematic regions -- where growth outstrips carbon fixation. In the parallel situation in

Macrocystis pyrifera it was assumed that the second category would also include young fronds arising from the base of the plants, where light could be limiting because of the depth of water and the surface canopy of adult fronds. Translocation in vascular plants involves the movement of photoassimilates into the phloem of the minor veins of the source leaves, and through the sieve tubes of the phloem to the sink regions where the assimilates can be unloaded; if there is no unloading, there may be feedback to the sources causing a drop in photosynthesis. Angiosperm leaves begin as sinks, but when half to three-quarters unfurled become sources, at first supplying their excess assimilates to the younger leaves above them, and later to stems, roots, storage organs, younger shoots, and fruit.

Although Macrocystis, by analogy, was thought to have a similar translocation pattern, Parker's experiments had not shown transport into young fronds, nor had they detailed which blades were sources of assimilates and which were sinks. The Macrocystis plant consists of meristematic regions separated by mature regions, and is considerably more complex than simple kelps such as Laminaria, in which it had been shown that the distal (mature) region of the lamina exported to the transition meristematic region at the junction of the stipe and lamina, and to haptera (Lüning 1969; Lüning et al. 1972, 1973). Even the giant kelp Nereocystis has this simple linear arrangement of source and sinks (Nicholson & Briggs 1972), which has recently been shown to be general in the Laminariales (Schmitz & Lobban 1976).

The objectives of the present work were to expand Parker's radiotracer experiments: to investigate translocation into young fronds, and to define source and sink regions of the frond. Experiments were carried out principally on the local species, Macrocystis integrifolia, but a brief study was also conducted on M. pyrifera in southern California to investigate depth effects on the pattern of carbon distribution as well as interspecies differences.

METHODS

I. Field procedures

Stipe elongation was used as an index of the growth rate of the plants: fronds tagged with numbered surveyor's tape were measured with a meter stick approximately weekly. The data were plotted and smooth curves drawn through them. Length increments over 5-day intervals taken from the curves were used to calculate percent daily elongation. Linear regression analysis of percent daily elongation versus $\log_{10}$ average stipe length in each 5-day interval yielded the "standard growth rate" (G) (North 1971), the y-intercept of the regression line, that is, the "percent daily elongation normalized to a frond length of one meter" (North, op. cit., p. 143). This statistic, which North has used extensively to compare growth rates of M. pyrifera over time and between populations, is normally given without units.

All translocation experiments were carried out in situ using SCUBA diving equipment. Normally a single blade somewhere on a frond was selected as the experimental blade, hereinafter referred to as the labeled blade; in a few experiments a group of blades was labeled. A clear polyethylene bag, with a serum cap held in the side by a short piece of plastic tubing, was sealed around the base of the pneumatocyst with a rubber band, enclosing about 2 litres of the surrounding seawater. Radioactive sodium bicarbonate was injected into the bag through the serum cap and mixed with the seawater by agitating the bag. Normally about 250 μCi $[^{14}C]$-$NaHCO_3$ was added (2.5 ml of stock solution).

Plastic bags have previously been used to incubate M. pyrifera blades with ^{14}C by Parker (1965) and by Towle & Pearse (1973). The latter authors suggested that photosynthesis may have been nutrient-limited in their 6 h experiments. In his 24 h experiments on production of marine macrophytes, Johnston (1969) found that if a ratio not exceeding 0.1-0.3 g dry weight alga per liter of seawater was used no nutrient or CO_2 deficiency effects were found. Weights of M. pyrifera blades range up to 1.5 g dry wt. (North 1971) (with the exception of sporophylls which are considerably heavier). This suggests that there may have been nutrient-limitation during my experiments; the effect would have been most pronounced when photosynthesis was highest. Short-term (1-8 h) experiments were carried out on both species of Macrocystis, but in order to have a measurable amount of radioactivity in the sinks I chose a 24 h duration for most of the experiments. A few 2-6 day experiments were carried out on M. integrifolia. (The use of larger bags would have done little to mitigate the nutrient-limitation problem inasmuch as a static layer of water would still form over the blade surface; however larger bags would have increased drag on the frond and the risk of the blade being torn away.)

At the end of the experiment the labeled frond and the young fronds associated with it were cut from the plant and brought to the surface (small plants were brought up whole), where the labeled blade was cut from the stipe with the bag of radioactive seawater still intact around it. The position of the labeled blade was marked with surveyor's tape. The fronds were transported moist to the laboratory by boat (a trip of from 10 min to 3 h). Plants in the short-term experiments were either sampled for analysis immediately or taken to the laboratory in darkened containers,

but no preservation or other special treatment was undertaken on plants from 24 h experiments. Durations given in the tables of data do not include transportation, handling, and drying times.

During the course of the experiments I labeled blades in every position on a frond from the apical scimitar to the frond initial. Plants in which I was able to find the primary frond or its remains (52 out of 97 experiments on M. pyrifera) could be aged by the number of fronds that had been formed. In the case of M. pyrifera the youngest plant had only the two primary fronds, each less than 1 m long; for M. integrifolia I conducted a series of experiments on very young plants, from the undivided lamina stage onwards. (These stages, and the terminology of fronds and their parts, are described in the section "Morphology and Development of Macrocystis.").

II. Laboratory techniques

The fronds were measured and a record made of the relative positions of the fronds and the blades. The fronds or parts were stretched out on lines to dry. Blades were then picked off and put into numbered bags or dishes. All blades on short fronds were sampled for ^{14}C content, but on longer fronds only the basal laminae (including sporophylls and frond initials), apical laminae (apical scimitar and immature free blades), and a few laminae on each side of the labeled blade were kept for sampling. The samples collected in California were returned to S.F.U. for analysis.

Throughout the results I have depicted selected experiments. These illustrations were drawn to show the ontogenetic relations of the fronds to each other, but do not show the actual spatial relation of the fronds (cf Fig 8).

It was not practical to sample thousands of blades quantitatively, because uptake of ^{14}C over a blade is uneven (cf. Fig. 13 and 18). Therefore analysis of total ^{14}C content was conducted on a single, weighed sample about 25 mg dry wt., from the proximal region (meristematic in immature blades) of each lamina, where most activity accumulated. Because of the qualitative nature of the analysis, loss of ^{14}C from blades during drying and storage was considered inconsequential, even though some volatile compounds may have escaped from the dried tissue. [Wallen & Geen (1968) found that approximately 31% of the radioactivity was lost from phytoplankton drying on membrane filters; this quantity did not increase over 8 weeks of storage. Considerably smaller losses would be expected from massive tissue such as Macrocystis laminae.]

The dry tissue was placed in a scintillation vial, rewetted with 0.1-0.2 ml water, and digested for liquid scintillation counting by the Mahin-Lofberg perchloric acid-hydrogen peroxide method (Lobban 1974). [This method was criticized by Fuchs & de Vries (1972), who claimed it did not give consistent results. However, Craigie (in preparation) has recently conducted extensive tests of the method and found that acid strength, temperature, and time of heating are all critical for quantitative work. Fuchs & de Vries did not re-wet their tissue samples, and thus their acid concentration was too high.] Raw data in counts per 5 or 10 min were corrected for quenching by an external-standard counting efficiency curve and converted to disintegrations per minute (dpm) by an off-line APL computer program. Since the background of the vials and cocktail could not be precounted, an average of 25 cpm was assumed and subtracted from the raw counts, but in view of the uncertainty of the background,

and on the basis of values obtained in several blank trials, I have chosen 100 dpm/10 mg dry wt as the lowest level of "significant" activity.

Autoradiographs of plant material were prepared by exposing X-ray film sheets for up to 12 days to tissue dried onto herbarium sheets.

A number of experiments on translocation in very small M. integrifolia was conducted in the laboratory, in a tank of running seawater. On the smallest plants it was necessary to use a plexiglas chamber sealed to the blade surface with a surgical glue (Lüning et al. 1972).

III. The study sites and species investigated

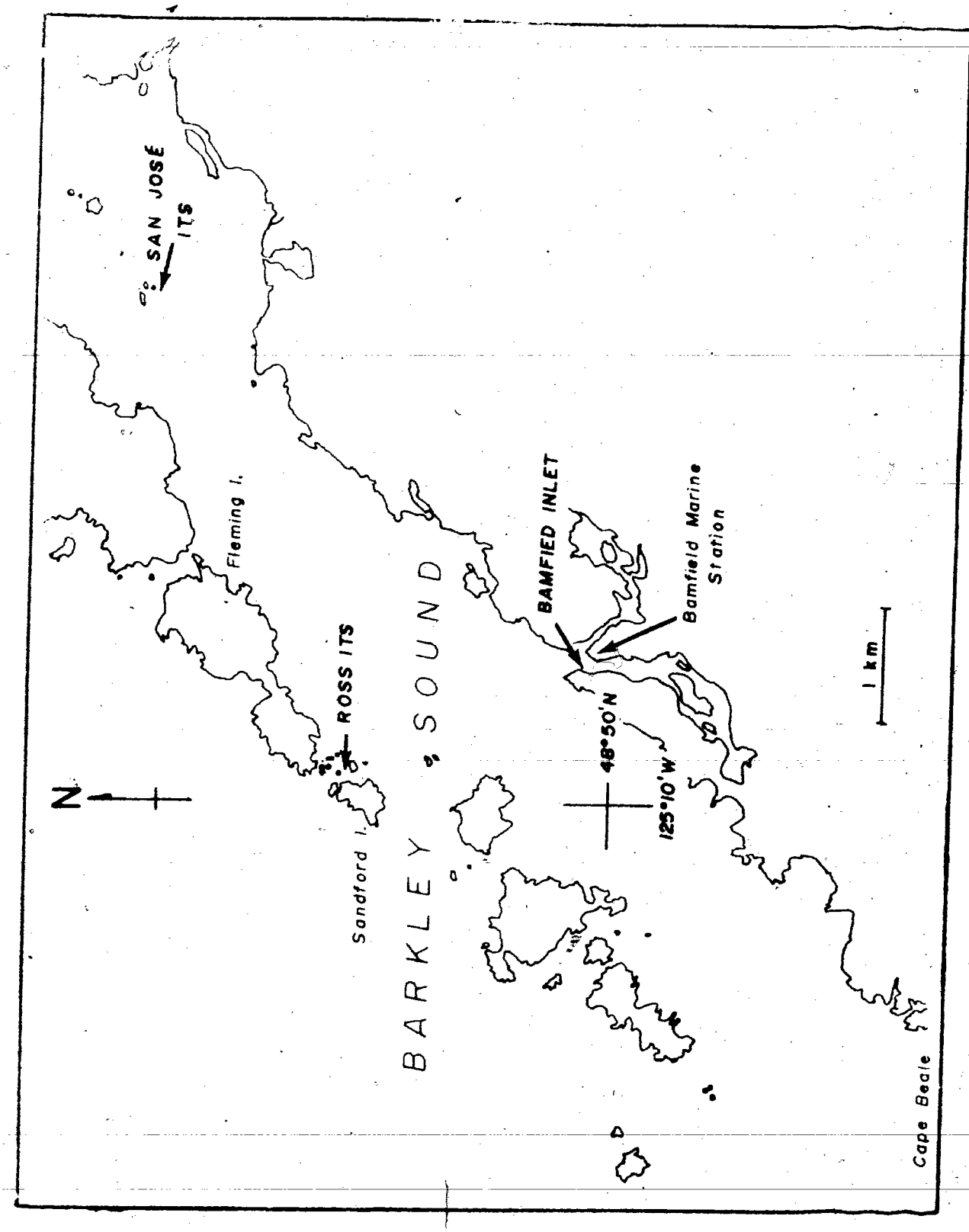
1. Macrocystis integrifolia Bory

This species occupies the northern part of the range of Macrocystis in North America, extending from Kodiak, Alaska to Monterey, California. It characteristically grows in areas somewhat protected from the full force of the open ocean, and can be found in very protected waters provided there is a modest amount of current. The total depth range of this species is from about 1 m above to 8 m below zero tide.

The plants of this species in Barkley Sound, Vancouver Island (Fig. 1) are all in rather sheltered waters, and grow in the shallower part of the depth range for the species. The conditions at the two principal study sites, Bamfield Inlet and Ross Islets, can be summarized as follows:

Bamfield Inlet: The kelp bed studied was on the east side of Mills Peninsula, Bamfield, near the mouth of the Inlet. The substrate is broken

Figure 1. Map of Barkley Sound, Vancouver Island, to show the locations of the study areas.


SAN JOSÉ ITS
Fleming I.
ROSS ITS
Sandford I.
BARKLEY SOUND
BAMFIED INLET
Bamfield Marine Station
48°50'N
125°10'W
1 km
N
Cape Beale

rock to about -2 m, below which are sediments. The plants are attached down to a depth of 1 m below zero tide. The site has weak currents, and is generally subject to little wave action, except during northerly winter storms.

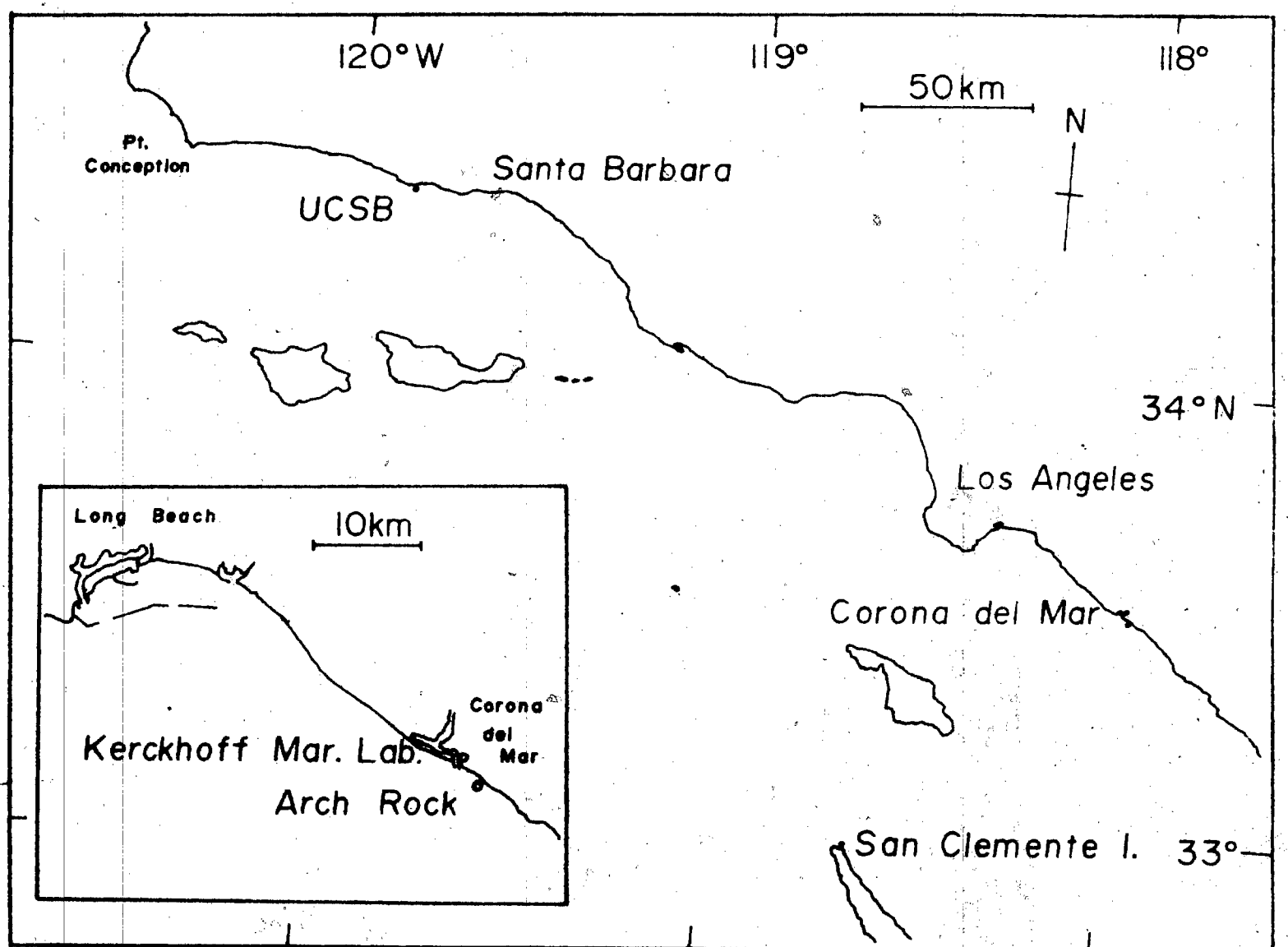
Ross Islets: Experiments were carried out in the kelp bed in the S.W. group of islets, where the plants grow down to about -3 m. The substrate is bedrock, partly overlain by sand and shell sand. The site is protected from wave action in spring and summer, but is subjected to strong surge during fall and winter. There is a moderate, chiefly northerly current.

The San José Islets plants are subjected to both moderate wave action, owing to the long fetch of S and W winds up Trevor Channel and SE storms across Numukamis Bay, and to moderate currents. The plants here were of particular interest as the deepest ones were 6-8 m below low water, a depth comparable to the M. pyrifera studied.

2. Macrocystis pyrifera (L.) C.A. Agardh

This species overlaps the southern extent of M. integrifolia, and is found as far as northern Baja California. Within this range several kinds of plants have been recognized. The type M. pyrifera has a conical holdfast, and the lower parts of the stipe are not flattened (Neushul 1971). This is marked contrast to M. integrifolia in which the bases of the stipes form a distinct rhizome. Neushul (1959, 1971) distinguished a form of M. pyrifera which has more flattened stipe bases than typical M. pyrifera yet lacks the rhizome of M. integrifolia. He

Figure 2. Map of the translocation study areas in southern California.


120°W
119°
118°
50km
N
Pt.
Conception
Santa Barbara
UCSB
34°N
Los Angeles
Long Beach
10km
Corona del Mar
Kerckhoff Mar. Lab.
Arch Rock
Corona
del
Mar
San Clemente I.
33°

felt that it was closest to M. angustifolia Bory (a southern hemisphere species -- Womersley 1954), and termed it "M. angustifolia northern hemisphere phase". It occurs at scattered locations in southern California, including the Santa Barbara region where some of my experiments were conducted. However, I observed a gradient of holdfast characters between these plants and typical M. pyrifera which I studied at Corona del Mar and San Clemente Island, and it is my opinion that all the Macrocystis in southern California should be refered to M. pyrifera (cf. Barrales & Lobban 1975, pp. 672-673). For the purposes of this dissertation the two groups of plants are treated separately -- not only because of this doubt, but also because they grew at different depths.

The study areas in southern California (Fig. 2) were as follows:

Corona del Mar (Newport Beach): the principal study site was near Arch Rock, about 2 km SE of the mouth of Newport Bay. The area is somewhat protected from the full force of ocean swells by the southern group of Channel Islands. Nevertheless, substantial swells were encountered, even at the seabed, on several occasions during the study (October and November 1974). The plants were attached 8-10 m below zero tide. Visibility was generally as poor as in British Columbia waters in summer. The substrate was bedrock, with some patches of sand.

A few plants were studied near the northern tip of San Clemente Island, where the plants grew deeper (to -15 m). The water there was very much less turbid than at the mainland stations. Wave exposure is probably rather less than at Corona del Mar, as the site was in the lee of the island. The substrate was similar, to the depth the plants grew,

turning to sediments at greater depths.

A few shallow-growing plants attached to the pilings of the Kerckhoff Marine Laboratory jetty and the rocks nearby (in the entrance to Newport Bay) were studied for comparison with B.C. Macrocystis. Overall, a considerable depth range of M. pyrifera was studied to examine the effect this factor might have on translocation.

A trip was made to the University of California at Santa Barbara (UCSB) to study translocation in "M. angustifolia northern hemisphere phase". These plants grew at -5 m on a basically sandy substrate and formed extensive, rather flattened holdfasts, and also grew attached to dead holdfasts (which apparently persist for a long time). Wave exposure is probably similar to Arch Rock. Visibility, at the time of my visit, was better than at Arch Rock.

MORPHOLOGY AND DEVELOPMENT OF *MACROCYSTIS*

A description of the morphology and development of *Macrocystis* species, based on the literature and my own observations, is presented here in order that the translocation results can be understood in terms of the growth of the plants.

The early development of *Macrocystis* has been described and illustrated by Brandt (1923), Skottsberg (1907), Neushul & Haxo (1963) for *M. pyrifera*, and by Scagel (1948) for *M. integrifolia*. It is the same in both species. Briefly summarized (Fig. 3), the initial split in the young plant (the undivided lamina stage) (Fig. 3b) is dichotomous, producing two blades, each of which begin to undergo unilateral divisions (Fig. 3 c-e) forming blades along an elongating stipe. The first two blades formed I refer to as frond-initials (Neushul 1971 calls them basal meristems). Each of these is capable of forming a new frond. The two or more blades above the frond-initials are sporophylls (in that they become fertile when the frond matures), and the remaining blades, formed later, usually remain sterile (Fig. 3h). Figure 4 shows in more detail a frond of *M. integrifolia* arising from the holdfast, to define the structures mentioned in the text.

The development of the holdfast and of later fronds differs somewhat between *M. pyrifera* and *M. integrifolia*. I will describe the later stages of *M. pyrifera*, and then show how *M. integrifolia* (which has been described by Scagel 1948) differs.

Figure 3. Development of Macrocystis fronds. (a) shows a frond initial or a very young plant. The young plant splits dichotomously (b), and then each blade begins unilateral division (c), first splitting off a frond initial. (d) shows the frond initial from (a), or one of the fronds of (c) dividing unilaterally; the newly-forming frond initial (1st frond initial) is shown with a split starting. In (e) this newly formed frond initial has separated from the apical scimitar; its subsequent development repeats (a) and (d). The apical scimitar from (e) is shown in (f) - (h) producing the 2nd frond initial (in f), and a sporophyll (in g). (h) shows a much later stage in the life of the frond [at this stage the 1st frond initial would be developing through (f) and (g)].

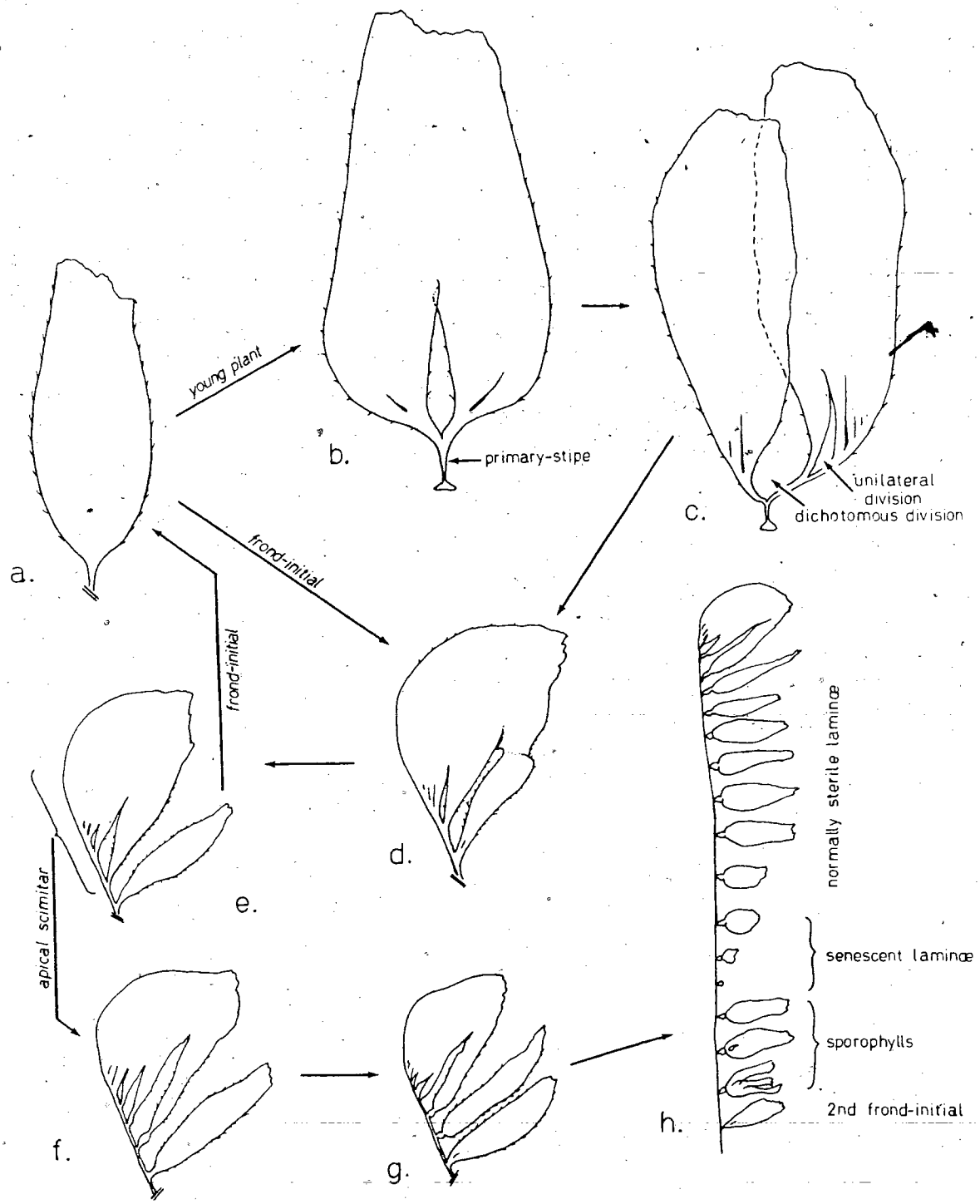

young plant
primary-stipe
unilateral division
dichotomous division
frond-initial
frond-initial
apical scimitar
normally sterile laminae
senescent laminae
sporophylls
2nd frond-initial
a.
b.
c.
d.
e.
f.
g.
h.

Figure 4. Drawing of a Macrocystis integrifolia frond, roughly to scale, to show the structures mentioned in the text.

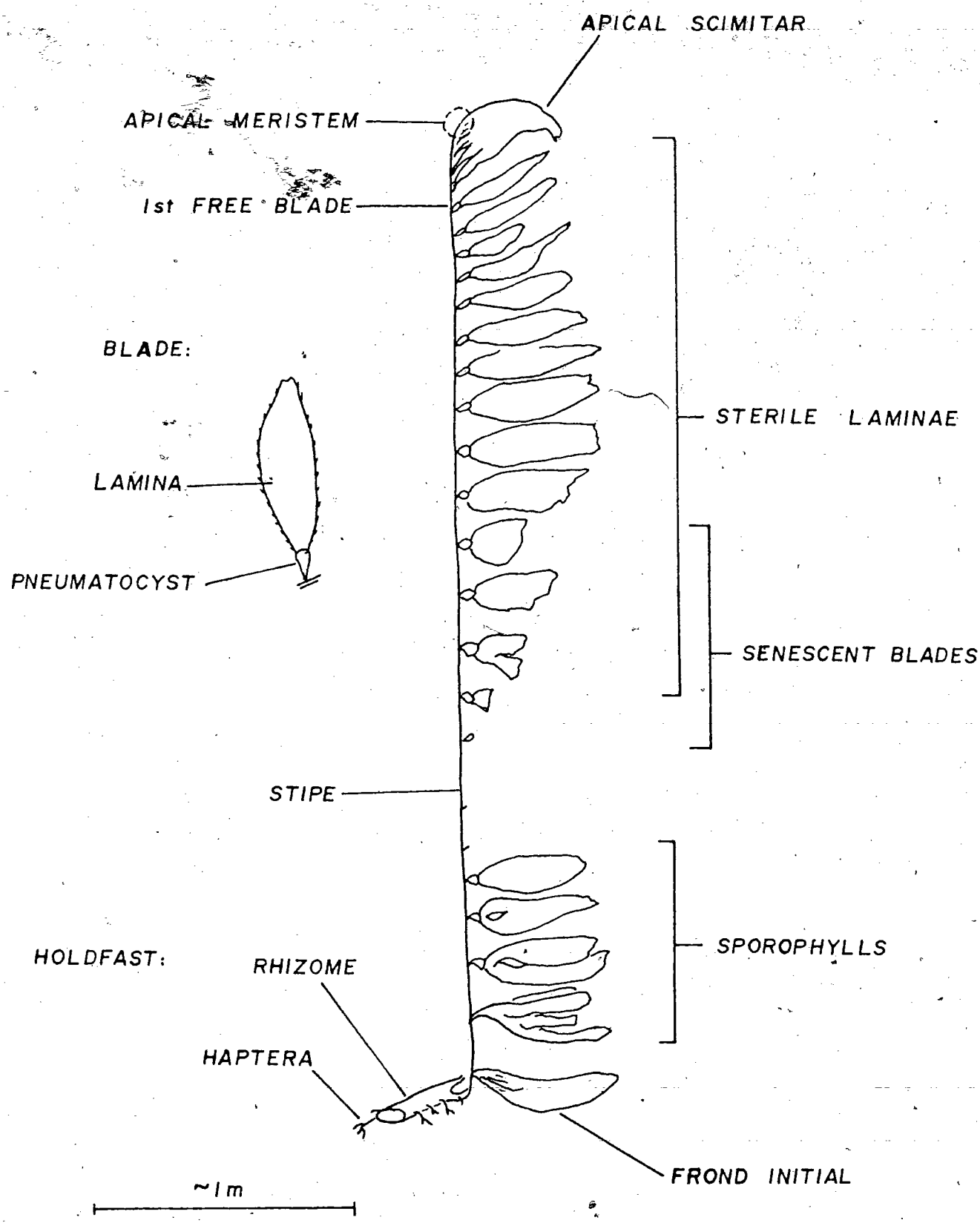

APICAL SCIMITAR
APICAL MERISTEM
1st FREE BLADE
BLADE:
LAMINA
PNEUMATOCYST
STERILE LAMINAE
SENESCENT BLADES
STIPE
SPOROPHYLLS
HOLDFAST:
RHIZOME
HAPTERA
FROND INITIAL
~1m

Figure 5. Diagram of a young Macrocystis plant, showing the two primary fronds (1^{o}), with the two 2^{o} fronds beginning to develop.

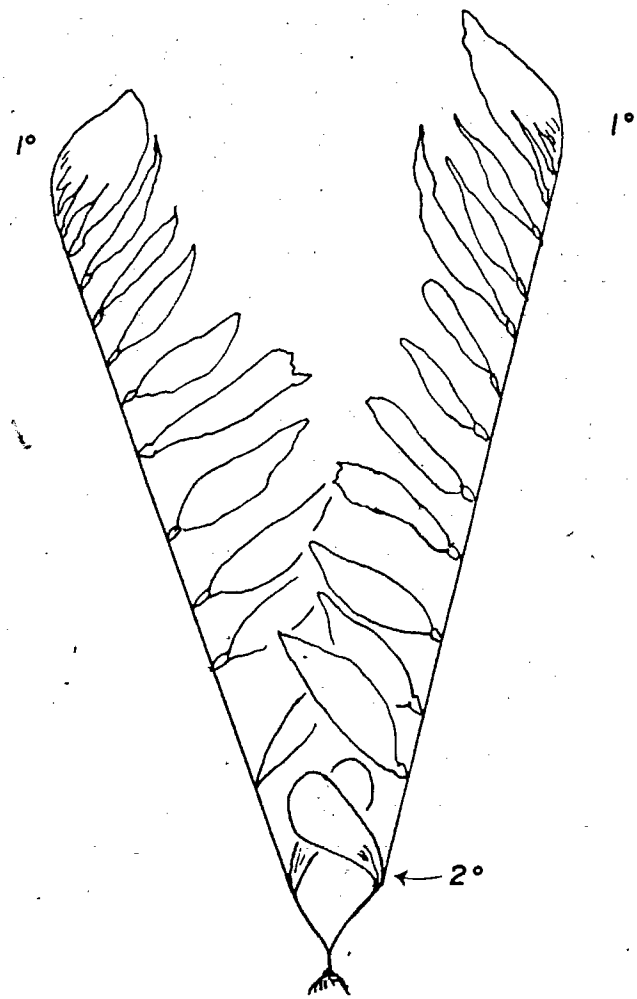
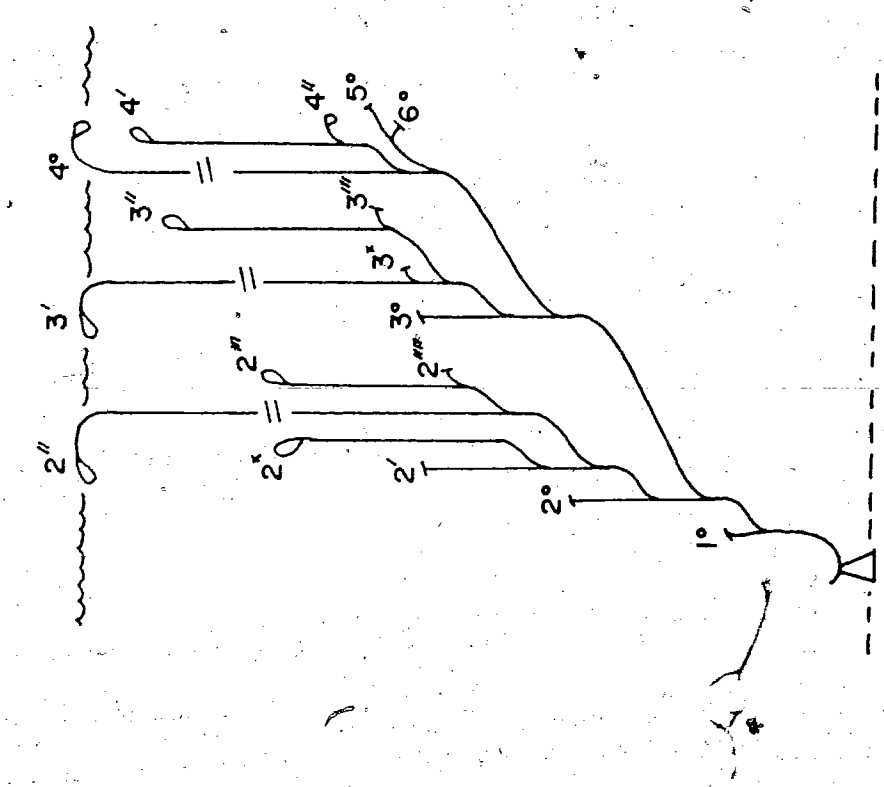
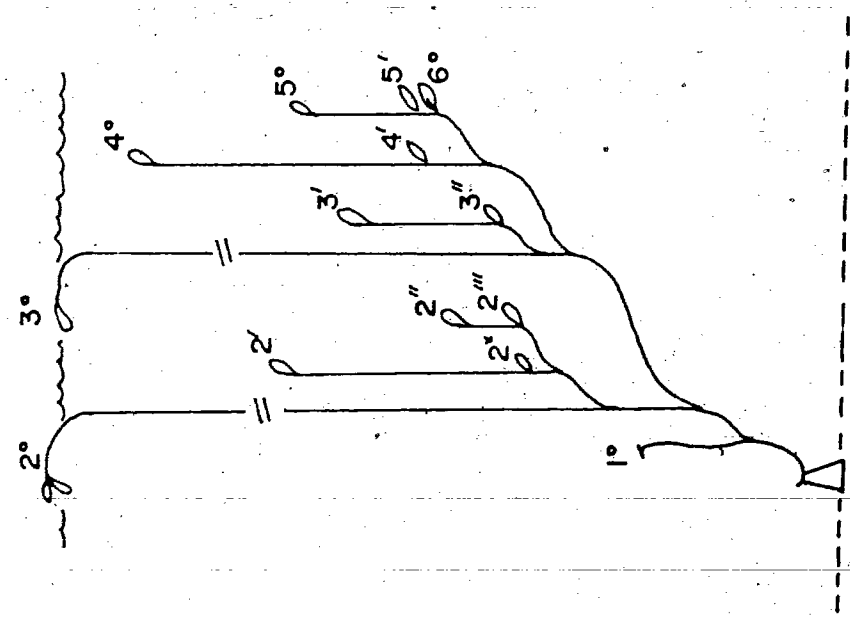

1°
1°
2°

Figure 6. Two stages in the later development of Macrocystis pyrifera (diagramatic). (a) a plant with 2^{o} and 3^{o} the surface-canopy fronds; (b) a plant with 2", 3', and 4^{o} the surface-canopy fronds. Both diagrams were prepared from actual specimens collected at Arch Rock. These diagrams do not reflect the actual spatial relationships of the fronds (cf. Fig. 8), inasmuch as the branches do not arise unilaterally from the parent fronds, but are shown this way to facilitate understanding translocation patterns.


4°
4'
4''
5°
6°
3''
3'''
3'
3°
3''
2'''
2''
2''''
2'
2°
1°


5°
5'
6°
4°
4'
3'
3''
3°
2''
2'''
2'
2''''
2°
1°

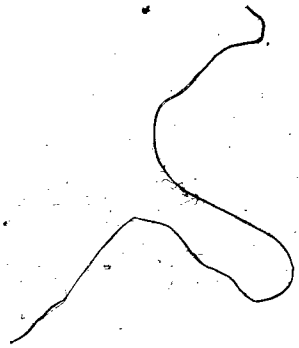
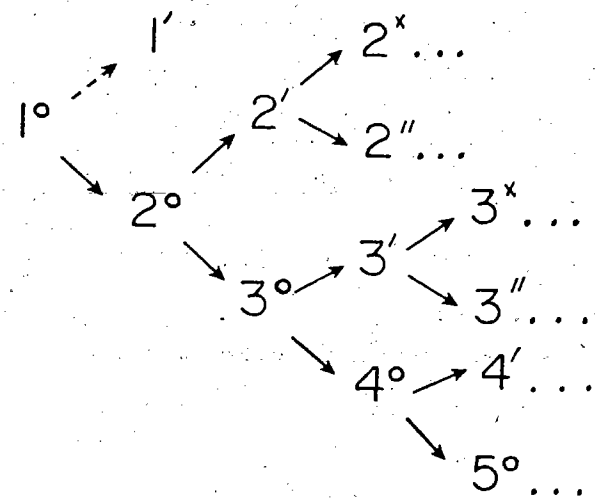
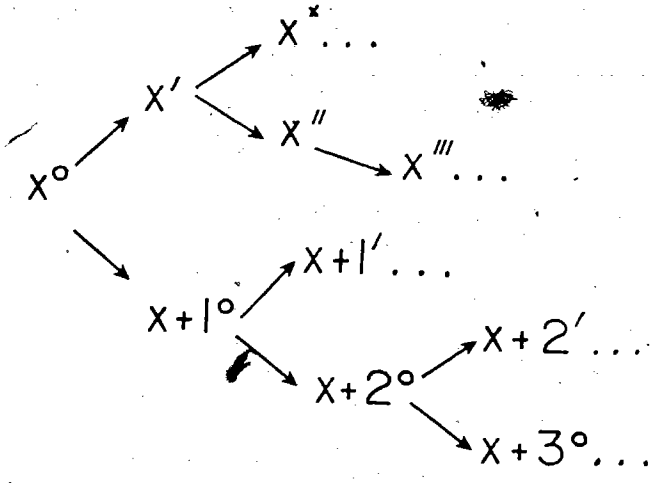


Figure 7. The developmental sequence of Macrocystis pyrifera. Top: development from the 1^{o} frond; Bottom: general development from the oldest known frond (x^{o}).


1°
1′
2°
2′
2ˣ...
2″...
3°
3′
3ˣ...
3″...
4°
4′...
5°...

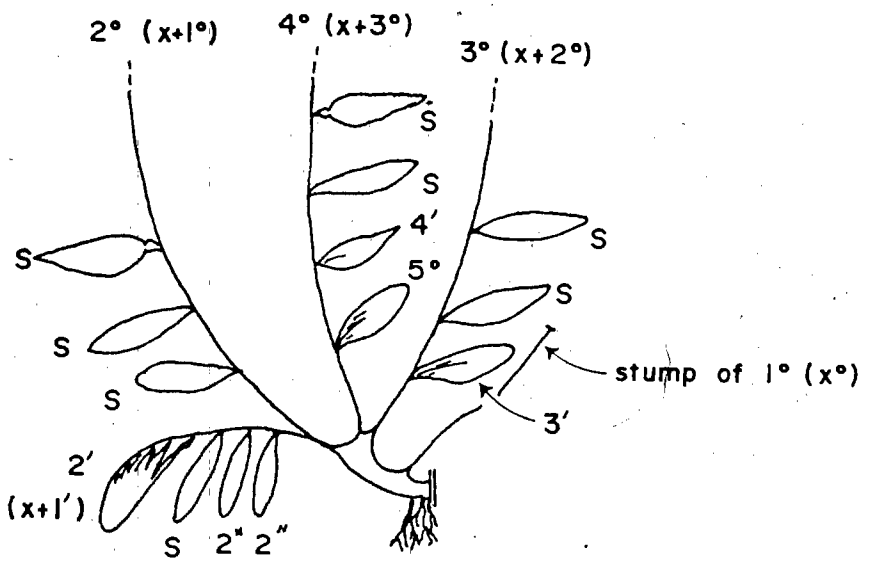

x°
x′
xˣ...
x″
x‴...
x+1°
x+1′...
x+2°
x+2′...
x+3°...

The first pair of fronds produced I refer to as the primary fronds (1^{o}) (Fig. 5). The first frond initial on each of these develops into the 2^{o} frond, but the second frond-initial rarely develops into a 1' frond. The next frond to be produced is the 3^{o}, from the first frond-initial of the 2^{o}. The general progression of the ^{o}-series of fronds can be stated as: $x^{o} \rightarrow x+1^{o} \rightarrow x+2^{o} \ldots$, where x^{o} is the oldest frond under study. The second frond-initial of 2^{o} develops soon after the 4^{o} frond begins to elongate; this frond I refer to as 2'. Similarly, the second frond-initial of 3^{o} develops into 3'. Each frond that is produced, with the exception of 1^{o}, forms two new fronds: $2^{o} \rightarrow 3^{o}$ and 2', $3^{o} \rightarrow 4^{o}$ and 3'. Similarly, 2' forms two fronds: 2" from the first frond-initial, and 2^{x} from the second frond-initial (Fig. 6a). The general outline of M. pyrifera development is shown in Fig. 7.

An older plant of M. pyrifera, showing the approximate relative sizes (ages) of the fronds, is given diagramatically in Fig. 6b: at this stage in the specimen shown 1^{o}, 2^{o}, 3^{o}, and 2' were all dead, only stumps of the stipes remaining, and 2"", 3^{x}, 3'", 4', 5^{o}, and 6^{o} had all been broken or grazed off. It is not possible to trace the fronds back to 1^{o} much after this stage because of the growing number of stumps and the developing holdfast. As the plant ages, haptera are produced from the bases of the older stipes, eventually burying the lower branch points in the conical mass of haptera.

The real spatial relation of the fronds of a young plant with six adult fronds is shown in Fig. 8, along with a diagram parallel to those in Fig. 6. This figure can also represent a portion of an old plant -- in that case the fronds are named x^{o}, $x+1^{o}$, etc.

Figure 8. Macrocystis pyrifera. (a) drawing of the base of one half of a small plant, showing the spatial relation of the fronds. (b) diagram of the same plant, parallel to the diagrams in Fig. 6. S = sporophyll.


2° (x+1°)
4° (x+3°)
3° (x+2°)
S
S
4'
5°
S
S
S
S
S
stump of 1° (x°)
3'
2'
(x+1')
S 2" 2"

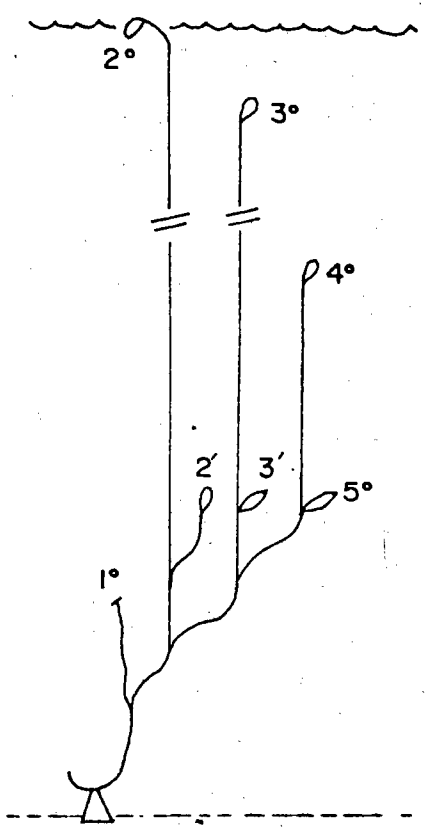
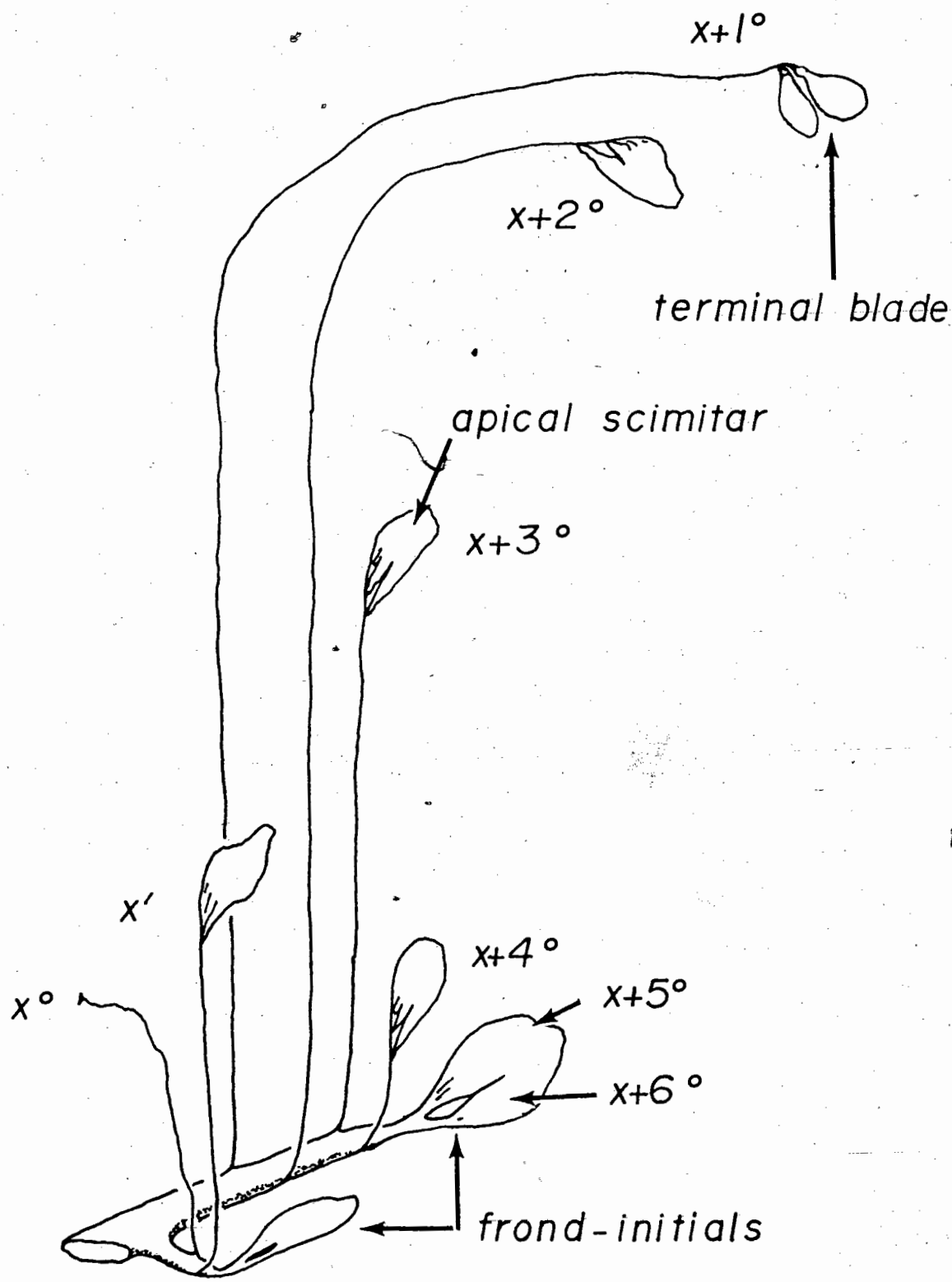

2°
3°
4°
2'
3'
5°
1°

Figure 9. Drawing of the younger part of a Macrocystis integrifolia plant, to show the spatial relation of the fronds arising from the rhizomatous holdfast (only the apical scimitars are shown).


x+1°
x+2°
terminal blade
apical scimitar
x+3°
x'
x°
x+4°
x+5°
x+6°
frond-initials

In the case of M. integrifolia the bases of the 1^{o} fronds begin to flatten out into the rhizome at about the time the 2^{o} fronds begin to develop. From then on the rhizome flattens ahead of frond development so that the appearance is of fronds arising from the top of the holdfast (Fig. 9). Branches occur in the rhizome where second frond initials develop into fronds. The development of second frond initials in M. integrifolia seems to be less frequent than in M. pyrifera.

The growth rate of M. integrifolia in British Columbia, as measured by stipe elongation, shows a large seasonal variation (Fig. 10), whereas M. pyrifera (North 1971) has a more or less uniform rate throughout the year in southern California. This difference in part reflects the different water temperature and light regimes in the two regions.

RESULTS

I. Translocation in M. integrifolia

A series of experiments was run May 4, 1976, to investigate short-term (1-7.5 h) translocation. The experiments were begun at 0800 PST under overcast and rain. The results (Fig. 11) clearly show a 4 h lag before export of ^{14}C was detectable. Activity was first detected in the stipe immediately above the labeled blade after 4 h; activity in other blades at this time was very slight. However, after 5.2 h considerable ^{14}C had accumulated in the blades towards the apex, with most found in the sampled blade closest to the source (three blades immediately above the labeled blade were not sampled). After 7.5 h the peak of ^{14}C accumulation had shifted toward the apex (Fig. 12).

The results of the 24 h experiments for Bamfield Inlet (1973) and Ross Islets (1975) have each been broken down into subseason units according to the trends in stipe elongation rates shown in Fig. 10. Because of the different locations, and the very different conditions in the two years, the results for each site will be treated separately. Very brief summaries of the data are given in the accompanying Tables; more complete data are given in the correspondingly numbered Appendix Tables. The complete set of data sheets has been deposited in the Data File of Depository of Unpublished Data, National Science Library, National Research Council of Canada, Ottawa, K1A OS2.

I was unable to correlate translocation pattern changes with a blade's number from the apex, because the freeing of a blade from the apical scimitar is a combination of splitting and tering, which is

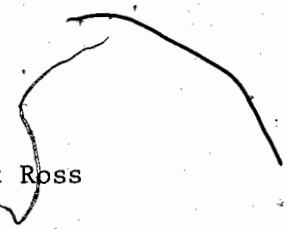


Figure 10. Histograms of the standard growth rates (G) of M. integrifolia fronds at Bamfield Inlet, 1973 (shaded), and at Ross Islets, 1975. (Standard growth rate is explained on page 4.) The seasonal trend is apparent in both years, although differing in detail.

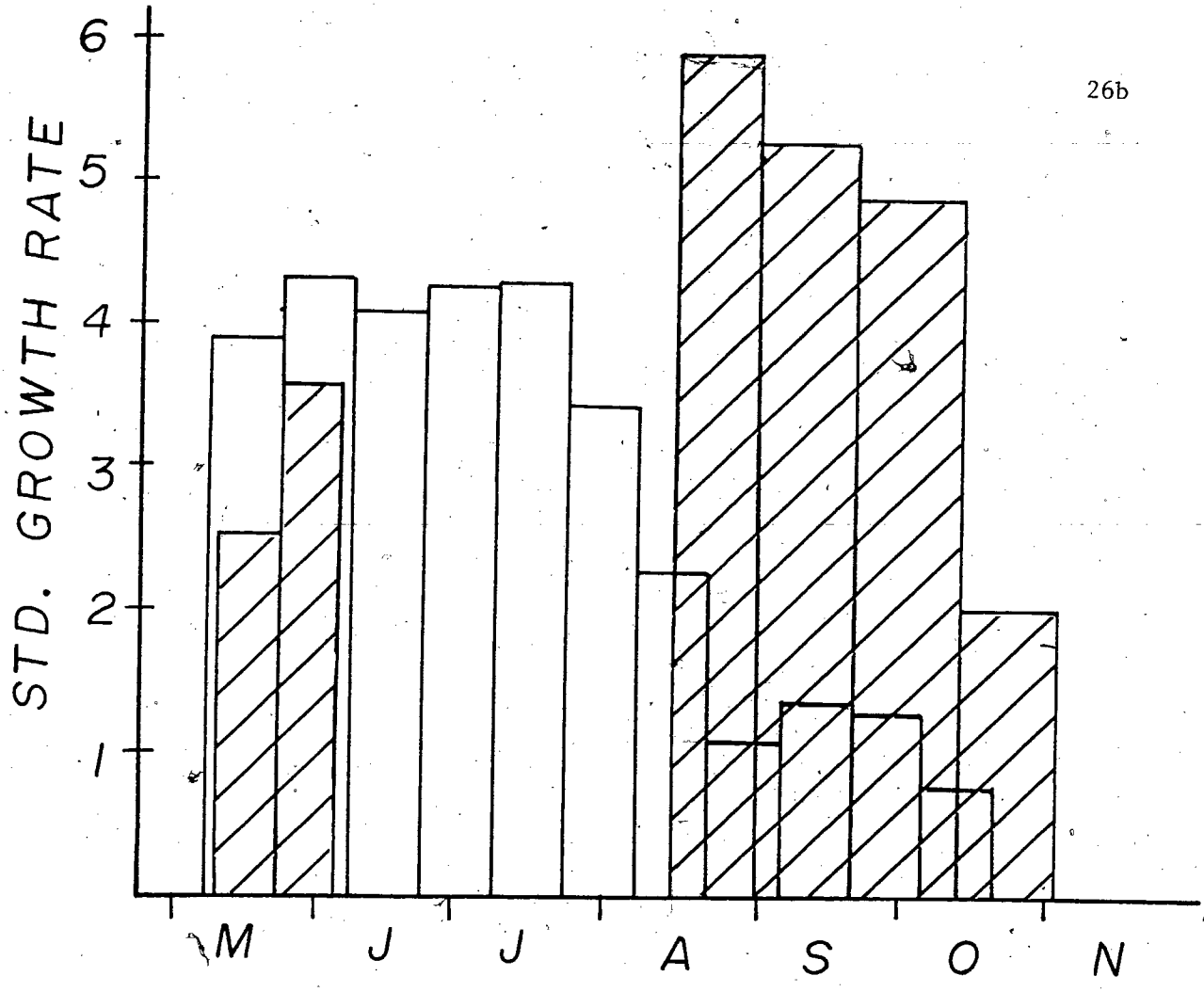

STD. GROWTH RATE
6
5
4
3
2
1
M
J
J
A
S
O
N

Figure 11. Results of the 3 h, 4 h, 5.2 h, and one of the 7.5 h experiments on M. integrifolia at Ross Its., May 4 1976. Activities in dpm are for the total sample, which consisted of two 17 mm diameter discs of proximal tissue from blades above the labeled blade; 3 discs along the length of labeled blades themselves. Labeled blades shown stippled; n.s. = not sampled. Source blades were 0.41, 0.68, 0.55, and 0.65 m respectively from the apices of their fronds.

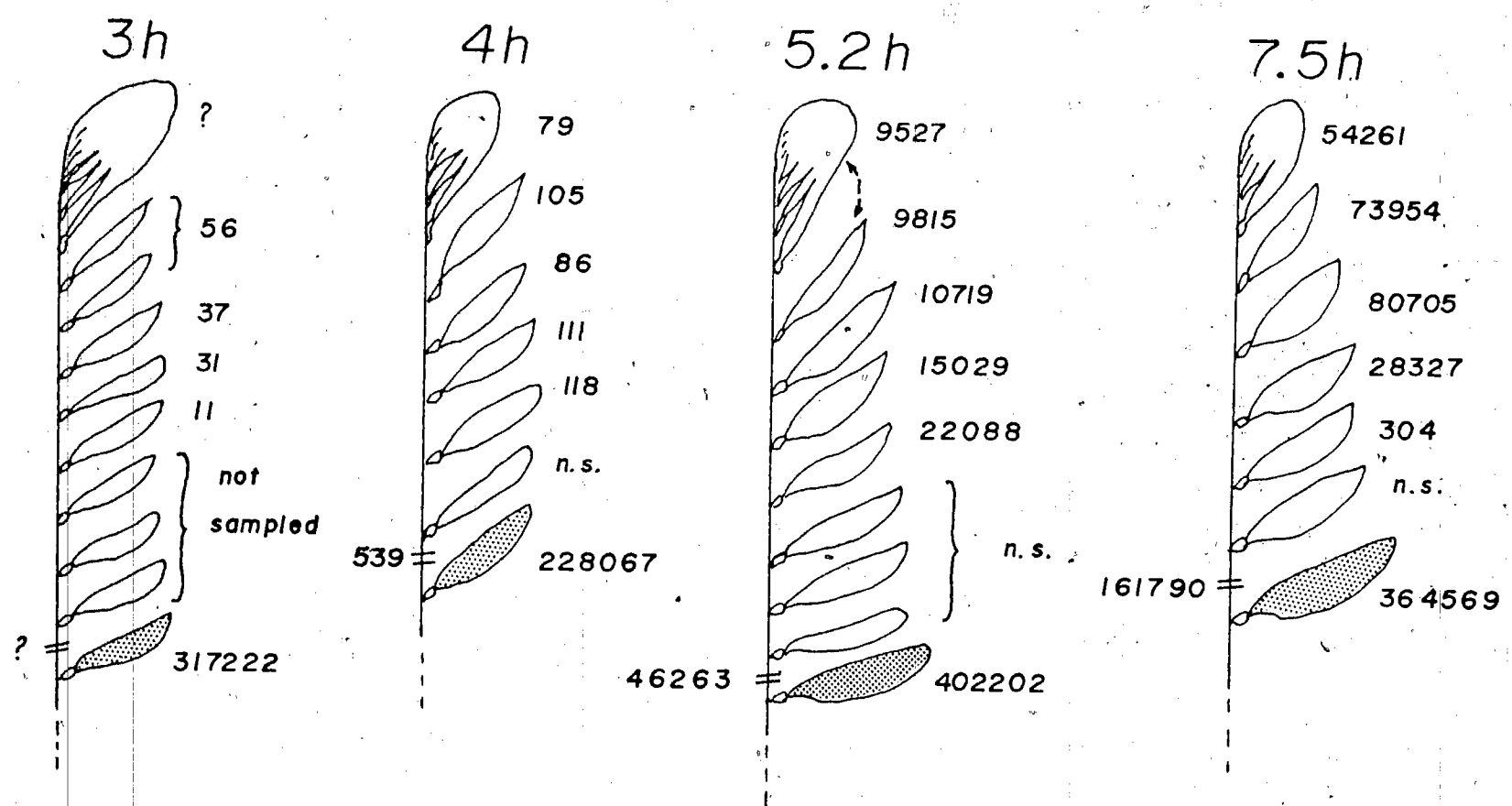

3h
?
56
37
31
11
not sampled
?
317222
4h
79
105
86
111
118
n.s.
539
228067
5.2h
9527
9815
10719
15029
22088
n.s.
46263
402202
7.5h
54261
73954
80705
28327
304
n.s.
161790
364569

Figure 12. Accumulation of radioactivity by the proximal region of young blades over time. Each curve shows the activity of the sample from the immature blades of one frond. The 4 h, 5.2 h and 7.5 h curves are for the experiments shown in Figure 15; the 24 h curve is from an experiment at Clarke-Owens, June 7 1975, and the quantity of ^{14}C in these blades should not be compared to the other curves. The peak of accumulation is seen to shift with time from close to the labeled blade to the first free blade. (Compare with Fig. 19) apiscim = apical scimitar.

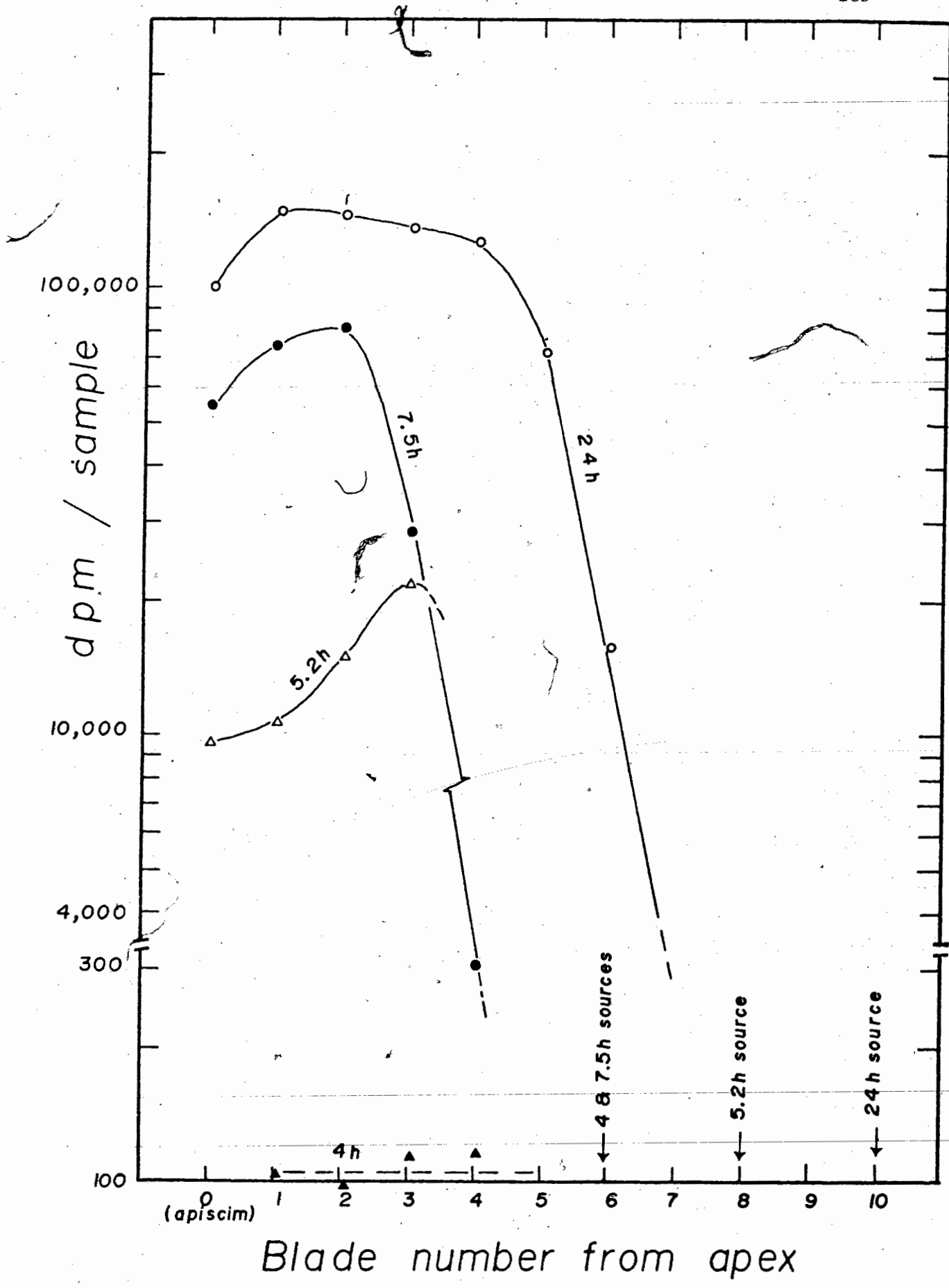
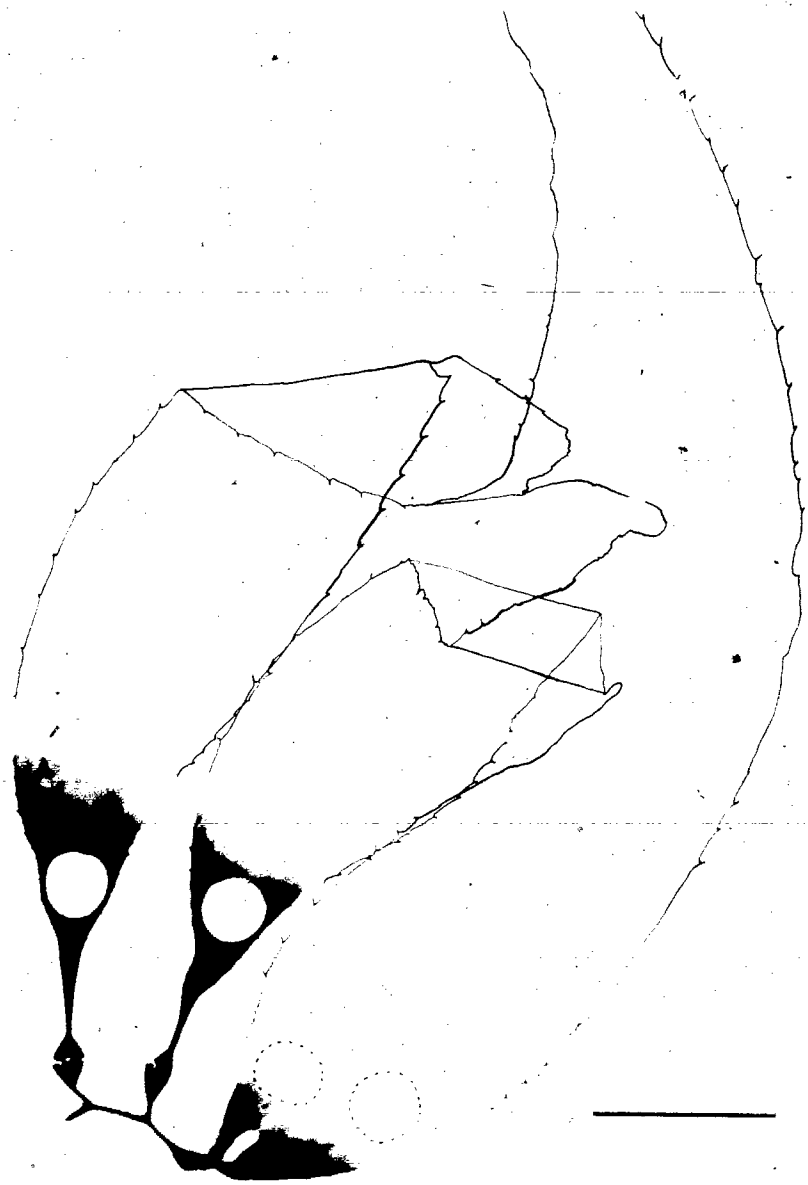

100,000
10,000
4,000
300
100
dpm / sample
7.5h
24h
5.2h
4 & 7.5h sources
5.2h source
24h source
4h
0
(apiscim)
1
2
3
4
5
6
7
8
9
10
Blade number from apex

Figure 13. Autoradiograph of the apex of a Macrocystis integrifolia frond to show uptake of ^{14}C by the proximal meristematic regions only. In this particular experiment the labeled blade was 0.68 m from the apex of the x^{o} frond; the apex shown in the autoradiograph was of the $x+1^{o}$ frond (0.16 m long). The radioactivity in the pairs of discs cut from the blades were 85,345 dpm and 1,016 dpm. (Plant #50, Bamfield Inlet, Sept. 16 1973.) Scale = 50 mm.



irregular, being partly a function of wave action (and handling). The results, throughout the dissertation, are therefore given in relation to the distance of the labeled blade from the apex (i.e. from the last split in the apical meristem). With a small number of experiments (264 adult plants) it is not possible to have labeled a blade at every centimeter from the apex, therefore a statement such as that upward export ceased about 2 m from the apex means that export was found from a blade 1.95 m from the apex (and from younger blades), but not from a blade 2.03 m from the apex (or older blades).

1. Bamfield Inlet, 1973

The results are best separated into two different periods of the year (Tables 1, 2): standard growth rate, G, rising in May-June, and G falling from the summer peak in August-October. There was in both groups an initial phase in the life of the blade during which there was import, but no export. Autoradiography (Fig. 13) shows that the proximal, meristematic part of the laminae, and the growing stipe and pneumatocysts, accumulated ^{14}C, but the distal regions of the laminae did not; there was a rather sharp cut-off between the importing and non-importing regions. When the blade was approximately 0.3 from the apex of the frond export began, and was at first exclusively upwards.

[A group of seven experiments was run in July 1974 at the Bamfield Inlet site to assess export from very young laminae. The distances of the labeled blades from the apices of their fronds were: 0.12, 0.12, 0.15, 0.20, 0.26, 0.40, and 0.50 m. Only in the last case was there significant translocation to the apical scimitar after 24 h (2,598 dpm/10 mg dry wt).]

Table 1. Synopsis of translocation experiments on M. integrifolia at Bamfield Inlet, May-June 1973. The results are arranged in order of increasing distance (d) of the labeled blade from the apex of the frond it was on. The conclusion from these experiments, in spite of several exceptions, is that downward export began from blades about 1.2 m from the apex. More complete data are given in Appendix Table 1 (p. 97).

Synoptic tables are presented for data given in the Appendix Tables with the same numbers (1-6 and 9-11) to provide an easily assessed summary of the direction of export. In all cases x^{o} was the labeled frond, and activity, A, in that column means upward translocation occurred. Activity in other columns means there was downward translocation from the labeled blade into the younger fronds. (A) = small amount of activity (less than 500 dpm/10 mg dry wt). Absence of particular juvenile fronds from the groups studied is indicated by --.

Table 1.

	Frond			
d	x^{o}	$X+1^{o}$	$x+2^{o}$	$x+3^{o}$
.30 m			--	--
.30	A			
.32			--	--
.34	A			--
.35			--	--
.38	A	A	A	A
.56	A			
.74	(A)	(A)	A	A
.83	A			--
.99	(A)	(A)	(A)	(A)
1.03	A			--
1.16	A			--
1.28	A	A	A	A
1.50	A			
2.23	A	A	A	A
3.23	A	(A)	(A)	

Table 2. Synopsis of translocation experiment results for M. integrifolia at Bamfield Inlet, August-October 1973, showing downward translocation from blades > 0.5 m from the apex. See legend of Table 1 (p. 31). More complete data given in Appendix Table 2 (p. 101).

	Frond			
d	x^o	$x+1^o$	$x+2^o$	$x+3^o$
.35	A			--
.39	A		--	--
.47	A			
.63	A	A	A	--
.68	(A)[1]	A		--
.90	(A)	A	A	(A)
1.04	A	(A)	A	--
1.07	A	A	--	--
1.07	A[2]	--	--	--
1.12	A	(A)		
1.15	A	A	A	(A)
1.53	A	A	A	
1.68	(A)	(A)	(A)	--
1.80	A	A	A	--
1.92*		A	A	--

--cont--

Table 2, cont.

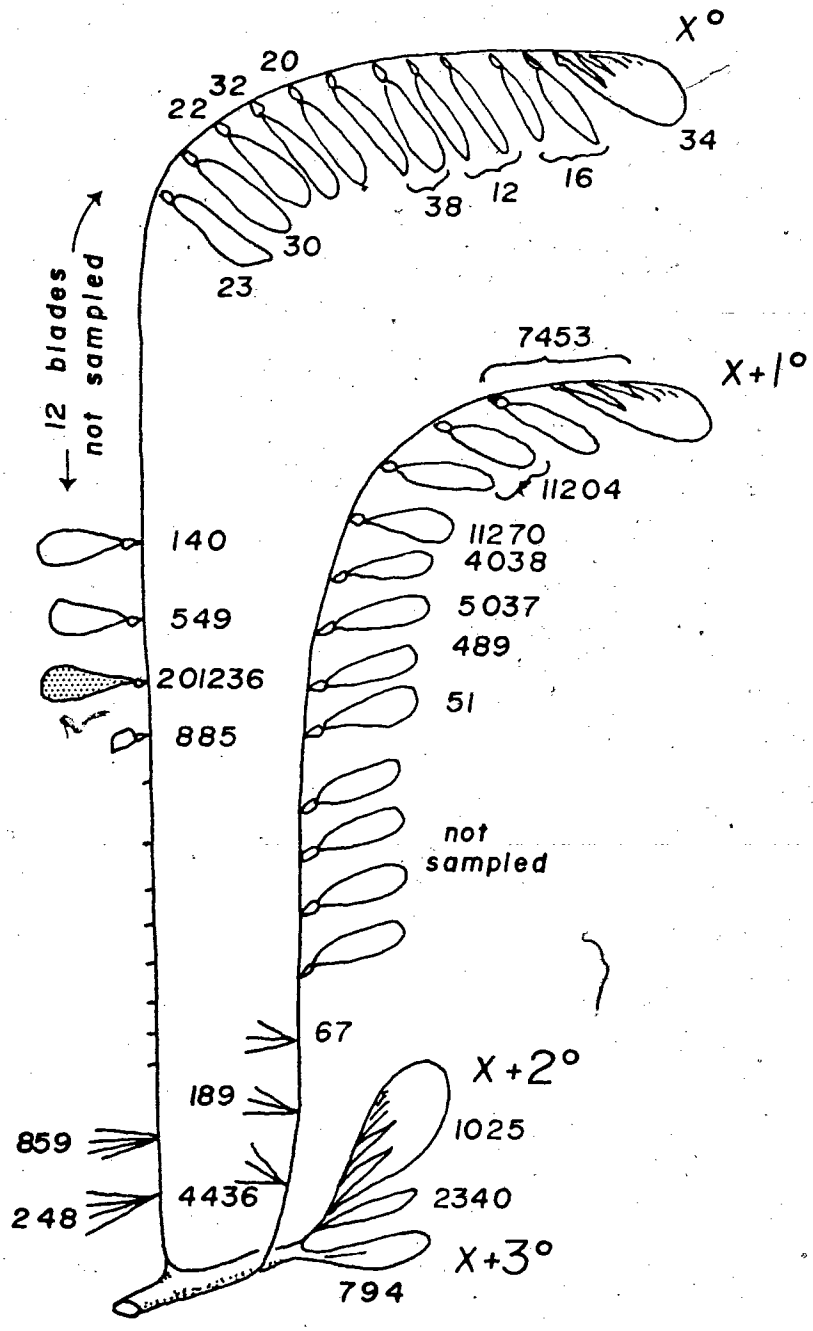
	Frond			
d	x^o	$x+1^o$	$x+2^o$	$x+3^o$
2.03*		A	A	A
2.40*		A	A	A
2.57*		A	A	A

* long-term experiments (48 h and 72 h)

'x^o apex damaged

$^2x'$: no activity

Figure 14. Example of translocation in the fall. The labeled blade, 2.03 m from the apex of the x^{o} frond, exported only downwards, to the sporophylls of x^{o} and to the apical regions of $x+1^{o}$, $x+2^{o}$, and $x+3^{o}$. (Plant #31, Bamfield Inlet, August 26-31: ^{14}C was applied for 24 h, and the plant harvested after a further 4 days of translocation. Frond lengths: x^{o} = 3.36 m; $x+1^{o}$ = 1.43 m.) Numbers are radioactivity in dpm/10 mg dry wt. Labeled blade shown stippled. Sporophylls in this diagram, and in other translocation diagrams are shown thus: ≫


X°
20
32
22
34
38
12
16
30
23
12 blades not sampled
7453
X+1°
11204
140
11270
4038
549
5037
489
201236
51
885
not sampled
67
X+2°
189
1025
859
4436
2340
248
X+3°
794

The direction of export from mature blades varied with season: in May-June (Table 1) export was only upwards until the blade was approximately 1.2 m from the apex, when export down the stipe and into the apices of juvenile fronds ($x+1^{o}$, $x+2^{o}$) and into frond initials ($x+3^{o}$, $x+4^{o}$) became well-established. Upward export continued even from very old blades (the oldest was 3.23 m from the apex). However, during August-October (Table 2) downward export began from much younger blades, at about 0.5 m from the apex, and upward export ceased by about 2 m from the apex. At this season there were many sporophylls, some with sori, and in many cases they accumulated significant activity (Fig. 14).

A series of experiments conducted in November 1973, at Wizard Islet, showed that there was very little transport at that time, which was after the end of the growing season. Such export as existed fitted the fall pattern.

2. Ross Islets, 1975

Experiments on the general translocation pattern were conducted in February, March, and August-November. The growth rate was not measured in February or March, but the plants were in excellent condition, and G was probably > 2; by May G was 3.9, as opposed to only 2.5 in May 1973 (Fig. 10). However, a very heavy settlement of epiphytic animals caused G to decline from mid July until the end of August when defoliation removed most of the heavily epiphytized mature laminae, leaving laminae only on the apical regions of the fronds and on very small fronds which

were only lightly epiphytized (Lobban 1976). As a result of these conditions, there was a number of rapid changes in the translocation pattern, which the experiments for the most part were too few to more than hint at.

All source blades in the February and March experiments were less than 0.7 m from the apex, and transport was only upward (Table 3).

Controls for harvesting experiments (described below) in mid June to late July showed erratic results, most likely due to frond-to-frond differences in the conditions of the source blades and the sinks (degree of epiphytism, etc.). Translocation practically ceased by the end of July, both at Ross Islets and at San Jose Islets (experiments July 25 and August 1). Experiments August 28 and September 16, and controls for September 14 harvesting experiments, showed rather erratic results again (Table 4): there was a change from a pattern close to the fall pattern in Fig. 15 to only-upward transport. This change was complete by September 24 experiments when there was export to the x^{o} apex only from all labeled blades, 0.15 m to 2.05 m from the apex (Table 4). During this time G rose a little from the low of 1.1 at the end of August, but remained less than 1.4 until the end of the growing season in October, when it again fell (Fig. 10). In November there was almost no translocation, as I had found at Wizard Islet in 1973 (page 35). The overall patterns of translocation in M. integrifolia are summarized in Fig. 15. Since the growth rates over the 1973 season (Fig. 10) followed a typical boreal climate growth curve, the results for Bamfield Inlet 1973 are taken as the basis for this diagram, supported by the February and March results from Ross Islets.

Table 3. Synopsis of translocation experiment results on M. integrifolia at Ross Islets, February and March 1975, showing only upward transport. See legend of Table 1 (p. 31). More complete data are given in Appendix Table 3 (p. 107).

	Frond			
d	x^o	$x+1^o$	$x+2^o$	$x+3^o$
.34 m	A		--	--
.35				
.37	(A)		--	--
.50	A		--	--
.56	A		--	--
.58	A	--	--	--
.58	A		--	--
.68	A	--	--	--
.69		--	--	--
.70	(A)		--	--

Table 4. Synopsis of translocation experiment results for M. integrifolia at Ross Islets, August-September 1975, showing a change from an irregular pattern in August to only-upward transport in September. See legend for Table 1 (p. 31). More complete data are given in Appendix Table 4 (p. 109).

	Frond				
d	x^o	$x+1^o$	$x+2^o$	$x+3^o$	x'
August 27-28					
.20	A			--	--
.27	A	A	A	--	
.37	A			--	--
.57	A			--	--
1.49		--	--	--	A
1.55		A	A	--	--
2.36	A		-(A)		--
2.64		--	--	--	
September 13-14 & 16-17					
.12		--	--	--	--
.12	A	--	--	--	--
.34				--	--
.35	A		--	--	--
.39	A			--	--
.51	A	--	--	--	(A)
.59	A	(A)	(A)	--	--

--cont--

Table 4, cont.

	Frond				
d	x^o	$x+1^o$	$x+2^o$	$x+3^o$	x'
2.29		--	--	--	--
September 23-24					
.15	A		--	--	--
.15	A		--	--	--
.25	A		--	--	--
.30	A		--	--	--
.32	A				--
1.03	A			--	--
2.05	A	--	--	--	--

Table 5. Synopsis of translocation experiment results for M. integrifolia at San Jose Islets in April and May 1976. More complete data are given in Appendix Table 5 (p. 113). See legend for Table 1 (p. 31).

	Frond				
d	x^o	$x+1^o$	$x+2^o$	$x+3^o$	$x+4^o$
.26		--			
.30		--	--	--	--
.49	A	--		--	--
.50	A	A		--	--
.54	A		--		--
.56	A	--	--	--	--
.60	A				--
.66		A	A	A	A
.70	A	A	A	A	--
.74	A	--	--	--	--
.90	A		--	--	--
.95	A	A	A	--	--
.97		A	A	A	--
1.00	A		A	A	--
1.36		x' :A			

3. Experiments on deep M. integrifolia

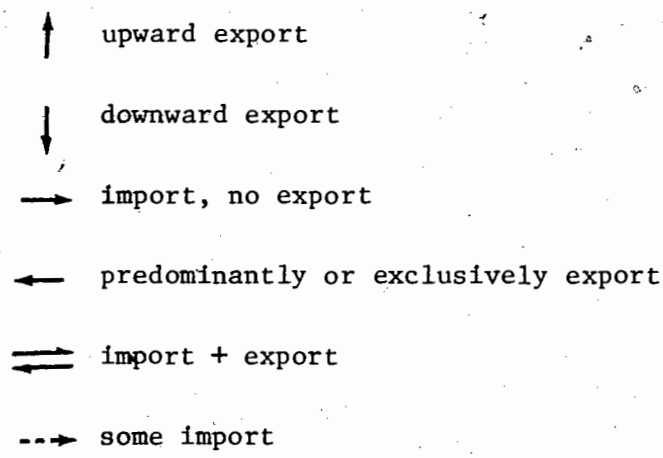
Two groups of experiments on plants 6.5 m below zero tide at San José Islets in July 1975 suggested a more consistent translocation pattern, somewhat different from the shallower plants, and much like the pattern I found in M. pyrifera (see below). The first group of experiments (Appendix Table 5) showed only upward translocation, but the second group, at the end of the month, showed no transport, as found at Ross Islets at that time.

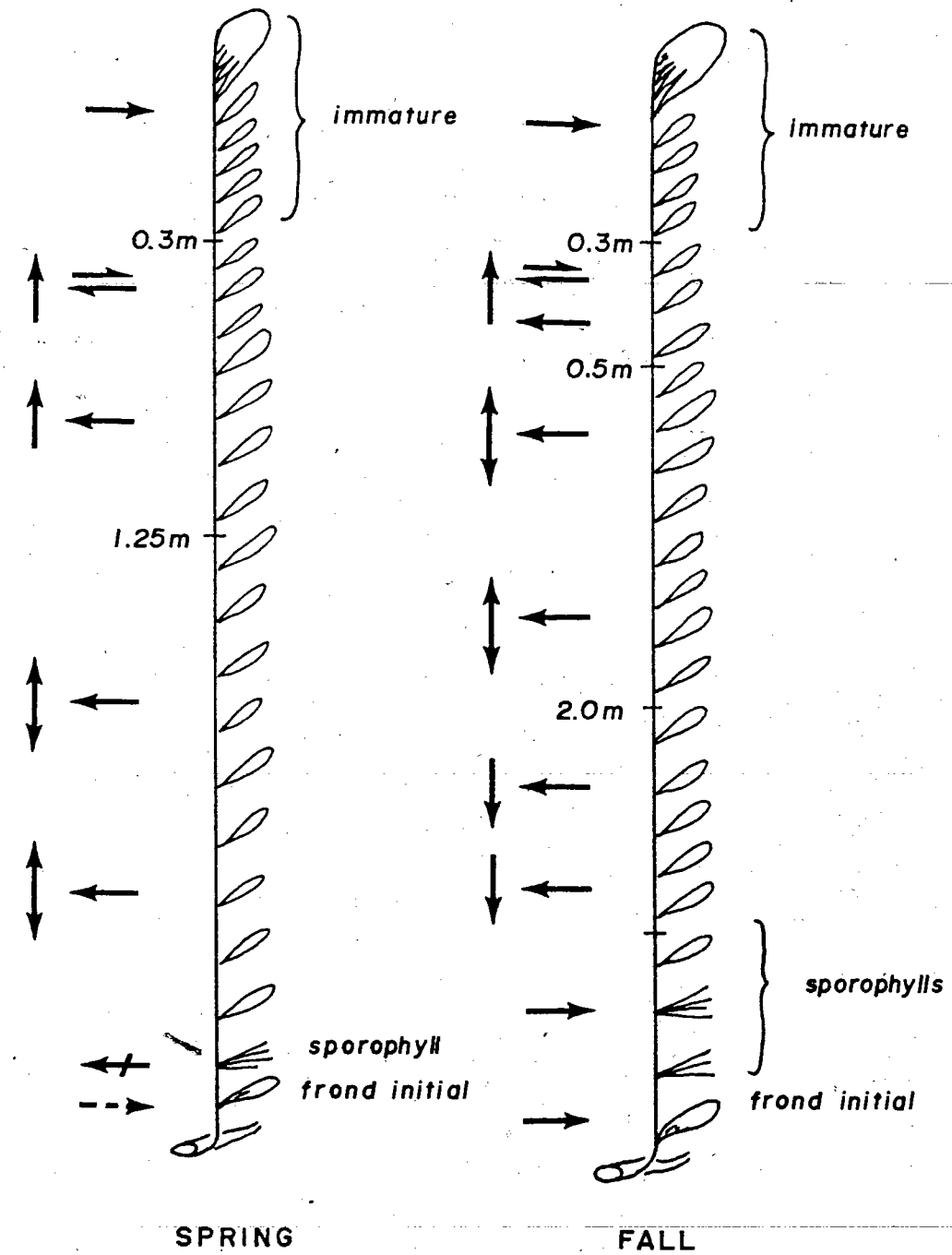
Further experiments on this population were carried out in April and May 1976. The results (Table 5) suggest that downward transport began from younger tissue than in Bamfield Inlet or Ross Islets plants at that season, between 0.6 and 1.0 m from the apex. However, the results were not as clear-cut as had been anticipated from the 1975 experiments.

4. Development of translocation in young plants

There was no export from the distal region of the "apical" blade, or the first free blade (2^{o} frond initial) in plants with the original lamina (cf. Fig. 3b) up to plants with the 2^{o} frond initial free of the apical scimitar (cf. Fig. 3e). Experiments on older plants showed that the export pattern from the first few blades to be cut off the apical scimitar was different from later blades at similar distances from the apex. The first blade to be formed (2^{o} frond-initial) exported from soon after being cut off the apical scimitar (approximately 0.1 m from

Figure 15. Diagramatic summary of Macrocystis integrifolia translocation pattern in spring and in fall, based principally on data from Bamfield Inlet plants, May-June, and August-October, respectively. Diagrams are not to scale. Arrows indicate import or export, and the direction of export:




immature
0.3m
1.25m
sporophyll
frond initial
SPRING
immature
0.3m
0.5m
2.0m
sporophylls
frond initial
FALL

the apex) at least until three more blades had been formed (Table 6; Fig. 16). It began to import when downward export began from the blades above it.

The second blade formed, which normally becomes a sporophyll, also began to export soon after being cut off the apical scimitar (about 0.07 m from the apex), and continued to export at least until 11 more free blades had been formed. The third blade, which might form sori, began export later, when there were 2-3 free blades above it (ca. 0.10-0.25 m from the apex); some downward export began around 0.75 m from the apex. Export may cease soon after the blade is 1 m from the apex, but there is only one experiment to give evidence on this.

As the number of blades on the frond increased, the distance from the apex to the source blade at which export began became closer to the distance found for adult fronds, approximately 0.3 m (Fig. 15).

Two experiments on the free blades of very small 2^{o} fronds showed no transport; on the contrary, all blades on such fronds are importing from the lower blades of 1^{o} (Fig. 17). In all subsequent frond generations, the first few blades on the $x+1^{o}$ do not export (see II.1, above).

Table 6. Synopsis of translocation experiment results on young plants of M. integrifolia. Experiments were conducted in the laboratory or in the field; more details in Appendix 6 (p. 116) A = activity found in the frond apex; 0 = no export. (See legend to Table 1 (p. 31).)

Blade number from base of frond	Total number of free blades															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	A	A		A												
2		A	A		A							A				
3				A	A	A		A	A	A				0		
4					0			A			A					
5												A		A		
6								0					A			
7							0	0	0							A
8										0		0				
9										0						

Figure 16. Experiment on a young plant of M. integrifolia showing export from a 2° frond-initial to the apex of the very short 1° frond. (Plant # 111, from the population transferred to Wizard It. Experiment in situ July 14-15 1974.) Numbers are dpm/10 mg dry wt. Labeled blade shown stippled. (The fronds have been twisted around (cf. Fig. 5) to show the blades and data more clearly.)

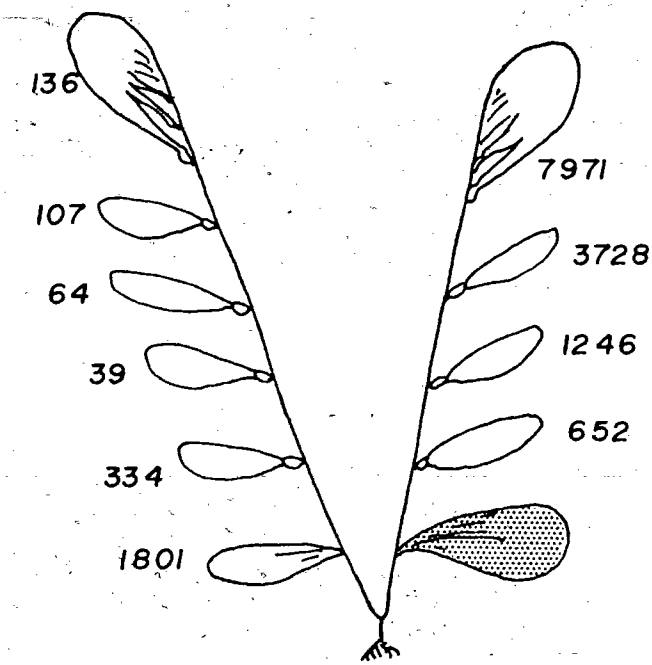
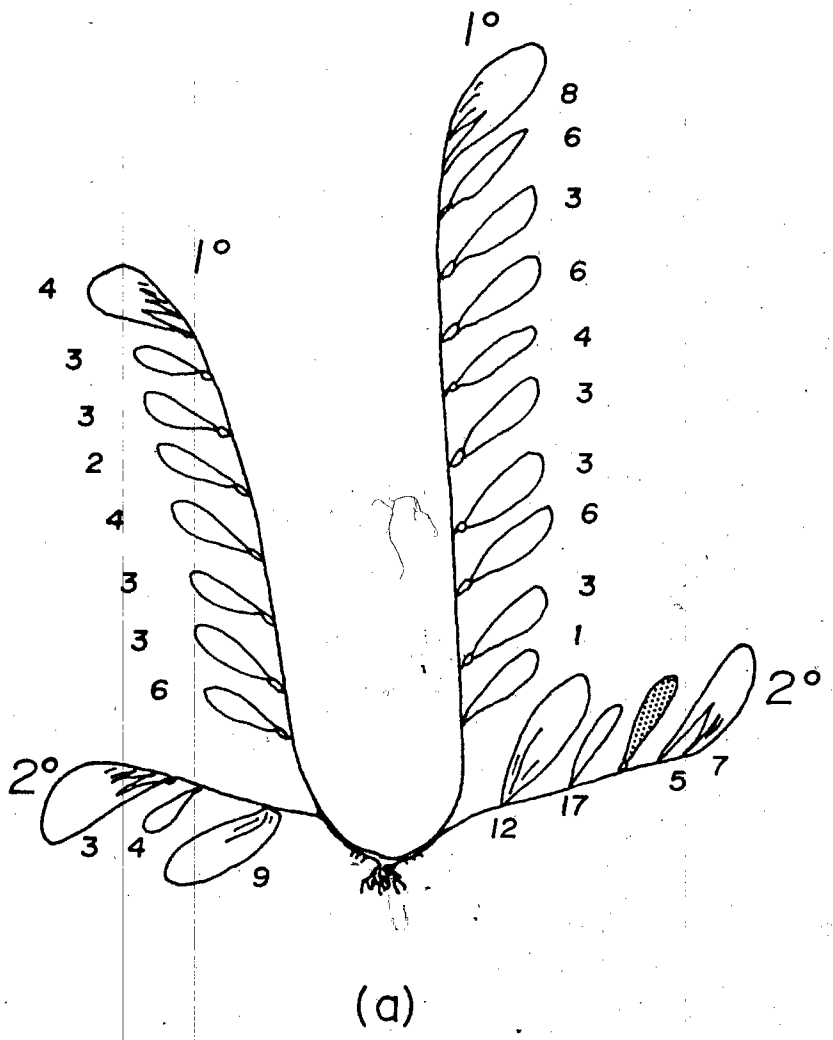
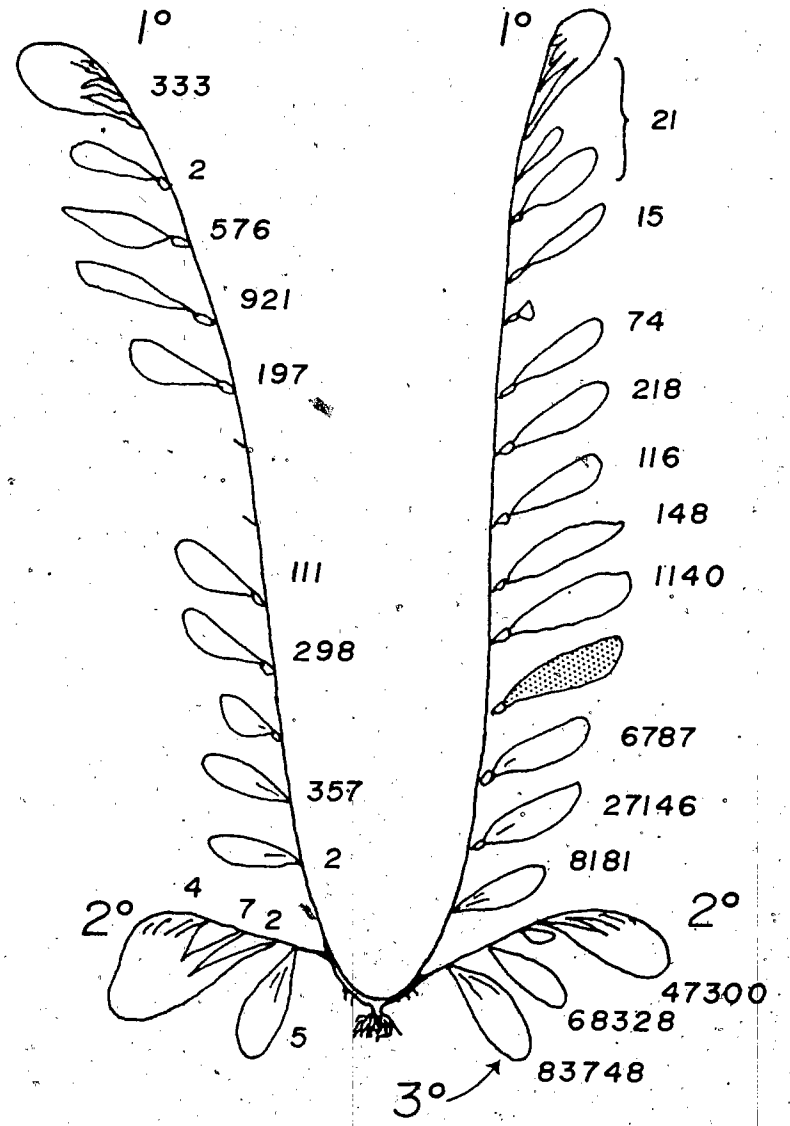

136
107
64
39
334
1801
7971
3728
1246
652

Figure 17. Translocation in young 2^{o} fronds of M. integrifolia: (a) labeled blade on the 2^{o} frond, showing no export; (b) labeled blade low on 1^{o}, showing import of assimilates by 2^{o}. (a: plant #137, August 12; b: plant #144, September 8 1974.) Numbers are radioactivity in dpm/10 mg dry wt. Labeled blade shown stippled.


1°
1°
2°
2°
4
3
3
2
4
3
3
6
8
6
3
6
4
3
3
6
3
1
3
4
9
12
17
5
7

(a)


1°
1°
2°
2°
3°
333
2
576
921
197
111
298
357
2
4
7
2
5
21
15
74
218
116
148
1140
6787
27146
8181
47300
68328
83748

(b)

Table 7. Translocation experiments: harvesting. Parts removed from the frond, or (*) already missing are listed under Parts Removed, along with the date removed if different from the date the experiment was begun. In column d, > indicates distance given is to the cut end of the stipe. A summary of direction of export is given: a large arrow indicates a large amount of ^{14}C moved, a small arrow a small amount.

Plant	Site/Date	Parts Removed*	d	Direction	Frond	Activ. in apiscim.	Activ. in blade below cut	Max. activ.
163	C-O/Jn 7	5 fr.bl.	.53	↕	x°	8,829	49,300	49,300
					x+1°	0	-	309
164	"	control	.59	↑	x°	98,270	-	147,900
165	"	(*) apiscim (no immature blades)	.30	•	x°	-	452	452
166	"	apical meristem	.50	0	x°	0	-	0
					x+1°	0	-	0
167	"	apiscim	> .37	↕	x°	-	37,020	77,770
					x+1°	208	-	208

continued

Table 7, continued

Plant	Site/Date	Parts removed*	d	Direction	Frond	Activ. in apiscim.	Activ. in blade below cut	Max. activ.
168	C-O/Jn 7	6 fr. bl.	.77	0	x^{o}	0	0	0
					$x+1^{o}$	0	-	0
169	"	5 fr. bl.	.86	↕	x^{o}	97,460	641	97,460
					$x+1^{o}$	4,751	-	4,751
170	"	apiscim + immature blades	>.34	↕	x^{o}	-	13,450	24,940
					$x+1^{o}$	392	-	392
171	"	apiscim + immature blades	>.42	↑	x^{o}	-	17,020	17,020
					$x+1^{o}$	0	-	0
210	R/Sep 14	control	.59	↕	x^{o}	24,090	-	28,550
					$x+1^{o}$	283	-	283
211	"	apiscim + 7 fr.bl., Sep. 9	ca.70	↓	x^{o}	-	0	0
					$x+1^{o}$	473	-	505
					$x+2^{o}$	1,626	-	1,626
					$x+3^{o}$	1,146	-	1,146

continued

Table 7 continued

Plant	Site/Date	Parts removed *	d	Direction	Frond	Activ in apiscim.	Activ. in blade below cut	Max. activ.
212	R/Sep 14	5 fr.bl. (+2 already missing)		↓	x°	288	259	288
		(Sep. 9)	>.65		x+1°	n.a.	-	0
					x+2°	0	-	0
213	"	control	.51	↑	x°	20,700	-	25,410
					x+1°	0	-	0
214	"	3 fr.bl. (+1 already missing)		↑	x°	22,950	319	29,340
		(Sep. 9)	.50		x+1°	0	-	0
					x+2°	0	-	0
215	"	apiscim + 1 small fr.bl.	>.50	↑	x°	-	8,820	8,820
		(2nd, 3rd fr.bl. already missing)			x+1°	0	-	0
		(Sep. 9)						
216	"	apiscim + 3 fr.bl. (Sep 9)	>.77	↓	x°	-	0	0
					x+1°	1,032	-	1,137
					x+2°	2,174	-	2,174
					x+3°	2,106	-	2,106

continued

Table 7, concluded.

Plant	Site/Date	Parts removed*	d	Direction	Frond	Activ. in apiscim.	Activ. in blade below cut	Max. activ.
217	R/Sep 14	apiscim (Sep. 9)		↑	x°	-	11,700	11,700

* Abbreviations used in this column:

apiscim = apical scimitar

fr.bl. = free blade

Sites: C-O = Clarke-Owens kelp bed

R = Ross Islets

5. Harvesting and translocation

Export from labeled blades on fronds lacking the apex was exclusively downwards (e.g. #13; 37, 43, 45 (Appendix Tables 1 and 2)); blades above the labeled blade did not accumulate activity. Similarly, there was no import by young fronds lacking the apex (#21; 37, 39).

Experiments conducted in 1975 (Table 7) showed that upward transport continued if either the apical scimitar (#214), or the immature free blades (#215, 217) were removed, but not if both were cut off (#211, 216). In a few experiments (e.g. #170, 171) there is an indication of a surge of assimilates upwards, towards the cut, immediately after cutting; but this surge is shown to be short-term (one or two days) by the prior-cut controls (Table 7), the fronds at Bamfield Inlet which lacked an apex, and the experiments in September (Table 7) in which the apex and/or immature blades were removed 4 days before the experiment was begun.

II. Translocation in Macrocystis pyrifera

Short-term experiments (Table 8) showed some translocation after 5 h, both to the apex of the labeled frond (C1, C4) and to the juvenile frond (C2). No activity was found outside the labeled blade in 1, 2, or 3 h experiments (C27-31), but this may be due to the labeled blades having been only about 1 m from the apex, where export is just beginning (see below).

Autoradiography (Fig. 18a, b) showed that, as in M. integrifolia, import of ^{14}C is only by the proximal, meristematic region of the blade. These figures show an increase in area accumulating activity as the blades matured. There was a gradation in activity from the pneumatocyst toward the distal part of the lamina. There was a smooth curve of activity in the 25 mg samples of blades (Fig. 19) versus blade number from the apex, with a peak in the blades immediately below the apical scimitar.

1. Macrocystis pyrifera at Arch Rock

This population was the one I studied the most. The results (Table 9) show that there was at first a period during which immature blades imported but did not export. As the distance of a blade from the apex approached 1 m export began (Table 9: C94 ff) (Fig. 20). The blade was still not fully grown at this stage, and import continued (Fig. 19). There was a transition region from about 0.75 m to 1.1 m during which export began, but I cannot determine from my experiments the distances from the apex which a blade was both importing and exporting.

Downward export began when the blade was about 3.6 m from the apex, the transition region in this case being rather wider than the first: from about 3.5-4.5 m from the apex. The two 2^{o} fronds in Fig. 21 show this difference in export direction with blade position.

The last phase in the export pattern was only-downward transport, and (or followed by) a period of senescence of the blades during which

Table 8. Results of short-term experiments on M. pyrifera, San Clemente I., October 8 and 21. In the Oct. 21 group (C27-C30) the length given (in brackets) is the amount of frond harvested, not total length. The labeled blades were removed from the bags at harvest, rinsed in unlabeled seawater, and dried in darkness. Experiments are arranged in increasing duration. A complete list of abbreviations and conventions used is given in the appendix.

Plant #	Duration (h)	Depth of labeled blade (m)	Distance lab. bl. to apex (m)	Activity in labeled bl. (10^3 dpm/10 mg)	Frond	Length (m)	Activity in apiscim	Max. activ. (dpm/10 mg)
C27	1	1.5	1.07	22	x^o*	(1.78)	0	0
C28	1	8.0	0.99	54	x^o*	(1.68)	0	0
C29	2	1.5	0.94	304	x^o*	(1.35)	0	0
C30	2	8.0	1.12	251	x^o*	(2.06)	0	0
C31	3	1.5	1.07	n.s.	x^o*	(1.40)	0	0
C4	5	14.0	0.31	n.s.	1^o*	0.98	429	496
					1^o	0.94	0	0
C1	5	13.0	1.59	n.s.	x^o*	3.39	268	363
					$x+1^o$	0.33	0	0
					$x+2^o$	0.07	0	0
C2	5	12.0	3.35	n.s.	x^o*	6.27	0	0
					x'	0.24	1175	1597
C3	5	11.0	5.38	n.s.	x^o*	9.63	0	0

Figure 18. Autoradiographs of the apices of (a) a mature frond (C90-2°), and (b) a young 1° frond (C11), in both cases on the same frond as the labeled blades, which were, respectively, 1.65 m and 0.60 m from the apex. The outlines of the non-radioactive parts of the blades have been drawn in. All the blades in (a) were attached to the apical scimitar before pressing; the jagged outline of the first free blade in (b) shows that it recently tore away from the apical scimitar. Scales = 50 mm.

b
a

Figure 19. Graph of activity in the single samples from the proximal regions of each lamina as a function of distance from the apex. This example is the juvenile frond of C6 (cf. Fig. 26) which had a length of 1.03 m. The source blade, labeled for 48 h, was on x°, which lacked the apex. Because the radioactive area increases in immature blades (cf. Fig. 18), this graph is not a representation of total import into the laminae (see text). Blades were probably mature from about #13 on.

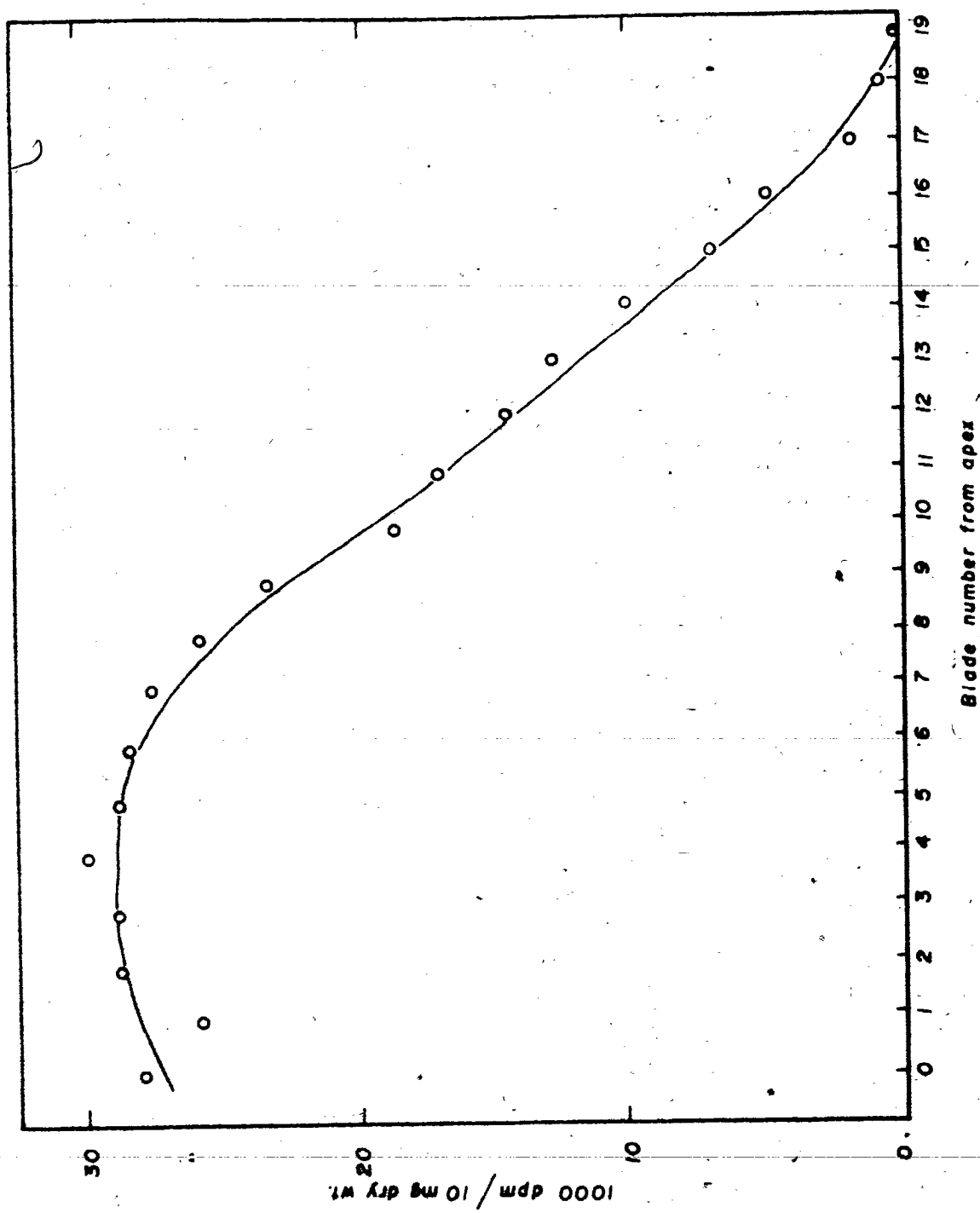

1000 dpm / 10 mg dry wt.
0
10
20
30
Blade number from apex
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19

Table 9. Synopsis of translocation experiments on M. pyrifera at Arch Rock. Upward export to x^o apex is seen in the .87 m experiment, and 1.27 m below; downward export is first seen about 3.6 m from the apex. See legend of Table 1 (p. 31). Further data given in Appendix Table 9 (p. 119).

	Frond			
d	x^o	$x+1^o$	$x+2^o$	x'
.18		--	--	--
.22			--	--
.25			--	--
.32		--	--	--
.38			--	--
.38		--	--	--
.39			--	--
.40			--	--
.46		--	--	--
.50		--	--	--
.59			--	--
.66		--	--	--
.87	A	--	--	--
1.04			--	--
1.27	A		--	--
1.65	A			
1.96	A	--	--	--

--cont--

Table 9, cont.

	Frond			
d	x^o	$x+1^o$	$x+2^o$	x'
1.98	A			
2.22	A		--	--
2.52	A		--	--
3.32	A			
3.45	A		--	--
3.61			--	--
3.64	A		A	A
4.62	A		--	--
5.13			A	A

export of currently-labeled photoassimilates declined. This phase had very diffuse boundaries, but began approximately 6 m from the apex.

Apical scimitars (C80, C86) and frond initials (C74-76, C78) did not export. Some export was found from sporophylls on very old fronds (C13, C79), but it was very low; sporophylls were often sinks (Fig. 26a, b). Sporophylls and frond initials imported from blades low on the frond which were also exporting to young fronds, and/or from the lower blades of $x\text{-}1^{o}$. No activity was found in the growing haptera samples (e.g. Fig. 21). The various phases of import and export are summarized in Fig. 22.

Downward export was directed to young fronds, rather than to older blades below the labeled blade. Any young frond close to the frond with the labeled blade received assimilates. Thus in C32 (Fig. 21) and C37 both 2' and 4^{o} contained activity from 2^{o}, and a very small amount of activity was also found in 3^{o}. However, 3^{o} was quite long, and the immature blades would have been supported chiefly by mature blades on the same frond. Activity did not pass from one side of the plant to the other (e.g. C43, C52; Fig. 24a, c.).

Fig. 23 shows the general case for export to juvenile fronds. The x^{o} would be supporting x", and x' if this was not long enough to support itself (cf. Fig. 21, C32-3^{o}); x^{o} would probably no longer support the ^{o}-series of fronds, since $x+1^{o}$ would be mature and supporting x+1' and $x+3^{o}$; $x+2^{o}$ would be about the same length and maturity as x'. When downward transport from $x+2^{o}$ begins it may support x+1' (as well as $x+3^{o}$ and $x+4^{o}$).

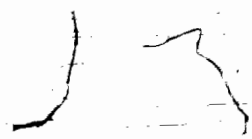


Figure 20. Example of an experiment on a blade, 1.92 m from the apex, exporting only upwards. Diagram not to scale. Labeled blade shown stippled, and marked with *. n.s. = not sampled.

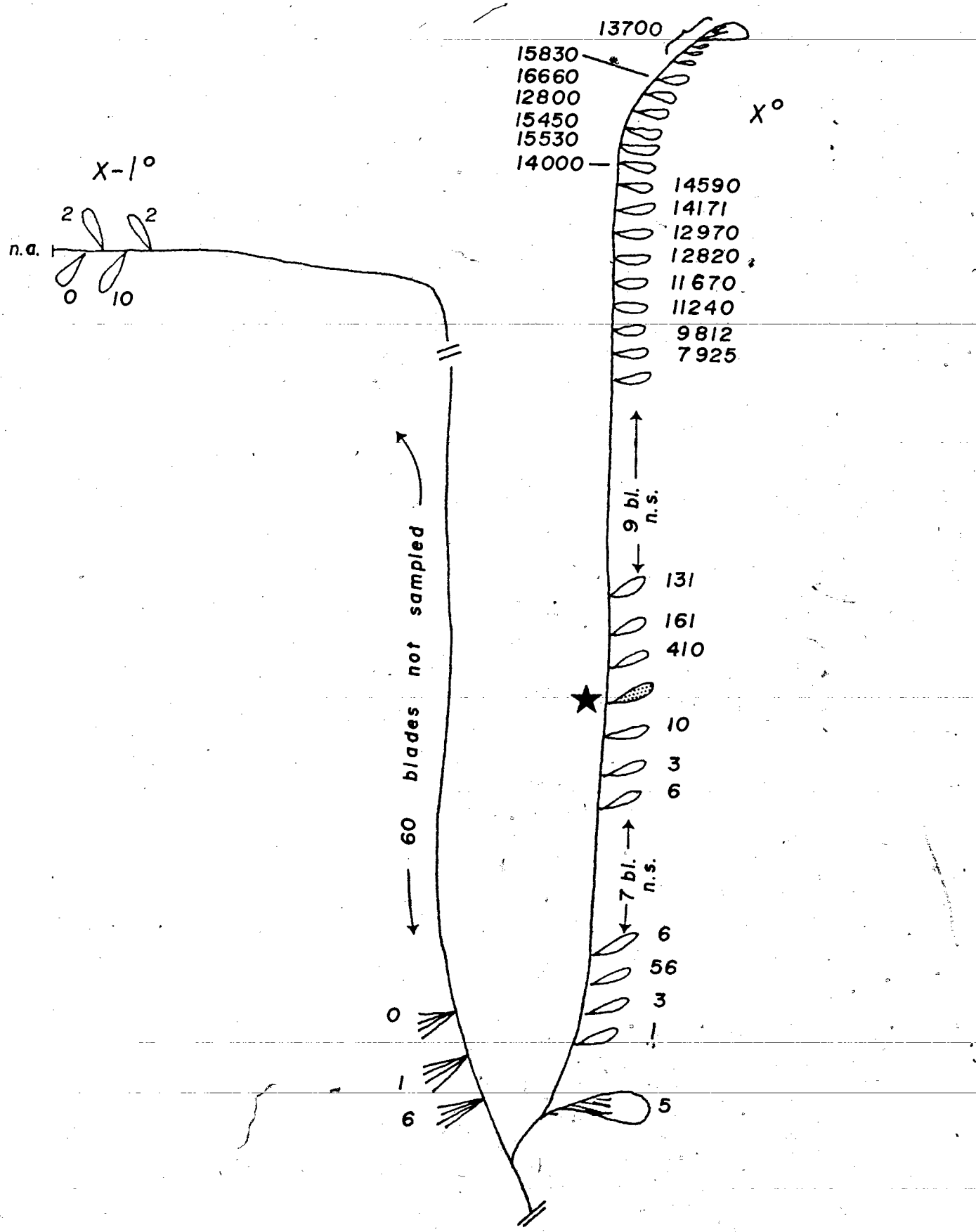

X-1°
2
2
n.a.
0
10
X°
13700
15830
16660
12800
15450
15530
14000
14590
14171
12970
12820
11670
11240
9812
7925
9 bl. n.s.
131
161
410
10
3
6
7 bl. n.s.
6
56
3
1
5
60 blades not sampled
0
1
6

Figure 21. Change from only-upward to upward and downward transport. The two halves of this plant were almost identical in frond lengths. The labeled blade was on the 2^{o} in each each. The two 1^{o}'s were absent. The labeled blade on C33 (right hand half) was 1.98 m from the apex (41st blade), and exported only to the 2^{o} apex; whereas the labeled blade of C32, 3.64 m from the apex (47th blade) exported both upward to the 2^{o} apex, and downward to the 2' and 4^{o} fronds, and, to a small extent to the 3^{o}. In other experiments it has been shown that activity from one half of the plant does not cross to the other. No activity was found in the haptera tips of this plant. Data in dpm/10 mg dry wt. Labeled blades shown stippled and marked with *.

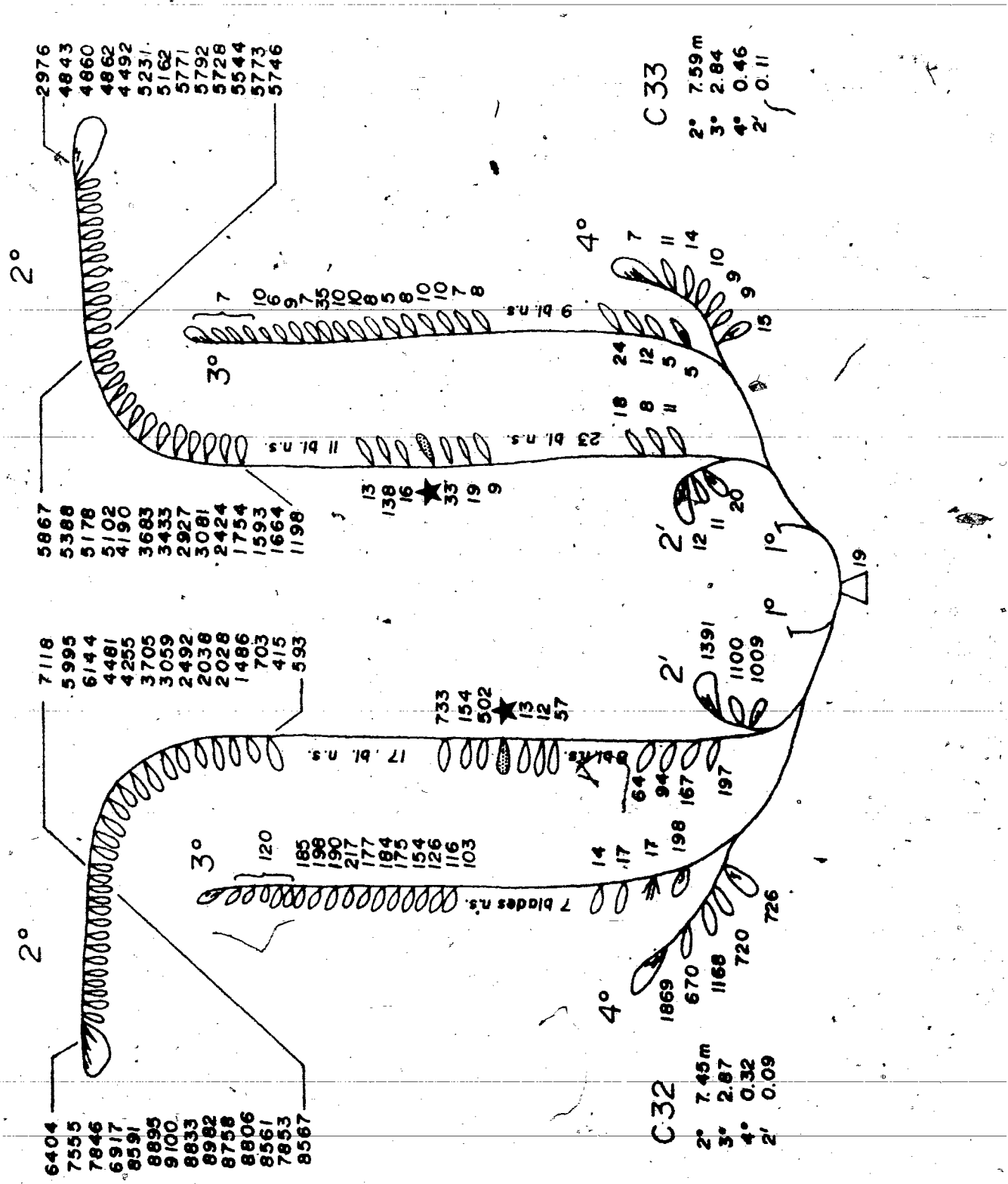
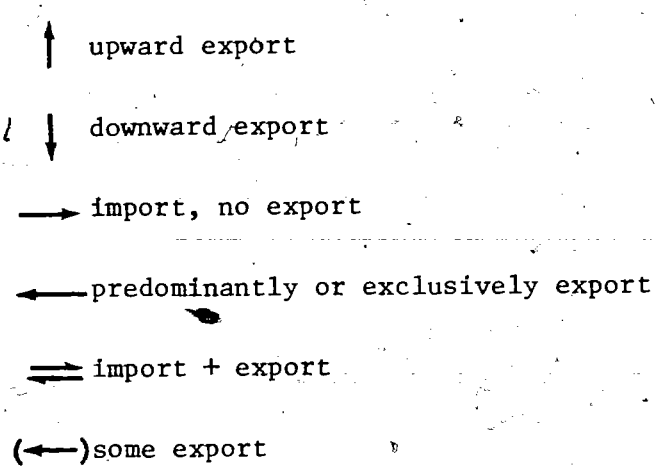

C33
2° 7.59m
3° 2.84
4° 0.46
2' 0.11
2°
3°
4°
2'
1°
9 bl n.s
11 bl n.s
23 bl n.s
17 bl n.s
7 blades n.s
2976 4843 4860 4862 4492 5231 5162 5771 5792 5728 5544 5773 5746
5867 5388 5178 5102 4190 3683 3433 2927 3081 2424 1754 1593 1664 1198
7118 5995 6144 4481 4255 3705 3059 2492 2038 2028 1486 703 415 593
6404 7555 7846 6917 8591 8895 9100 8833 8982 8758 8806 8561 7853 8567
C32
2° 7.45m
3° 2.87
4° 0.32
2' 0.09

Figure 22. Diagram, not to scale, to summarize import/export, and export direction patterns in mature fronds of Macrocystis pyrifera. Downward transport takes assimilates out of the frond to juvenile fronds, usually without labeling blades below the source except sporophylls and frond initials.



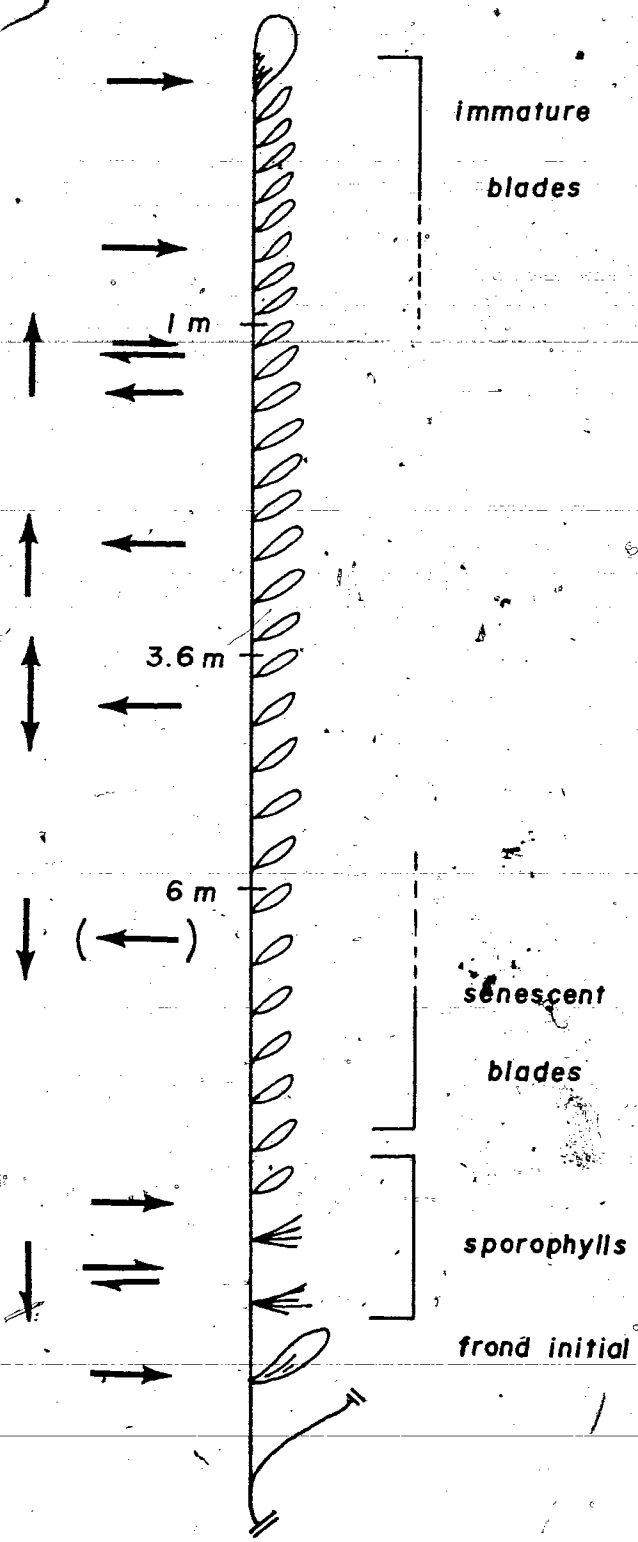
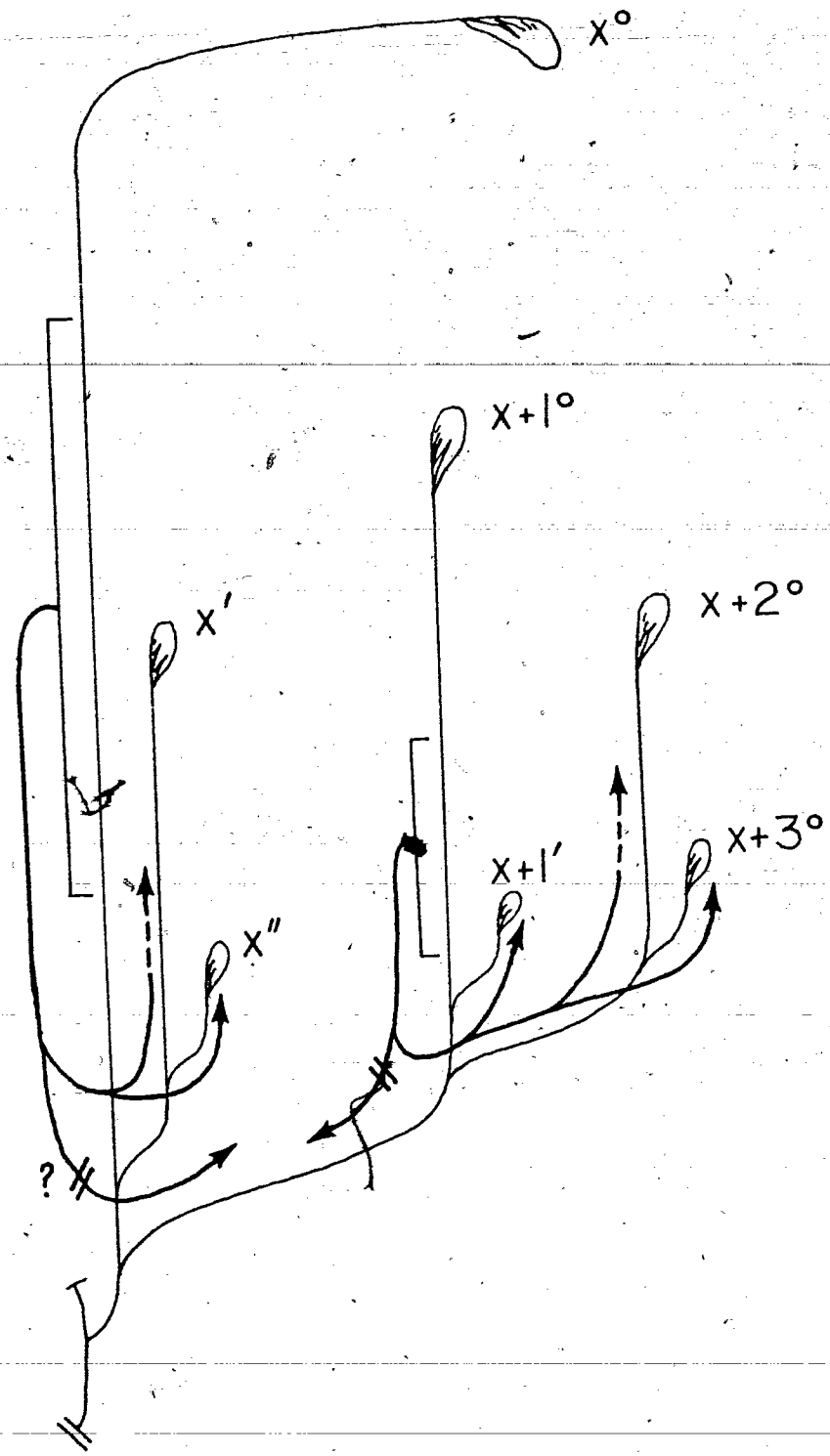

immature
blades
1 m
3.6 m
6 m
senescent
blades
sporophylls
frond initial

Figure 23. Diagram, not to scale, of export from source blades on mature fronds of M. pyrifera which are exporting partly or wholly downwards. In this general diagram, the $x+1^{o}$ would be similar to the 2^{o} of C32 (Fig. 21). Further details in the text.


X°
X+1°
X'
X+2°
X+1'
X+3°
X"
?

2. Macrocystis pyrifera at Kerckhoff Marine Laboratory

In contrast to the well-defined pattern of export and import found in the Arch Roch population, the translocation pattern in plants growing 1-2 m below low water in Newport Bay was less clear (Table 10), although basically the same as at Arch Rock. Of course, because the fronds were much shorter than those at Arch Rock -- only about 3 m long when full grown -- the transition regions are not expected at the same distances from the apex.

Within the experiments carried out, all fronds showed transport to the apex of the labeled frond, except C40 in which there was no transport at all. Although the blade number and distance from the apex in this frond would reasonably suggest the blade was mature, blades closer to the apex (e.g. C47, C45, C42) did show upward transport; in all these cases the blades were not fully grown. Import frequently dropped off sharply 5-10 blades behind the apex (Fig. 24a, c; compare with Fig. 19), suggesting that blades are formed slowly enough that the first few free blades have enough mature tissue to export photoassimilates. The closest blades to the apex that were labeled were on C52 (7th blade) and C45 (8th blade), both of which showed upward transport.

Transport was exclusively upwards until the source blade was about 1 m from the apex: C46 and C43 also showed downward translocation, although in C46 (Fig. 24b) the closest young frond with an apex was 4' (3' bore the labeled blade), and ^{14}C was not found outside the 3'.

Table 10. Synopsis of translocation experiment results for M. pyrifera at Kerckhoff Marine Laboratory. See legend for Table 1 (page 31). More complete data are given in Appendix Table 10 (p. 124).

	Frond				
d	x^o	$x+1^o$	$x+2^o$	x'	other
.32	A	(A)	--	--	A
.44	A		--	--	
.46	A		--	--	
.51	A	--	--	--	
.55			--	--	
.60	A		--	--	
.61	A			--	
.66	A	--	--	--	
.74	A	--	--	--	
.90	A		--	--	
1.03	A		--	--	
1.32	(A)		--	--	
1.37	A		A	A	--

Figure 24. Examples of experiments at Kerckhoff Marine Laboratory, M. pyrifera 1-2 m below low water. Labeled blades stippled and marked with *.

(a) C52: The experiment with the labeled blade closest to the apex, nevertheless showing both upward and downward transport. Note that no activity crossed into the right hand group of fronds. Note the sharp drop in import between the 3rd and 5th free blades from the apex of the labeled frond (4^{o}). Source blade was judged to be "only just mature" at the time of the experiment.

(b) C46: The oldest M. pyrifera studied, as far as could be determined. In the K.M.L. plants the haptera did not obscure the lower dichotomies, so that it was possible to trace fronds further than in Arch Rock plants. Translocation was upwards and downwards, but not out of the frond. Note that the labeled frond's juvenile (3") lacked the apex.

(c) C43: The experiment with the labeled blade farthest away from the apex, showing both upward and downward translocation. Note that although the 3^{o} and 4^{o} on the side of the labeled frond received ^{14}C, and 3^{o} and 4^{o} on the other side did not. Note the sharp drop in import between the 12th and 13th free blades on the labeled frond (2^{o}).

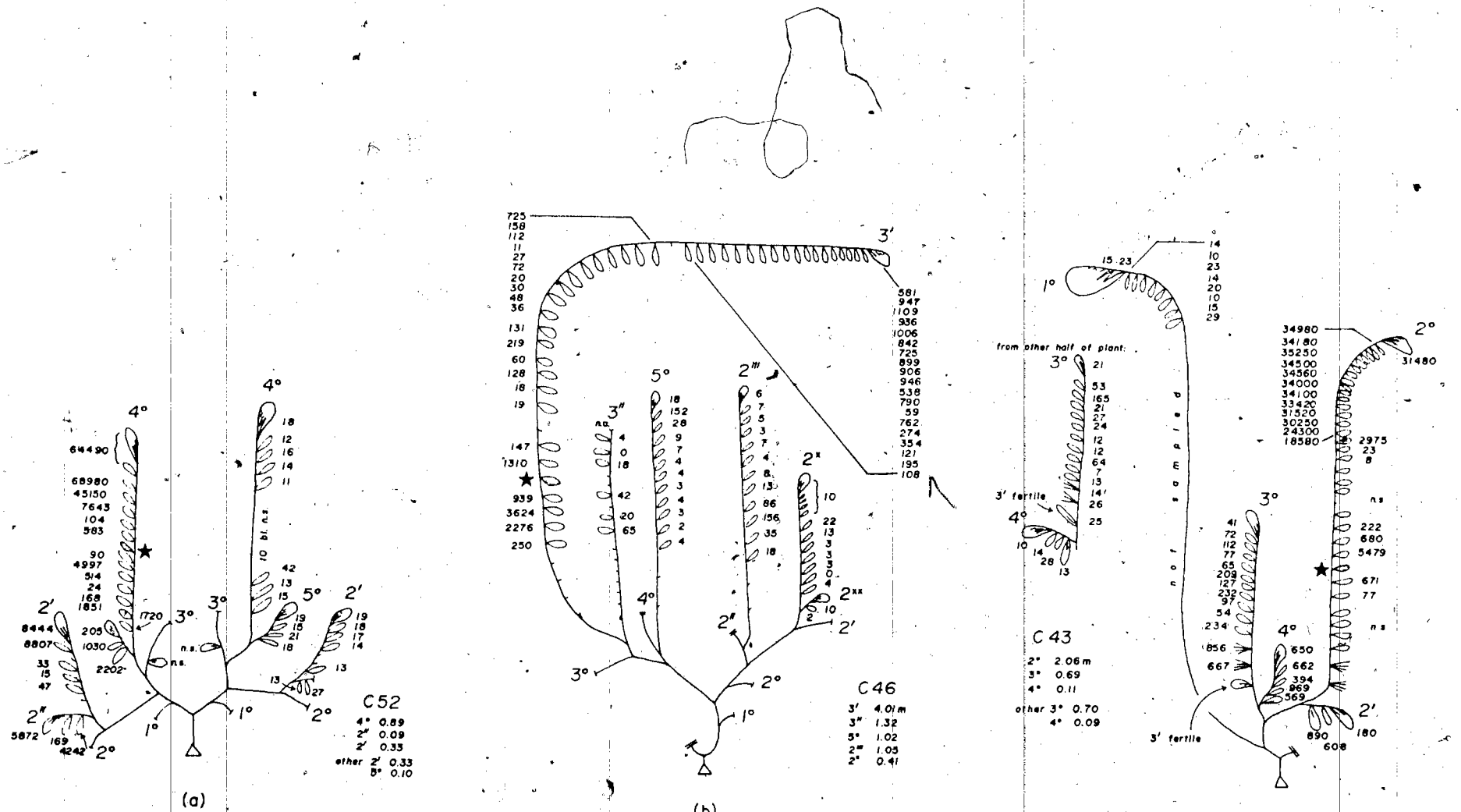

(a)
C52
4° 0.89
2‴ 0.09
2′ 0.33
other 2′ 0.33
5° 0.10
(b)
C46
3′ 4.01m
3″ 1.32
5° 1.02
2‴ 1.05
2° 0.41
(c)
C43
2° 2.06m
3° 0.69
4° 0.11
other 3° 0.70
4° 0.09
from other half of plant
3′ fertile
3′ fertile

Table 11. Synopsis of translocation experiment results, Santa Barbara. See legend of Table 1 (page 31). More details are given in Appendix Table 11 (p. 127).

	Frond			
d	x^o	$x+1^o$	$x+2^o$	other
.43		--	--	--
.44	A	--	--	
.75	A	--	--	
.75	A	--	--	
1.22		--	--	
1.52	A	--	--	
1.68	A[1]	A	--	--
1.80	A		--	--
1.94	A		--	
2.35	A		--	
2.77	A		--	--
3.00	A	--	--	
3.93		(A)	(A)	--
4.44	A		--	
6.26			--	
6.54			--	--
6.64		(A)	(A)	--
7.90		--	--	A

[1] x^o lacked apex - activity in base of frond only.

Table 12. Translocation from source blades on primary fronds. Experiments at Arch Rock, California. See Appendix for list of abbreviations and conventions.

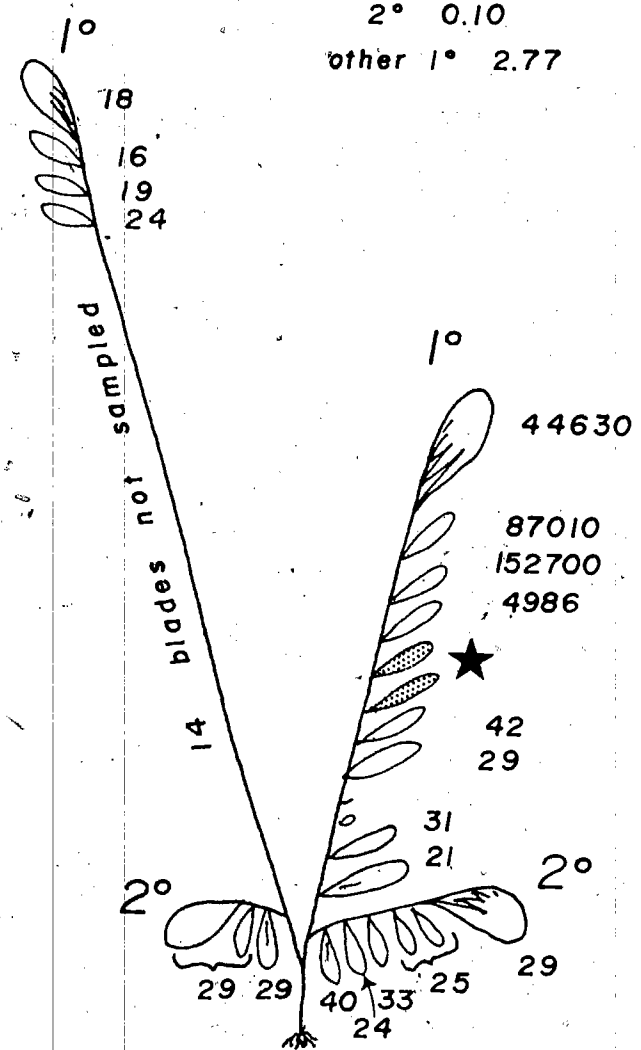
Notes:
1. Source = 2nd + 4th free blades (3rd missing)
2. Source = 4th + 5th free blades
3. Radioactive: see Fig. 22b.

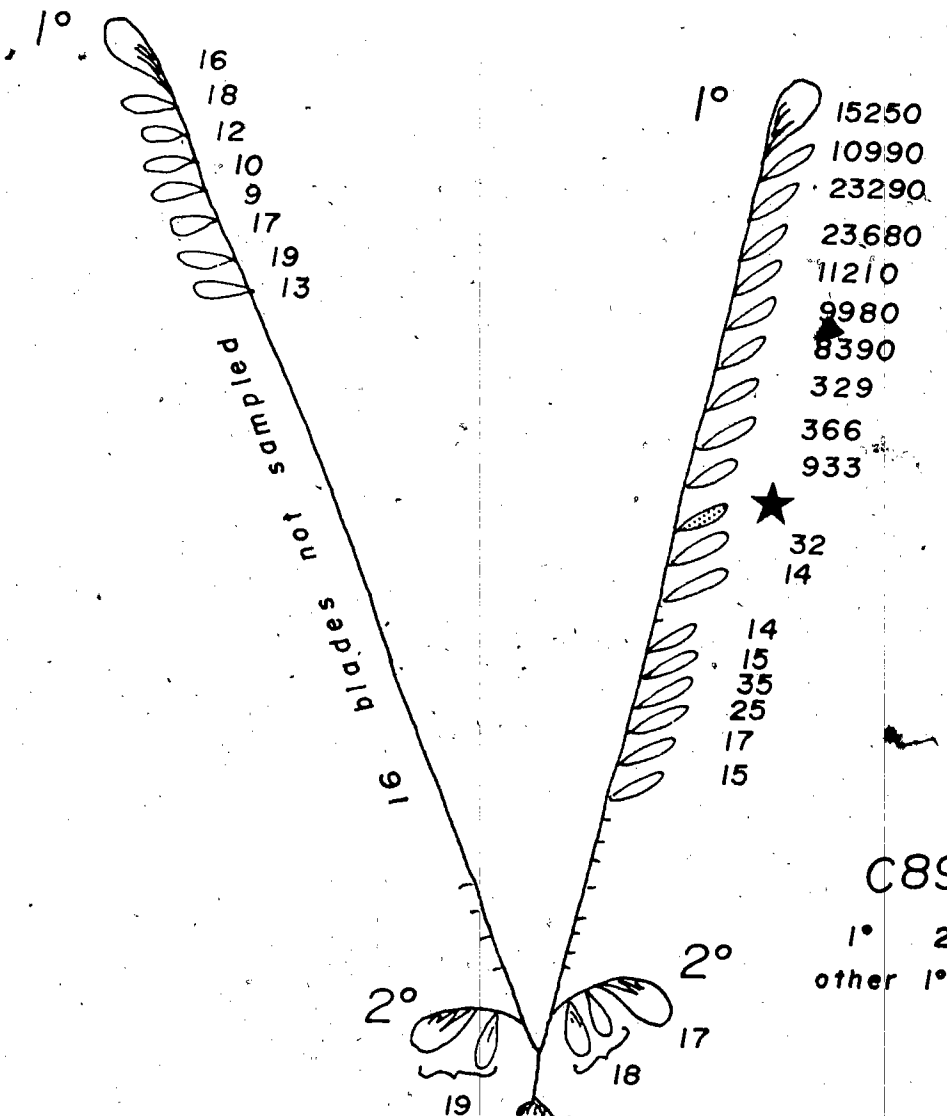
Plant	d (m)	frond	length (m)	activity in apical scimitar	maximum activity
C85	.15 [1]	1°*	2.46	1270	1643
		2°	.64	0	0
		1°	.79	0	0
C96	.18 [2]	1°*	ca.1.04	44630	152700
		2°	.10	0	0
		1°	2.77	0	0
		2°	.10	0	0
C91	.36	1°*	.86	24980	43260
		2°		n.a.	0
		1°	.79	0	0
		2°	.08	0	0
C89	.49	1°*	2.79	15250	23680
		2°	ca..10	0	0
		1°	3.25	0	0
		2°	ca..10	0	0
C92	.59	1°*	3.23	46240	46240
		2°	.17	0	0
		1°	3.72	0	0
		2°	.28	0	0
C11	.60	1°*	2.12	(Note 3)	(1195)
		2°	.10	0	0
		1°	1.08	n.a.	327
		2°	.10	0	0

Figure 25. Two examples of export by blades on primary (1^{o}) fronds. Note that the source blades in C96 are well within the region importing in C89. Labeled blades were 0.18 and 0.49 m from the apices, respectively, in the region in which in subsequent frond generations there is only import (cf. Fig. 22).

C96

1°* 1.04m
2° 0.10
other 1° 2.77

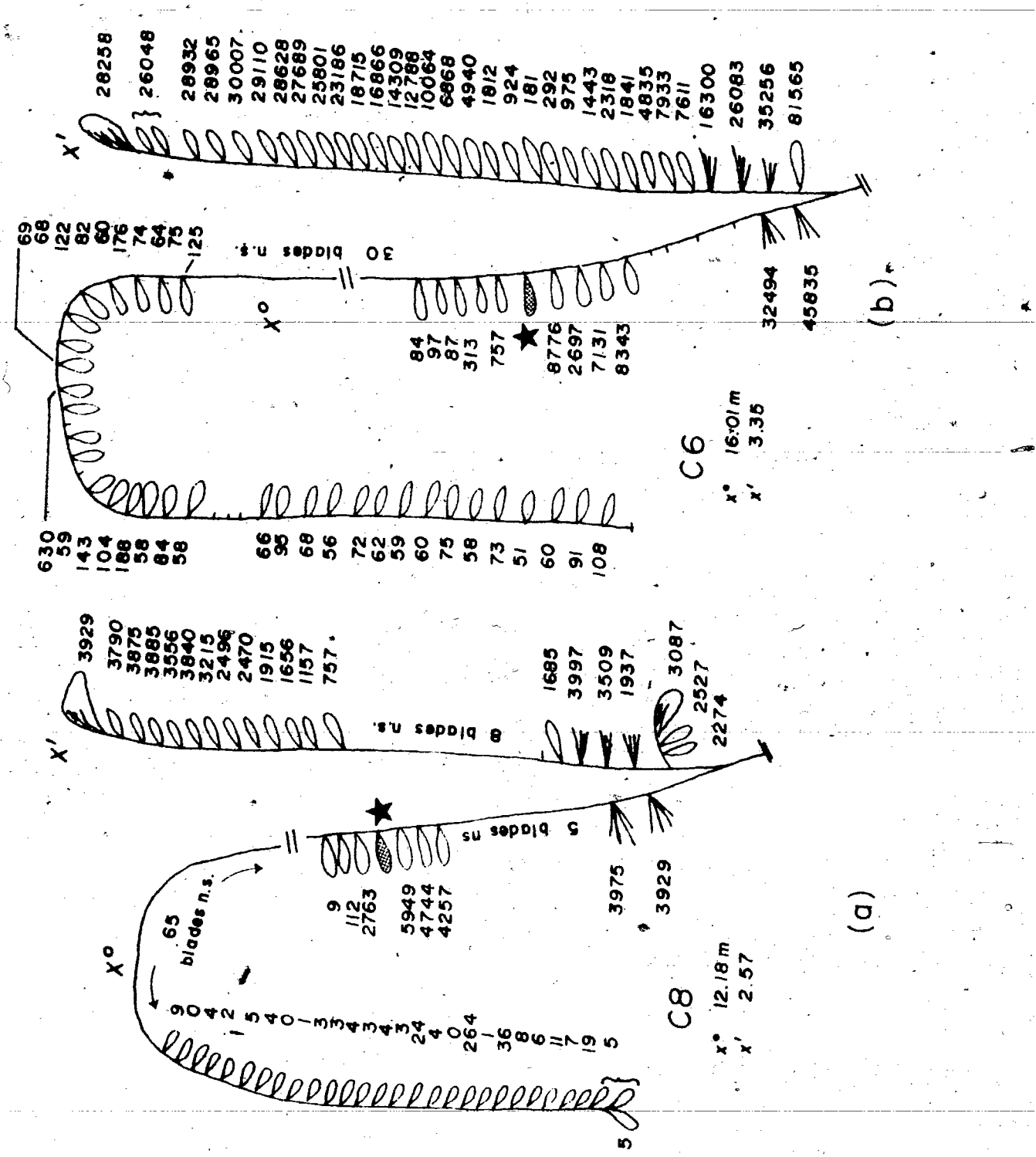




C89

1° 2.79m
other 1° 3.25

Figure 26. Effect of apex loss on translocation to the juvenile frond. Both cases are M. pyrifera from Arch Rock, and were exposed continuously to ^{14}C for 48 h (Table 9). (a) C8: labeled blade on frond with terminal blade (nongrowing apex), radioactivity in samples from sporophylls of x^o and sporophylls and apex of the juvenile frond of the order of 10^3 dpm/10 mg dry wt. (b) C6: very similar pair of fronds, but with x^o lacking the apex, activity in samples from juvenile frond and base of x^o of the order of 10^4 dpm/10 mg dry wt. Labeled blades shown stippled and marked with *.


28258
26048
28932
28965
30007
29110
28628
27689
25801
23186
18715
16866
14309
12788
10064
6868
4940
1812
924
181
292
975
1443
2318
1841
4835
7933
7611
16300
26083
35256
81565
X'
69
68
122
82
60
176
74
64
75
125
30 blades n.s.
X°
32494
45835
(b)
84
97
87
313
757
8776
2697
7131
8343
C6
x° 16.01 m
x' 3.35
630
59
143
104
188
58
84
58
66
95
68
56
72
62
59
60
75
58
73
51
60
91
108
3929
3790
3875
3885
3556
3840
3215
2496
2470
1915
1656
1157
757
1685
3997
3509
1937
3087
2527
2274
8 blades n.s.
5 blades ns
3975
3929
9
112
2763
5949
4744
4257
65
blades n.s.
C8
x° 12.18 m
x' 2.57
(a)

3. Macrocystis at Santa Barbara

The translocation results (Table 11) show a similar pattern to plants at Arch Rock. Export began in younger tissue, at around 0.45 m from the apex, but this is probably because the plants were growing in shallower water than Arch Rock plants, and were therefore shorter. Export was exclusively-upwards until the blade was about 3 m from the apex, below which the little export found was chiefly downward into young fronds. (C70 stands as an exception: its labeled blade, 4.4 m from the apex, exported only upwards.)

4. Translocation in 1° fronds of M. pyrifera

Export from labeled blades on 1° fronds began in much younger tissue than was the case for later-formed fronds (Table 12). Source blades 0.15-0.60 m from the apex showed only upward translocation. The region of import + export seems to be wider than in later fronds (Fig. 25).

5. Translocation in fronds lacking the apex

During the course of this study several labeled blades were on fronds lacking the apex; in addition, the young frond of C46 lacked the apex. There was no upward transport in any of these cases. Comparison of C6 and C8 (Table 9; Fig. 26), or C71 and C72 (Table 11), shows that there was an increase in translocation to the young frond if the labeled frond lacked the apex.

DISCUSSION

I. Translocation pattern in Macrocystis

In Macrocystis, assimilates from the many mature, source blades between the immature blades and the sporophylls on a frond are partitioned between the nearby apical growing points (strong sinks) and the sporophylls, frond initials, and probably the holdfast (weak sinks). Translocation in this genus thus follows the mature-source to meristematic-sink pattern described for Laminaria spp. and other small kelps (Lüning et al. 1973; Nicholson & Briggs 1972; Schmitz & Srivastava 1974, 1975, 1976; Schmitz & Lobban 1976), but a new dimension is added since as many as 4 apices may receive assimilates simultaneously from any given source blade, depending on (1) the position of the source in relation to the apex of its frond, and (2) the lengths of the nearby juvenile fronds. The translocation pattern of a blade can be correlated with its distance from the apex, which is a measure of its maturity. Similarly, import into a juvenile frond depends on its maturity: fronds of about 2 m length in M. integrifolia, 3 m in M. pyrifera, have mature blades, and no longer import.

The short-term experiments on M. integrifolia show a lag period of about 4 h before ^{14}C is detectable in the frond other than in the labeled blade. This lag, which is not found in higher plants (cf. Fisher 1975), can be interpreted as the time taken for (1) uptake and fixation of labeled bicarbonate, (2) build-up of ^{14}C in the pool of assimilates to

be loaded into the sieve-element system, (3) time for the loading and translocation of these labeled assimilates, and (4) time for accumulated ^{14}C to reach 100 dpm/sample. Parker's (1965) single experiment on an intact frond of M. pyrifera in situ showed a small amount of activity in the apex, 2.5 m from the labeled blade, after 4 h. I obtained slightly higher values in my 5 h experiments on this species, but did not find export after only 3 h.

The distance of the blade from the apex at which export began correlates, in M. integrifolia, with the distance where Sharp (1974) found lamina expansion to be almost completed (0.3 m from the apex). I have no data on the position of the blade in M. pyrifera at which lamina expansion is complete, but on the basis of the translocation results I would expect it to be between 0.5 and 1.0 m from the apex. On the basis of vascular plant findings (Turgeon & Webb 1973, 1975), as well as evidence from other kelps (Lüning et al. 1973; Schmitz & Srivastava 1975, 1976; Schmitz & Lobban 1976), I expect that the distal region of the immature blades, which autoradiography showed to be non-importing, would be supplying assimilates to the proximal region. I have not conducted experiments to verify this, and it may be that it only supports its own growth.

The graph of activity in the sample from each blade (Fig. 19) is by no means a graph of assimilate import by blades. However, in conjunction with the smooth increase in lamina area accumulating ^{14}C, seen in the autoradiographs, a curve for total import and export by the laminae

would probably be similar in shape to the graph for Cucurbita pepo L. given by Turgeon & Webb (1975, fig. 7).

Low activity (and occasionally high activity) was often found in mature blades, particularly those close to the labeled blade. In Macrocystis this might be attributed to the reticulate nature of the sieve element system and the fact that the filaments are not organized into discrete bundles. However, many blades along the transport path did not accumulate detectable radioactivity in 24 h. Wu & Thrower (1973) point out that Aronoff's (1955) report of no movement of labeled assimilates from one leaf to an older leaf has been confirmed many times. However, the following statements by Canny & Askham (1967) perhaps offer an explanation of activity in mature blades: "The mature leaf is a highly specialized exporter of sugar and cannot be made to reverse its polarity. Yet it is equally well known to all who have made this kind of autoradiograph that there is almost always a faint image produced by a mature leaf which is dismissed as being insignificant. ... It seemed to us that this faint image ... might represent the labeled contents of the phloem translocation system diffused about the leaf during drying, and dimmed by shielding of interposing tissue." They concluded that tracer may spread into an exporting leaf, against a net movement of non-tracer, but only as far as the unloading boundaries. I point this out especially since my method of drying would have allowed tracer from the whole stipe between the source blade and the mature blade in question to have diffused into the blade. Although it has more recently been shown that

certain conditions, such as darkness or CO_2-starvation can reverse the polarity (Heyser et al. 1975; Schmitz & Srivastava 1975), radioactivity in mature blades of Macrocystis can likely be dismissed from a consideration of translocation under normal conditions.

There is both export and import from blades of Macrocystis for a short (but as yet undetermined) time as they approach maturity. The magnitude of export and import is much greater than could be accounted for by diffusion against a flow of non-tracer assimilates. Temporary bi-directional translocation when export first begins is well known in vascular plants, and is a consequence of export from the tip of the leaf and import by the base (Jones & Eagles 1962; Turgeon & Webb 1973). It is a little harder to see how such bi-directional transport is accomplished in a reticulate system of sieve elements than in discrete phloem bundles, but selective callose deposition may well play a role in separating the importing and exporting parts of the reticulum.

Certain of the M. pyrifera experiments indicate a decline in accumulation of radioactivity in the proximal regions of immature laminae with increasing age of the labeled blade. However, other experiments showed that other factors must play major roles in determining the amount of radioactivity in the sinks, which my single-sample, qualitative experiments were not designed to resolve. These factors might include total photosynthesis of the labeled blades (dependent on health, light conditions, etc.), growth rates of the sinks, temperature during the experiment, depths of source and sinks, and so forth.

My experiments do not take into account carbon fixed by the blade before the experiment began. If senescing laminae export storage carbon, as for example tobacco leaves have been found to do (Shiroya et al. 1961), there could be substantial undetected translocation to younger blades or fronds, and this material would also dilute any newly-fixed carbon being exported.

Translocation in 1° fronds, which grow without benefit of a parent frond, shows a different pattern from that in subsequent frond generations. Export was found from sporophylls and frond initials when they had just been freed from the apical scimitar, until mature sterile blades had been formed.

II. Translocation and the environment of M. integrifolia and M. pyrifera

Two features of the environments which differ significantly between M. integrifolia and M. pyrifera, and affect translocation, are seasonal fluctuations, and the depths of the plants.

The transition regions -- where downward translocation begins, and where upward transport ceases -- change with season in M. integrifolia, and are modified by changes in growth rate. I interpret this change as a change from principally upward transport supporting growths of existing fronds which have survived the winter, to principally downward transport supporting sporophylls (reproduction) and production of new fronds (propagation and overwintering). Growth of M. pyrifera in

southern California varies little throughout the year (North 1971), so that one does not anticipate changes in translocation pattern from growth to storage (Lüning et al. 1973 found that Laminaria saccharina, which grows all year, translocated throughout the winter, whereas L. hyperborea ceased growth in the fall and stored assimilates in the lamina for the flush of spring growth). Nevertheless, the experiments on M. pyrifera, which were all conducted in October and November, may not represent a year-round pattern of translocation. At that time the nitrate and nitrite concentrations were very low in the surface waters at Arch Rock and San Clemente Island (North & Anderson 1975). North (1975) noted that, "The kelp bed at Cameo Shores [Arch Rock] displayed a quite noticeable canopy deterioration at this time [October 21 1974], presumably from adverse water temperatures during summer and early fall." It could be that subsurface blades (which were labeled in my experiments) were exporting more to their own frond apices at this time, at the expense of the juvenile fronds, in order to supplement the apical nitrogen supply. The translocate of Macrocystis is known to contain a high proportion of amino acids (Parker 1966; Schmitz unpublished), and it is quite possible that the apical blades could retain the amino acids for growth, and excrete the excess carbon; immature blades of M. integrifolia have been shown to excrete ^{14}C received from a source blade below (Fankboner & Druehl, 1976), and two phytoplankters have been shown to take up amino acids from seawater and preferentially retain the nitrogen (Stevens & North 1971). The fates of the carbon and the nitrogen in the translocation stream have not been investigated, nor is

the composition of Macrocystis exudates known. (Some nitrogenous materials -- as well as carbohydrates -- were exuded from Laminaria spp., following desiccation stress (Sieburth 1969).) The quantity of assimilates received by the juvenile fronds, as far as I can judge from my qualitative experiments, is low. The young fronds are growing in deep, poorly lit water, and are likely dependent on assimilates from the parent frond for growth (Sargent & Lantrip 1952). North (1968) showed a decrease in the growth rate of young fronds when their connection to the parent frond was severed. (However young tissues of Laminaria have been found to have extraordinarily high rates of dark-CO_2-fixation, both in light and in darkness (Willenbrink, pers. comm.) and this might also be so in Macrocystis.) If the adult frond apices in my experiments were indeed serving as unusually strong sinks, the translocation pattern at other times of year could be expected to differ from the one I found in the following ways: (1) if more ^{14}C were imported by the young fronds it might become detectable within the 24 h experimental period; (2) upward export might begin later, and would probably end sooner; (3) downward translocation would probably begin sooner.

The actual distances from the apex to the transition regions depend on the overall length of a full grown frond. In M. integrifolia (1-2 m below low water) export began at 0.3 m from the apex, while downward transport began about 1.2 m from the apex in spring, 0.5 m in fall. For M. pyrifera the transition regions were at about 0.5 and 3.0 m at Santa Barbara (5 m below low water), and 1 m and 3.5 m from the apex at

Arch Rock (8-10 m below low water). As far as I can determine from the low number of experiments, export in the shallow M. pyrifera in Newport Bay begun 0.15-0.3 m from the apex. The results of M. integrifolia were rather more variable than those from M. pyrifera, which I attribute partly to the more fluctuating environment of the shallower plants. In general the shallower the plant, the shorter the fronds, and the closer the transition regions to the apex.

Macrocystis has a surface canopy which shades deeper parts of the plant, but also provides assimilates to them. The deeper the tissue, of course, the less light it will receive, because of light attenuation by the water column, and the more important will be the assimilates received from older parts of the plant. As a young frond grows, it develops mature blades and elongates into greater illuminated water, and import from the other fronds declines and eventually ceases. Thus translocation to juvenile fronds should be more important in M. pyrifera than in M. integrifolia.

III. Harvesting, and apical dominance

The immediate effect of cutting the apex of an M. integrifolia frond was, apparently, the creation of a sink at the wound; ^{14}C accumulated in the blade(s) immediately below the cut. The explanation of the surge of transport may be simply that it is a physical function of severing the sieve tubes: Milburn (in Hébant 1975, p. 222) suggested

that the cut " ...goes a very long way to draining the turgor pressures from the whole system." If this is the case, then the sieve sap which replaces the sap which was exuded could contain a considerable amount of ^{14}C in my labeling experiments. There would then be a diffusion of ^{14}C against, or in the absence of, flow from the mature blades near the cut (Canny & Askham 1967). Whatever the explanation for the activity near the cut, the effect is a short-term one, one or two days at most, and subsequently the assimilates which were going to the apex of the cut frond are redistributed to the remaining sinks -- apices of young fronds, and sporophylls at the base of the cut frond. In my qualitative experiments this increase is not apparent in M. integrifolia, but can be seen in M. pyrifera; the change in pattern is clear in both species.

Clendenning (1968) thought that harvesting affected the kelp chiefly by increasing the penetration of light, and decreasing translocation. However, harvesting seems to increase the translocation to the young fronds. The combined effects of translocation and light should result in the canopy reforming faster than would be predicted from the growth rates of the young fronds alone. Of course, the amount of extra carbon they receive will depend on the amount of mature tissue left on the parent frond -- there must be a point where the amount of source tissue lost is equal to the amount of sink lost; if more tissue is cut off, growth of the young fronds will be impaired. Severing long fronds completely from kelp plants resulted in a marked decrease in the

growth rates of the short fronds (North 1968). But, as North (op. cit.) found, the overall reaction of a plant to cutting was very variable, depending particularly on the amount of tissue in the canopy, amount removed, and the light increase resulting from cutting.

The difference in translocation to the labeled frond apex compared with the juvenile frond apex, and the very marked increase in export to the juvenile frond when the apex of x^{o} of M. pyrifera is lost, indicates apical dominance in Macrocystis. The question of hormonal activity in kelps is still very much open, but evidence is accumulating to implicate hormones not only in translocation, but also in fructification and senescence.

IV. Translocation in Macrocystis and in vascular plants

The pattern of import and export from maturing laminae of Macrocystis shows great similarity to the pattern well known in many dicotyledons (Shiroya et al. 1961; Hale & Weaver 1962, fig. 23; Thrower 1967; Larson & Gordon 1969): immature leaves import only, but when half to three-quarters expanded begin export, first upwards, then downwards out of the shoot to storage or younger meristems. The massive support of flowers and fruit in angiosperms contrasts with the generally low import of ^{14}C by sporophylls of Macrocystis, but production of flowers and fruit occurs late in the life of the plant (or in the particular growing season), and often involves relatively massive structures. In

contrast, sporophylls are among the first blades formed (cf. p. 13), and they are already large when split off the apical scimitar. Frequently, but not always, the sporophyll branches and may become very large. However, this takes place over the whole life of the frond (about 6 mo. -- North 1961) and even beyond (since the lower part of the stipe bearing the sporophylls frequently remains when the rest of the frond has decayed). Photosynthesis in the sporophyll can partly meet the respiration requirements (L.D. Druehl, in prep.). It is therefore not surprising to find that, in a 24 h period, the amount of radioactivity accumulated in sporophylls is low compared to fast-growing tissue.

Macrocystis also differs somewhat from dicotyledons in the change from import to export. Because the distal part of the developing lamina is part of the already-formed apical scimitar, there is little growth in it (the proximal part of the lamina is meristematic), and no import into the distal region of either the apical scimitar or the free blades. In dicotyledons the whole leaf area is involved in expansion, and at first the whole leaf imports (Turgeon & Webb 1973). Subsequently, the importing area shrinks toward the proximal part of the leaf, and the distal region then begins to export, first to the proximal part, and then, while the leaf is still importing, out of the leaf to younger leaves (Turgeon & Webb 1973, 1975; Geiger 1975; Webb & Gorham 1964).

Although there are analogies between Macrocystis and dicotyledons, there are also interesting analogies with monocotyledons,

particularly some of the grasses, where tillering is analogous to new frond production in Macrocystis. In the vegetative state of certain grass plants, leaves (e.g. corn: Hofstra & Nelson 1969) and tillers (rye: Sagar & Marshall 1966; Marshall & Sagar 1968) are interdependent. I have no evidence from Macrocystis pyrifera, but in M. integrifolia the frond initial on the primary frond supported the apical blades until the frond had about 12 blades; thereafter the frond initial did not export. Frond initials on subsequent fronds, in both species, did not export, and there is no movement from younger fronds to older even when the younger frond lacks the apex. When rye internodes began to expand, and especially when the inflorescence was formed, the meristems and leaf insertions became more separated (Ryle & Powell 1972), and interdependence changed to the familiar pattern of export upward from upper leaves, downward from lower leaves (Rawson & Hofstra 1969; Ryle & Powell 1972). A close analogy exists between Macrocystis and Agropyron repens (L.) Beauv. (couch grass): in the seedling stage of this grass assimilates from the leaves supported the primary shoot and root meristems; later tillers began to grow and were supported by the primary shoot, but no activity passed from the tillers to the primary shoot (Rogan & Smith 1974). The beginning of export from cereal leaves may begin later than in dicots, because of the highly polarized growth from a proximal meristem (Felippe & Dale 1972). In M. integrifolia the onset of export was shown to coincide with maturity of the lamina.

Perhaps the greatest difference in translocation pattern between

Macrocystis and land plants is that in the latter root and shoot growth are of the same order, and a large proportion of the leaves ~~assimilates~~ go to the roots. In Macrocystis hapteron growth is relatively slow, in terms of biomass added, and import is correspondingly low. (The haptera are weakly pigmented, but it has not yet been shown whether a significant amount of the growth comes from their own photosynthesis.)

It is beyond the scope of this study to consider the mechanism by which the observed movement of ^{14}C takes place. However, it should be remembered that the structure of sieve elements in kelps is very different from sieve tubes of vascular plants: (1) the sieve elements are fully functional cells, with a full cytoplasm (some even retain the nucleus), and abundant vesicles (Schmitz & Srivastava 1974, 1975, 1976; Schmitz in Johnson 1975, p. 72), and lack companion cells (Ziegler 1963; Parker & Huber 1965; Schmitz & Srivastava op. cit.; Parker 1971); (2) the reticulum they form is much finer and more open than in vascular plants, with many more anastomoses than angiosperms (Aloni & Sachs 1973; Schmitz & Srivastava 1974). Despite these recent studies on kelp sieve elements, studies on Macrocystis pertain largely or exclusively to the sieve plates (Wille 1885; Oliver 1887; Sykes 1908; Esau et al. 1953; Accortini 1960; Ziegler 1963; Parker & Philpott 1961; B. Parker 1964; J. Parker 1964; reviewed by Esau 1969). Schmitz & Srivastava (1974a) recently demonstrated a high turnover of ATP in sieve elements of Macrocystis integrifolia. In Laminaria digitata, Penot et al. (1976) showed inhibition by cyclohexamide of long-distance ion transport (e.g. ^{32}P).

There are many problems which remain. Some, such as the fate of C- and N-compounds imported by young tissue, and how the reticulate sieve element system might be divided between upward and downward transport, have been raised in the foregoing discussion. Some other important questions are: the kinetics of loading assimilates into the sieve elements, of transport, and of unloading; and the role of hormones in regulation of translocation patterns. My studies have at best defined the problems, and provided the necessary background against which to begin more detailed, and quantitative experiments, leading ultimately, one hopes, to an understanding of the mechanism of translocation in brown algae. While comparison with land plant translocation is instructive in evaluating results on algae, and in pointing out directions of research that are likely to be fruitful, one needs to be careful to not carry the analogies too far. Current thinking on evolutionary relationships between plants places the higher brown algae on a branch well separated, by non-translocating algae, from land plants, and it is unreasonable to presuppose homologies between algal and vascular plant translocation; rather, they are an example of parallel evolution.

REFERENCES

Accortini, J. 1960. Observaciones sobre el aparato secretor y conductor de Macrocystis pyrifera C. Ag. Tecnicas para su visualizacion. Com. Museo Argent. Cien. Nat. Bern. Rivadavia (Botan.) 1 (8): 11-20.

Aloni, R. & T. Sachs. 1973. The three-dimensional structure of primary phloem systems. Planta (Berl.) 113: 345-353.

Aronoff, S. 1955. Translocation from soybean leaves. II. Plant Physiol. 30: 184-185.

Aronoff, S., J. Dainty, P.R. Gorham, L.M. Srivastava & C.A. Swanson (eds.) 1975. Phloem Transport. Plenum Press, New York, 636 pp.

Barrales, H.L. & C.S. Lobban, 1975. The comparative ecology of Macrocystis pyrifera, with emphasis on the forests of Chubut, Argentina. J. Ecol. 63: 357-377.

Brandt, R.P. 1923. Potash from kelp. Early development and growth of the giant kelp, Macrocystis pyrifera. U.S. Dept. Agric. Bull. 1911. 40 pp.

Canny, M.J. & M.J. Askham, 1967. Physiological inferences from the evidence of translocated tracer: a caution. Ann. Bot. (n.s.) 31: 409-416.

Clendenning, K.A. 1968. Harvesting effects on canopy invertebrates and on kelp plants. In, W.J. North & C.L. Hubbs (eds.) Utilization of kelp bed resources in southern California. Calf. Dept. Fish & Game, Fish Bull. 139, pp. 219-222.

Crafts, A.S. 1939. The relation between structure and function of the phloem. Amer. J. Bot. 26: 172-177.

Esau, K. 1969. The Phloem. Handbook of Plant Anatomy V (2). 505 pp.

Esau, K., V.I. Cheadle & E.M. Gifford, Jr. 1953. Comparative structure and possible trends of specialization of the phloem. Amer. J. Bot. 40: 9-19.

Fankboner, P.V. & L.D. Druehl. 1976. In situ accumulation of marine algal extracellular products by a polycheate worm. Experimentia 32: 1391-1392.

Felippe, G.M. & J.E. Dale. 1972. The uptake of $^{14}CO_2$ by developing first leaves of barley and partition of the labelled assimilates. Ann. Bot. (n.s.) 36: 411-418.

Fisher, D.B. 1975. Translocation kinetics of photosynthates. In, S. Aronoff et al. (eds.) Phloem Transport. Plenum Press, N.Y, pp. 327-358.

Fuchs, A. & F.W. de Vries. 1972. Comparison of methods for the preparation of ^{14}C-labeled plant tissues for liquid scintillation counting. Intl. J. Appl. Radiation Isotopes 23: 361-369.

Geiger, D.B. 1975. Phloem loading and associated processes. In, S. Aronoff et al. (eds.) Phloem Transport. Plenum Press, New York, pp. 251-281.

Hale, C.R. & R.J. Weaver. 1962. The effect of developmental stage on direction of translocation of photosynthate in Vitis vinifera. Hilgardia 33: 89-131.

Hébant, C. 1975. Discussion. In, S. Aronoff et al. (eds.) Phloem Transport. Plenum Press, New York, pp. 211-224.

Heyer, W., O. Leonard, R. Heyser, E. Fritz & W. Eschrich. 1975. The influence of light, darkness, and lack of CO_2 on phloem translocation in detached maize leaves. Planta (Berl.) 122: 143-154.

Hofstra, G. & C.D. Nelson. 1969. The translocation of photosynthetically assimilated ^{14}C in corn. Can. J. Bot. 47: 1435-1442.

Johnson, R.P.C. 1975. Discussion. In, S. Aronoff et al. (eds.) Phloem Transport. Plenum Press. New York, pp. 63-78.

Johnston, C.S. 1969. The ecological distribution and primary production of macrophytic marine algae in the eastern Canaries. Int. Rev. ges. Hydrobiol. 54: 473-490.

Jones, H. & J.E. Eagles. 1962. Translocation of ^{14}carbon within and between leaves. Ann. Bot. (n.s.) 26: 505-510.

Larson, P.R. & J.C. Gordon. 1969. Leaf development, photosynthesis, and C^{14} distribution in Populus deltoides seedlings. Amer. J. Bot. 56: 1058-1066.

Lobban, C.S. 1974. A simple, rapid method of solubilizing algal tissue for scintillation counting. Limnol. Oceanogr. 19: 356-359.

Lobban, C.S. 1976. Growth, translocation and harvesting interactions in Macrocystis integrifolia. Final report to B.C. Marine Resources Branch, Victoria, 88 pp.

Lüning, K. 1969. Growth of amputated and dark-exposed individuals of the brown alga Laminaria hyperborea. Mar. Biol. 2: 218-223.

Lüning, K., K. Schmitz & J. Willenbrink. 1972. Translocation of ^{14}C-labeled assimilates in two Laminaria species. Proc. Intl. Seaweed Symp. 7: 420-425.

Lüning, K., K. Schmitz & J. Willenbrink. 1973. CO_2 fixation and translocation in benthic marine algae. III. Rates and ecological significance of translocation in Laminaria hyperborea and L. saccharina. Mar. Biol. 23: 275-281.

Marshall, C. & G.R. Sagar. 1968. The interdependence of tillers in Lolium multiflorum Lam. - a quantitative assessment. J. Exptl. Bot. 19: 785-794.

Neushul, M. 1959. Studies on the growth and reproduction of the giant kelp, Macrocystis. Ph.D. Thesis, Univ. Calif. Los Angeles. 134 pp.

Neushul, M. 1971. The species of Macrocystis, with particular reference to those of North and South America. In, W.J. North (ed.) The Biology of Giant Kelp Beds (Macrocystis) in California. Nova Hedwigia Beih. 32: 211-222.

Neushul, M. & F.T. Haxo. 1963. Studies on the giant kelp, Macrocystis. I. Growth of young plants. Amer. J. Bot. 50: 349-353.

Nicholson, N.L. & W.R. Briggs. 1972. Translocation of photosynthate in the brown alga Nereocystis. Amer. J. Bot. 59: 97-106.

North, W.J. 1961. Lifespan of the fronds of the giant kelp Macrocystis pyrifera. Nature (Lond.) 190: 1214-1215

North, W.J. 1968. Effects of canopy cutting on kelp growth: comparison of experimentation with theory. In, W.J. North & C.L. Hubbs (eds.) Utilization of kelp bed resources in southern California. Calif. Dept. Fish & Game, Fish Bull. 139: 223-254.

North, W.J. 1971. Growth of individual fronds of the mature giant kelp, Macrocystis. In, W.J. North (ed.) Biology of Giant Kelp Beds (Macrocystis) in California. Nova Hedwigia Beih. 32: 123-168.

North, W.J. 1972. Observations on populations of Macrocystis. In, I.A. Abbott and M. Kurogi (eds.) Contributions to the Systematics and Ecology of North Pacific Benthic Marine Algae. Jap. Soc. Phycol, Tokyo, pp. 75-92.

North, W.J. 1975. Evaluating oceanic farming of seaweeds as sources of organics and energy. Semi-annual report to Natl. Sci. Found. (Mimeo) 53 pp.

North, W.J. & B.N. Anderson. 1975. Evaluating oceanic farming of seaweeds as sources of organics and energy. Semi-annual report to Natl. Sci. Found. (Mimeo) 120 pp.

Oliver, F.W. 1887. On the obliteration of the sieve-tubes in Laminarieae. Ann. Bot. 1: 95-117.

Parker, B.C. 1963. Translocation in the giant kelp Macrocystis. Science 140: 891-892.

Parker, B.C. 1964. Chemical nature of sieve tube callus in Macrocystis. Phycologia 4: 27-42.

Parker, B.C. 1965. Translocation in the giant kelp Macrocystis. I. Rates, direction, quantity of C^{14}-labeled organic products and fluorescein. J. Phycol. 1: 41-46.

Parker, B.C. 1966. Translocation in Macrocystis. III. Composition of sieve tube exudate and identification of the major C^{14}-labeled products. J. Phycol. 2: 38-41.

Parker, B.C. 1971. Studies of translocation in Macrocystis. In, W.J. North (ed.) The Biology of Giant Kelp Beds (Macrocystis) in California. Nova Hedwigia Beih. 32: 191-195.

Parker, B.C. & J. Huber. 1965. Translocation in Macrocystis. II. Fine structure of the sieve tubes. J. Phycol. 1: 172-179.

Parker, J. 1964. Further notes on the sieve plates of Macrocystis pyrifera. Protoplasma 58: 681-684.

Parker, J. & D.E. Philpott. 1961. The ultrastructure of sieve plates of Macrocystis pyrifera. Bull. Torrey Bot. Club. 88: 85-90.

Penot, M., J.Y. Floc'h, & M. Penot. 1976. Physiologie comparée des transports à longue distance chez les végétaux supérieurs et chez les algues marines. Phycologia 15: 299-308.

Rawson, H.M. & G. Hofstra. 1969. Translocation and remobilization of ^{14}C assimilated at different stages by each leaf on the wheat plant. Austr. J. Biol. Sci. 22: 321-331.

Reinke, J. 1876. Beitrage zur Kenntnis der Tange. Jahrb. Wiss. Bot. 10: 317-382.

Rogan, P.G. & D.L. Smith. 1974. Patterns of translocation of ^{14}C-labelled assimilates during vegetative growth of Agropyron repens (L.) Beauv. Z. Pflanzenphysiol. 73: 405-414.

Ryle, G.J.A. & C.E. Powell. 1972. The export and distribution of ^{14}C-labelled assimilates from each leaf on the shoot of Lolium temulentum during reproductive and vegetative growth. Ann. Bot. (n.s.) 36: 363-375.

Sagar, G.R. & C. Marshall, 1966. The grass plant as an integrated unit -- some studies of assimilate distribution in Lolium multiflorum Lam. Proc. 9th Intl. Grassland Congr. pp. 493-497.

Sargent, M.C. & L.W. Lantrip. 1952. Photosynthesis, growth and translocation in giant kelp. Amer. J. Bot. 39: 99-107.

Scagel, R.F. 1948. An investigation on marine plants near Hardy Bay, B.C. Report to Prov. Dept. Fish.; Occ. Pap. 1. 70 pp.

Schmitz, K. & C.S. Lobban, 1976. A survey of translocation in Laminariales (Phaeophyceae). Mar. Biol. 36: 207-216.

Schmitz, K. & L.M. Srivastava. 1974. Fine structure and development of sieve tubes in Laminaria groenlandica Rosenv. Cytobiologie 10: 66-87.

Schmitz, K. & L.M. Srivastava. 1974a. The enzymatic incorporation of ^{32}P into ATP and other organic compounds by sieve-tube sap of Macrocystis integrifolia. Planta (Berl.) 116: 85-89.

Schmitz, K. & L.M. Srivastava. 1975. On the fine structure of sieve tubes and the physiology of assimilate transport in Alaria marginata Postels and Ruprecht. Can. J. Bot. 53: 861-876.

Schmitz, K. & L.M. Srivastava. 1976. The fine structure of sieve elements of Nereocystis lütkeana. Amer. J. Bot. 63: 679-693.

Sharp, G.J. 1974. The impact of Tegula pulligo, Gmelin on tissue loss from Macrocystis integrifolia, Bory in Barkley Sound, Vancouver Island, British Columbia. M.Sc. Thesis, Simon Fraser University. 114 pp.

Shiroya, M., G.R. Lister, C.D. Nelson & G. Krotkov. 1961. Translocation of C^{14} in tobacco at different stages of development following assimilation of $C^{14}O_2$ by a single leaf, Can. J. Bot. 39: 855-864.

Sieburth, J.McN. 1969. Studies on algal substances in the sea. III. The production of extracellular organic matter by littoral marine algae. J. Expt. Mar. Biol. Ecol. 3: 290-309.

Skottsberg, C. 1907. Zur Kenntnis der Sub-Antarktischen und Antarktischen Meeresalgen. I. Phaeophyceen. Wiss. Ergebn. Schwed. Sud-Polar-Exped. IV (6). 172 pp.

Steinbiss, H.H. & K. Schmitz. 1973. CO_2-Fixierung und Stofftransport in benthischen marinen Algen. V. Zur autoradiographischen Lokalisation der Assimilattransportbahnen im Thallus von Laminaria hyperborea. Planta (Berl.) 112: 253-261.

Stevens, G.C. & B.B. North. 1971. Extrusion of carbon accompanying uptake of amino acids by marine phytoplankters. Limnol. Oceanogr. 16: 752-757.

Sykes, M.G. 1908. Anatomy and histology of Macrocystis pyrifera and Laminaria saccharina. Ann. Bot. 22: 291-325.

Thrower, S.L. 1967. The pattern of translocation during leaf ageing. Symp. Soc. Exptl. Biol. 21: 483-506.

Towle, D.W. & J.S. Pearse. 1973. Production of the giant kelp, Macrocystis, estimated by in situ incorporation of C^{14} in polyethylene bags. Limnol. Oceanogr. 18: 155-159.

Turgeon, R. & J.A. Webb. 1973. Leaf development and phloem transport in Cucurbita pepo: transition from import to export. Planta (Berl.) 113: 179-191.

Turgeon, R. & J.A. Webb. 1975. Leaf development and phloem transport in Cucurbita pepo: carbon economy. Planta (Berl.) 123: 53-62.

Wallen, D.G. & G.H. Geen. 1968. Loss of radioactivity during storage of ^{14}C-labeled phytoplankton on membrane filters. J. Fish. Res. Bd. Canada. 25: 2219-2224.

Webb, J.A. & P.R. Gorham. 1964. Translocation of photosynthetically assimilated C^{14} in straight-necked squash. Plant Physiol. 39: 663-672.

Will. H. 1884. Zur Anatomie von Macrocystis luxurians Hook. fil. et Harv. Botan. Zeit. 42: 801-808 + 825-83

Wille, N. 1885. Siebhyphen bei den Algen. Ber. deutsch. Bot. Ges. 3: 29-31.

Williams, R.D. 1964. Assimilation and translocation in perennial grasses. Ann. Bot. (n.s.) 28: 419-425.

Womersley, H.B.S. 1954. The species of Macrocystis with special reference to those on southern Australian coasts. Univ. Calif. Publ. Bot. 27: 109-132.

Wu, A. & L.B. Thrower. 1973. Translocation into mature leaves. Plant & Cell Physiol. 14: 1225-1228.

Ziegler, H. 1963. Untersuchungen über die Feinstruktur des Phloems. II. Die Siebplatten bei der Braunalge Macrocystis pyrifera (L.) Ag. Protoplasma 57: 786-799.

Ziegler, H. & I. Ruck. 1967. Untersuchungen über die Feinstruktur des Phloems. III. Die "Trompetenzellen" von Laminaria-Arten. Planta (Berl.) 73: 62-73.

APPENDIX

TABLES 1-6 + 9-11

Appendix Tables: More complete data are given here than in the synoptic tables in the text for the results of the various groups of translocation experiments. A copy of the full set of data sheets, with the complete data for all the experiments, has been lodged in the Data File of Depository of Unpublished Data, National Science Library, National Research Council of Canada, Ottawa.

The following list of abbreviations and conventions applies to all the Tables in the Appendix, as well as to Table 7 (pages 47-50), Table 8 (page 53), and Table 12 (page 67).

Unless otherwise noted experiments were of 24 h duration, with continuous feeding with ^{14}C.

Activity is given in dpm/10 mg dry wt. Maximum activity means the highest sample dpm in the apical scimitar and associated immature blades.

0 dpm means "less than 100 dpm/10 mg dry wt" (see page 7).

d (m) = distance from the labeled blade to the apex of the labeled frond.

date = date of harvest (end of experimental period)

apiscim = apical scimitar

fr. bl. = free blade

fr. init. = frond initial

n.a. = no apex

n.s. = not sampled

? = contamination suspected

Abbreviations for study sites in Barkley Sound: R = Ross Islets; C-O = Clarke-Owens; SJ = San José Islets; BMS = Bamfield Marine Station; BI = Bamfield Inlet; WI = Wizard Islet.

* indicates the labeled frond.

Table 1. Results of translocation experiments on M. integrifolia at Bamfield Inlet, May-June 1973.

Plant	date	d (m)	frond	length (m)	activity in apiscim	maximum activity
10	June 20	.30	1^{o}*	2.26	10052	10052
			2^{o}	.67	0	0
			3^{o}	fr.init.	209	-
			1^{o}	2.31	0	0
11	June 20	.30	x^{o}*	2.20	0	0
			$x+1^{o}$	.23	0	0
			$x+2^{o}$	fr.init	0	-
6	June 5	.32	1^{o}*	2.04	0	446
			2^{o}	.49	0	0
			1^{o}	2.29	0	0
13	June 24	(.33)	1^{o}*	(1.37)	n.a.	0
			2^{o}	.08	345	-
			1^{o}	.91	653	730
			2^{o}	.27	4076	4076
			3^{o}	fr.init.	211	-
7	June 5	.34	x^{o}*	1.27	5508	27361
			$x+1^{o}$	.55	0	338
			$x+2^{o}$	.12	0	0
5	June 5	.35	x^{o}*	2.60	0	0
			$x+1^{o}$	.76	0	0

Table 1, cont.

Plant	date	d(m)	frond	length (m)	activity in apiscim	maximum activity
19	June 28	.38	1^{o}*	1.28	341472	341472
			2^{o}	.11	9447	9447
			3^{o}	fr.init.	10369	-
			4^{o}	fr.init.	16928	-
			1^{o}	1.48	0	0
			2^{o}	.09	0	0
21	June 28	.56	x^{o}*	2.40	2965	4921
			$x+1^{o}$	.59	n.a.	0
			$x+2^{o}$	fr.init.	273	-
15	June 24	.74	x^{o}*	2.56	280	280
			$x+1^{o}$	1.21	n.a.	456
			$x+2^{o}$	-	303	950
			$x+3^{o}$	fr.init.	598	598
22	June 28	.83	x^{o}*	1.45	50313	64043
			$x+1^{o}$	.27	0	0
			$x+2^{o}$	fr.init.	0	0
16	June 24	.99	x^{o}*	3.67	0	179
			$x+1^{o}$	1.40	271	309
			$x+2^{o}$	.78	489	489
			$x+3^{o}/4^{o}$	fr.init.	366	366

Table 1, cont.

Plant	date	d (m)	frond	length (m)	activity in apiscim	maximum activity
3	May 23	Note 1	x^{o}*	1.39	1014	1769
			$x+1^{o}$	.32	0	0
26	June 28	1.03	x^{o}*	2.05	7820	9767
			x'	.30	0	0
			x''	fr.init.	0	0
18	June 28	1.16	x^{o}*	2.10	61812	64886
			x'	.26	0	0
			x''	fr.init.	0	0
9	June 20	1.28	x^{o}*	1.78	8558	10253
			$x+1^{o}$	1.40	2390	2390
			$x+2^{o}$	.72	2933	2933
			$x+3^{o}$	fr.init.	3708	-
14	June 24	Note 2	x^{o}*	2.71	588	588
			$x+1^{o}$	.85	113	161
			$x+2^{o}$	.21	707	707
			$x+3^{o}$	fr.init.	464	-
24	June 28	1.50	x^{o}*	3.52	3572	7000
			$x+1^{o}$(x'?)	.72	0	0
			$x+2^{o}$(x''?)	fr.init.	0	-
			$x+3^{o}$(x'''?)	fr.init.	0	-

Table 1, cont.

Plant	date	d (m)	frond	length (m)	activity in apiscim	maximum activity
17	June 28	2.23	x^{o}*	2.90	9357	11768
			$x+1^{o}$	1.40	2037	2761
			$x+2^{o}$	.11	19853	19853
			$x+3^{o}$	fr.init.	11049	11049
23	June 28	3.23	x^{o}*	4.45	1514	5217
			$x+1^{o}$(x'?)	.72	363	512
			$x+2^{o}$(x"?)		186	255
			$x+3^{o}$(x"'?)	fr.init.	0	-
20	June 28	-	x^{o}	1.73	n.a.	0
			$x+1^{o}$	.54	0	0
			$x+2^{o}$	fr.init.	0	0

Notes. 1. labeled blade number 12 of 19

2. labeled blade number 29 of 36

Table 2. Results of translocation experiments on M. integrifolia at Bamfield Inlet, August-October 1973.

Plant	date	d(m)	frond	length (m)	activity in apiscim	maximum activity
39	Sep 1	.35	2°*	.70	97820	131731
			3° and 4°		0	0
			other 1°,2°,3°,4°		0	0
43	Sep 1	(.37)	x°*	2.42	n.a.	0
			x+1°	.54	8571	21445
			x+2°	fr.init.	23661	-
			x+3°	fr.init.	11851	-
47	Sep 16	.39	x°*	2.65	153481	1512473
			x+1°	1.00	0	0
			x+2°	-	190	190
			x+3°	fr.init.	110	-
28	Aug 27	.40	x°*	2.23(Note 1)	145	413
			x+1°	2.07	377	377
			x+2°	.29	686	1141
			x+3°	fr.init.	1432	-
27	Aug 27	.47	x°*	1.84	34685	50944
			x+1°/2°	fr.init.	0	0
61	Oct 13 (Note 2)	.46	x°*	(.84)	n.a.	0(Note 3)
			x+1°	.50	13921	28720
			x+2°	fr.init.	1050	-

Table 2, cont.

Plant	date	d (m)	frond	length (m)	activity in apiscim	maximum activity
29^4	Aug 28	.63	1^{o}*	1.76	17727	48571
			2^{o}	.15	76943	76943
			3^{o}	fr.init.	2993	-
			1^{o}	1.21	407	498
50^5	Sep 16	.68	1^{o}*	1.15	584	584
			2^{o}	.41	1016	85345
			3^{o}	fr.init.	196	-
			2^{o}	.16	151	151
			3^{o}	fr.init.	0	-
37	Sep 1	(.80)	x^{o}*	(3.27)	n.a.	0
			$x+1^{o}$	(1.35)	n.a.	0
			$x+2^{o}$	.49	167	1006
			$x+3^{o}$	fr.init.	0	-
59^2	Oct 13	.87	x^{o}*	2.68	20813	42143
			x'		n.a .	19899
			x"	fr.init.	34688	-
36	Sep 1	.90	x^{o}*	3.22	0	0
			$x+1^{o}$	2.20	1126	1302
			$x+2^{o}$	.81	2065	6419
53	Sep 21	(.91)	x^{o}*	(3.60)	n.a.	358 (Note 3)
			$x+1^{o}$	1.35	2144	7424
			$x+2^{o}$	.31	2411	7105
			$x+3^{o}$	fr.init.	1374	-

Plant	date	d(m)	frond	length	activity in apiscim	maximum activity
32^6	Aug 31	(1.01)	x^o*	(1.93)	n.a.	0
			$x+1^o$	1,18	16610	23153
			$x+2^o$		49179	49179
			$x+3^o$	fr.init.	25557	-
38	Sep 1	1.04	x^o*	2.70	12037	14960
			$x+1^o$	.43	198	198
			$x+2^o$	fr.init.	997	-
44	Sep 16	1.07	x^o*	2.74	888	1488
			$x+1^o$	.67	2633	3537
52	Sep 21	1.07	x^o*	2.26	8708	23636
			x'	fr.init.	0	-
54	Sep 21	1.12	x^o*	3.83	13114	36206
			$x+1^o$	1,44	173	173
			$x+2^o$	.17	0	0
			$x+3^o$	fr.init.	0	0
48	Sep 16	1.15	x^o*	2.23	242	1019
			$x+1^o$	.60	4940	15062
			$x+2^o$	fr.init.	5856	-
			$x+3^o$	fr.init.	325	-
51	Sep 21	(1.22)	x^o*	3.77	n.a.	0
			$x+1^o$	.90	1756	1756
			$x+2^o$	fr.init.	690	-

Plant	date	d(m)	frond	length (m)	activity in apiscim	maximum activity
45	Sep 16	(1.24)	x°*	(4.09)	n.a.	0
			x+1°	.91	9365	10174
			x+2°		4948	4948
			x+3°	fr.init.	1154	-
60[2]	Oct 13	1.25	x°*	5.31	(Note 1)	142(Note 3)
57	Sep 21	1.53	x°*	2.43	1590	4702
			x+1°	.40	9138	6932
			x+2°	fr.init.	0	-
			x+3°	fr.init.	823	-
58	Sep 21	1.68	x°*	3.75	510	510
			x+1°	1.03	169	243
			x+2°	fr.init.	363	-
55	Sep 21	1.80	x°*	4.22	1378	1378(Note 3)
			x+1°	1.09	602	634(Note 3)
			x+2°		608	7390
33[7,8]	Sep 1	1.92	x°*	2.84	0	0
			x+1°	1.39	4638	8388
			x+2°/3°	fr.init.	28271	-
31[6]	Aug 31	2.03	x°*	3.36	0	0
			x+1°	1.43	7453	11270
			x+2°		1025	2340
			x+3°	fr.init.	794	-

Table 2, cont.

Plant	date	d(m)	frond	length (m)	activity in apiscim	maximum activity
65^2	Oct 13	2.40	x^o*	4.66	251	251 (Note 3)
			$x+1^o$	1.17	7423	13238 (Note 3)
			$x+2^o$	fr.init.	3772	-
			$x+3^o$	fr.init.	8363	-
64^2	Oct 13	2.57	x^o*	3.92	0	0 (Note 3)
			$x+1^o$	1.54	9745	13991 (Note 3)
			$x+2^o$		17343	18390
			$x+3^o$	fr.init.	1873	-
63^2	Oct 13	-	x^o*	(2.09)	n.a.	0
			$x+1^o$	(.79)	n.a.	0 (Note 3)
			$x+2^o$	fr.init.	30676	37165
			$x+3^o$	fr.init.	51399	-
35^8	Sep 1	-	x^o*	(1.24)	n.a.	0
			$x+1^o$	1.94	102	395
			$x+2^o,3^o$	fr.init.	0	-
34^7	Sep 1	-	1^o*	(.99)	n.a.	0
			2^o	fr.init.	134465	-
			1^o	1.24	18108	40196

Table 2, cont.

Notes. 1. x^{o} with terminal blade

2. 72 h continuous label

3. High activity in sporophylls

4. 24 h label, 48 h experiment

5. Apex damaged. This experiment shown in Schmitz & Lobban (1976), fig. 7.

6. 24 h label, 5 day experiment

7. 24 h label, 6 day experiment

8. labeled blade senescent

Table 3. Results of translocation experiments on M. integrifolia at Ross Islets, February and March, 1975.

Plant	date	d (m)	frond	length (m)	activity in apiscim	maximum activity
147	Feb 9	.34	x^{o}*	1.35	5368	9930
			$x+1^{o}$	.17	0	0
148	Feb 9	.35	x^{o}*	1.73	0	0
			$x+1^{o}$	.82	0	0
			$x+2^{o}$	.17	0	0
			$x+3^{o}$	fr.init.	0	0
150	Feb 9	.37	x^{o}*	1.33	0	346
			$x+1^{o}$	fr. init.	0	0
149	Feb 9	.50	x^{o}*	1.11	8780	11980
			$x+1^{o}$	.30	0	0
151	Feb 9	.56	x^{o}*	1.51	67790	79690
			$x+1^{o}$	.42	0	0
153	Mar 9	.58	x^{o}*	1.24	22290	23890
155	Mar 9	.58	x^{o}*	1.18	1174	1796
			$x+1^{o}$	fr.init	496	-
154	Mar 9	.68	x^{o}*	1.78	946	1273
152	Mar 9	.69	x^{o}*	1.70	0	0

Table 3, cont.

Plant	date	d (m)	frond	length (m)	activity in apiscim	maximum activity
156	Mar 9	.70	x^{o}*	1.57	213	213
			$x+1^{o}$	.80	0	0

Table 4. Results of translocation experiments on M. integrifolia at Ross Islets, August-November 1975.

Plant	date	d (m)	frond	length (m)	activity apiscim	maximum activity
August 27-28						
203	Aug. 28	.37	x^{o}*	1.80	1,526	1,728
			$x+1^{o}$	.80	0	0
			$x+2^{o}$	.11	0	0
204	"	1.55	x^{o}*	2.77	0	0
			$x+1^{o}$	.38	441	605
			$x+2^{o}$	fr.init.	640	989
205	"	.57	x^{o}*	2.40	70,750	76,870
			$x+1^{o}$	.41	0	0
			$x+2^{o}$	.08	0	0
206	"	.27	x^{o}*	3.10	1,969	1,992
			$x+1^{o}$	.67	731	855
			$x+2^{o}$	.59	650	650
			x'	fr.init.	311	525
207[1]	"	1.49	x^{o}*	4.80	0	0
			x'	.12	917	2,293
		.20	$x+1^{o}$	1.95	627	664
			$x+2^{o}$	.95	0	2,328
			$x+3^{o}$	fr.init.	763	1,883

Table 4, cont.

Plant	date	d (m)	frond	length (m)	activity apiscim	maximum activity
208	"	2.36	x^{o}*	4.18	0	1,031
			$x+1^{o}$	2.80	0	0
			$x+2^{o}$	.45	0	0
			$x+3^{o}$	fr.init.	295	-
209	"	2.64	x^{o}*	3.94	0	0
			x'	fr.init.	235	457
September 13-14 and 16-17						
210	Sept. 14	.59	x^{o}*	2.22	24,090	28,550
			$x+1^{o}$	.27	283	283
			$x+2^{o}$	.04	276	277
213	"	.51	x^{o}*	2.60	20,700	25,410
			x'	fr.init.	349	-
218	Sept. 17	.35	x^{o}*	2.62	36,140	43,320
			$x+1^{o}$	.15	0	0
	"	2.29	x^{o}*	8.35	0	0
			x'	.68	0	0
220	"	.12	x^{o}*	1.60	0	0
			$x+1^{o}$	3.60	n.a.	0
221[2]	"	.12	x^{o}*	7.45	70,000	91,950

Table 4, cont.

Plant	date	d (m)	frond	length (m)	activity apiscim	maximum activity
222[3]	"		x^o*	(4.92)	n.a.	-
			$x+1^o$	2.49	n.a.	0
			$x+2^o$	.17	567	635
223	"	.34	x^o*	5.82	0	0
			$x+1^o$	1.10	0	0
			$x+2^o$	.16	0	0
224[3]	"		x^o*	(9.20)	n.a.	3,560
225	"	.39	x^o*	2.84	43,700	45,140
			$x+1^o$	.34	0	0
			$x+2^o$	.06	0	0
September 23-24						
226	Sept. 24	.30	x^o*	2.00	27,620	34,440
			$x+1^o$		0	0
227	"	.25	x^o*	1.88	83,870	84,150
			$x+1^o$	.18	0	0
228	"	.32	x^o*	4.40	43,070	43,520
			$x+1^o$	1.85	n.a.	n.s.
			$x+2^o$	.35	0	0
			$x+3^o$	.07	0	0
229[4]	"	.15	x^o*	1.44	n.a.	11,010
			$x+1^o$	.12	0	0

Table 4, cont.

Plant	date	d (m)	frond	length (m)	activity apiscim	maximum activity
230	"	.15	x^o*	3.27	40,590	41,740
			$x+1^o$	.92	n.a.	0
231	"	2.05	x^o*	4.31	6,926	8,715
232	Sept. 24	1.03	x^o*	4.09	17,250	22,940
			$x+1^o$	1.22	0	0
			$x+2^o$	.07	410	0
November 14-15						
233[5]	Nov. 15	.10	x^o*	.42	0	0
			$x+1^o$	fr.init.	0	0
234	"	.21	x^o*	1.28	188	1,461
			$x+1^o$		n.a.	0
235[5]	"	.21	x^o*	1.83	274	471
			$x+1^o$		0	0
236	"	.17	2^o*	.78	0	0
			3^o, 4^o		0	0
			other 2^o, 3^o		0	0

Notes:
1. both x^o and $x+1^o$ labeled
2. terminal blade on x^o
3. x^o apex lost during harvesting
4. apical scimitar + 1 free blade missing from x^o apex
5. apical scimitar in poor condition on x^o

Table 5. Results of translocation experiments on *M. integrifolia* at San José Islets.

Plant	date	d (m)	frond	length (m)	activity in apiscim	maximum activity
1975 experiments.						
185	July 17	1.03	x^{o}*	5.83	11430	14560
			$x+1^{o}$	3.14	0	0
			$x+2^{o}$	.39	0	0
187	July 17	1.34	x^{o}*	9.41	10910	14020
186	July 17	1.62	x^{o}*	7.19	10830	12200
184	July 17	1.77	x^{o}*	6.57	11420	11420
			$x+1^{o}$	(2.52)	n.a.	0
			$x+2^{o}$	1.23	0	0
			$x+3^{o}$,x'	fr.inits.	0	0
183	July 17	1.96	x^{o}*	4.13	13900	13900
			$x+1^{o}$	2.24	0	0
1976 experiments						
258	May 11	.26	x^{o}*	3.31	-	467
			$x+2^{o}$	1.24	402	402
			$x+3^{o}$	.21	513	513
			$x+4^{o}$	fr.init.	293	-
262	May 11	.30	x^{o}	2.42	0	275

Table 5, cont.

Plant	date	d(m)	frond	length (m)	activity in apiscim	maximum activity
246	Apr 22	.49	x^{o}*	1.45	24440	34930
			$x+2^{o}$	fr.init.	0	0
259	May 11	.50	x^{o}*	1.25	24311	24311 (Note 1)
			$x+1^{o}$	.08	1550	1550
			$x+2^{o}$	fr.init.	1386	-
261	May 11	.54	x^{o}*	3.24	2465	2465
			$x+1^{o}$	2.80	808	808
			$x+3^{o}$	.41	507	507
245	Apr 22	.56	x^{o}*	2.09	1752	1752
260	May 11	.60	x^{o}*	2.47	18779	20073
			$x+1^{o}$	1.89	129	355
			$x+2^{o}$	1.00	295	347
			$x+3^{o}$	,11	165	165
241	Apr 22	.66	x^{o}*	1.86	0	0
			$x+1^{o}$	1.16	14190	15250
			$x+2^{o}$	.48	24910	26520
			$x+3^{o}/4^{0}$	fr.init.	21450	28820
242	Apr 22	.70	x^{o}*	1.45	23350	23940
			$x+1^{o}$	.26	5758	16230
			$x+2^{o}$	.09	5479	5479
			$x+3^{o}$	fr.init.	2393	-

Table 5, cont.

Plant	date	d (m)	frond	length (m)	activity in apiscim	maximum activity
243	Apr 22	.90	x^{o}*	1.44	28630	29830
			$x+1^{o}$	fr.init.	0	0
264	May 11	.95	x^{o}*	2.22	3845	3845(Note 1)
			$x+1^{o}$	.38	31802	51630
			$x+2^{o}$	fr.init.	32370	-
238	Apr 22	.97	x^{o}*	1.81	0	0
			$x+1^{o}$	.62	2826	3562
			$x+2^{o}$	fr.init.	2214	-
			$x+3^{o}$	fr.init.	2438	-
263	May 11	1.00	x^{o}*	2.34	13022	13834
			$x+1^{o}$	1.80	0	253
			$x+2^{o}$	.53	27777	33218
			$x+3^{o}$	fr.init.	14025	-
237	Apr 22	1.36	x^{o}*	2.36	0	0(Note 1)
			x'	fr.init.	8434	-

Notes. 1. High activity in sporophylls

Table 6. Translocation experiments on young M. integrifolia. Export from blades on young 1° fronds. Experiments are grouped to show export from a particular blade as more blades are formed above it. Conditions: L = in laboratory; C = chamber used for labeling; D = continuous illumination. Experiments in situ at: W = Wizard It., July 9-Sep 8 1974; BI = Bamfield Inlet, fall 1973; R = Ross Its, July 1974.

Blade (# from base)	total # fr. bl.	d (m)	sink (if any)	maximum activity	plant # & conditions
Apiscim	0	0		0	103; L,C
1 (2°)	1	ca..12	1°*	54587	102; L,C
	1	ca..12		0	97; L,C,D
	2	.07	1°*	1058	93; L,C,D
	4	ca..18	1°*	340	113; W
	4	ca..28	1°*	7971	111; W
2	2	.07	1°*	16850	100; L
	2	.07		0	101; L
	3		1°*	94258	99; L
	5	.15	1°*	524193	105; W
			2°(fr.init.)	6407	
	12	.84	1°*	1097	131; W
			2°	13507	
			other 1°	3073	
			2°	9542	
3	4	.23	1°	470	107; W

Table 6, cont.

Blade (# from base)	total # fr.bl.	d (m)	sink (if any)	maximum activity	plant # & conditions
3, cont	4	.18	1°*	1790	108; W
			2°	1924	
	5		1°*	779	106; W
	5	.17		0	109; W
	6		1°*	348910	98; L,D
	6	.11	1°*	12631	114; W
	8	.37	1°*	70670	129; W
	9	.53	1°*	2437	135; W
	9	.70	1°*	10982	134; W
	10	ca. .70		0	110; W
	10	.77	1°*	22248	139; W
			2°	4000	
4	5	.10		0	104; W
	8	.19	1°*	971493	132; W
	11	.45	1°*	21433	130; W
5	14	1.14	1°*	0	144; W
			2°	68328	
			3°(fr.init.)	83748	
	12	.60	1°*	51274	40; BI
6	8	.10		0	142; W
	13	.74	1°*	19303	42; BI
	13	.62	1°*	81745	56; BI

Table 6, cont.

Blade # from base	total # fr.bl.	d (m)	sink (if any)	maximum activity	plant #, & conditions
7	7	.06		0	136; W
	8	.07		0	141; W
	9	.08		0	138; W
	16	.81	1°*	26518	41; BI
8	10	.09		0	143; W
	12	.18		0	68; BI
9	10			0	122; R
	12	1.79		0	146; W

Table 9. Results of translocation experiments on M. pyrifera at Arch Rock, October and November 1974.

Plant	d (m)	frond	length (m)	activity in apiscim	max. activ.
C80	0	2'*		apiscim = source	0
		4°, 5°		0	0
C86	0	x°*		apiscim = source	0
C84	.18	x°* (Note 1)		0	0
C77	.22	2'*		0	0
		2°, 4°, (n.a.), 5°, 2"		0	0
C81	.25	x°*		0	0
		x+1°		0	0
C20	.32	x°*		0	0
C82	.38	2'* (Note 2)		0	1,007
		2", 5°, 4° (n.a.)		0	0
C88	.38	x°* (Note 2)		0	0
C83	.39	2'*		0	0
		2", 4°, 5°		0	0
C87	.40	x°*		0	0
		x+1°		0	0
C25	.46	x°*		0	0

Table 9, cont.

Plant	d (m)	frond	length (m)	activity in apiscim	max. activ.
C14	.50	x^{o}*		term. blade	0
		$x+1^{o}$		408	784
C24	.50	x^{o}*		0	0
C95	.59	3^{o}*		0	0
		2^{o}, 4^{o}		0	0
C38	.66	4^{o}*		342 (Note 3)	
		2', 2", 2^{o}, 3^{o}		0	0
C94	.87	3^{o}*		24,350	35,520
		2^{o}, other 3^{o}		0	0
C36	1.04	3^{o}*		781 (Note 3)	
		4^{o}, 2', 2^{o}		0	0
C 9#	1.27	2'*		82,050	86,300
		2", 3', 5^{o}		0	0
C90	1.65	2^{o}*		15,920	15,920
		3^{o}, 4^{o}, 2'		0	0
C18	1.96	x^{o}*		13,700	16,660
C33	1.98	2^{o}*		2,916	5,867
		2', 4^{o}, 3^{o}		0	0
C35	2.22	3^{o}*		4,145	9.450
		2^{o}, 2', 4^{o}, 1'		0	0

Table 9, cont.

Plant	d (m)	frond	length (m)	activity in apiscim	max. activ.
C 7#	2.52	4^{o}*		15,870	16,320
		5^{o}, 3^{o}, 3', 2^{o}, 2', 2"		0	0
C93	3.32	2^{o}*		3,152	3,498
		2', 1^{o}, 4^{o}, 3^{o}		0	0
C34	3.45	3^{o}*		3,177	7,505
		2^{o}, 2', 4^{o}		0	0
C97	3.61	3^{o}*		0	0
		4^{o}, 2', 2^{o}		0	0
C32	3.64	2^{o}*		6,404	9,100
		2'		1,391	1,391
		4^{o}		1,869	1,869
		3^{o}		0	198
C39	4.62	3^{o}*		1,750	3,344
		2^{o}		term.blade	0
		2', 4^{o}		0	0
C37	5.13	2^{o}*		0	0
		2'		316	316
		4^{o}		185	757
		3^{o}		0	0
C 8#	8.40	x^{o}*		term.blade	0
		$x+1^{o}$		3,929	3,929

Table 9, cont.

Plant	d (m)	frond	length (m)	activity in apiscim	max. activ.
C 5#	10.90	x°*		n.a.	0
		x+1°		13,270	14,300
C 6#	12.22	x°*		n.a.	0
		x+1°		28,258	30,007
		Plants in which source was a sporophyll or frond-initial:			
C74	0	2"* (Note 4)		-	-
		2', 5°		0	0
C78	0	2'* (frond initial)		-	-
	2° (n.a.), 3°, other 2° (n.a.)			0	0
		other 3°, 4°		0	0
C76	0	3'* (frond initial)		-	-
		3°		0	0
		4°		0	363(Note 5)
		5°		12,300	12,300
C75	0	5°* (frond initial)		-	-
	(.25 from apex	4°		747	946
	of 4°)	3°		147	344(Note 5)
		2°, 2'		0	0
C79	?	2° (sporophyll*)		n.a.	0
		2'		4,801	5,761
		5°		0	0

Notes. 1. First 4 free blades = source

Table 9, cont.

2. 3 blades labeled; activity declines from sources
3. Steady decline from labeled blade
4. Whole 2" (apiscim + 3 fr.bl.) was labeled
5. In base of frond only
6. # = 48 h experiment

Table 10. Results of translocation experiments on M. pyrifera at Kerckhoff Marine Laboratory (1.5-2.5 m below low water), October 25-26 and 29-30 1974.

Plant	d	frond	activity in apical scimitar	max. activ.
C52	.32	4°*	64,490	68,980
		5°	205	3,202
		2'	8,444	8,807
		2"	5,872	
		1°, 2°, 3°: gone		
		4°, 2', 5°, of other side		0
C47	.44	3°*	95,470	107,700
		4°, 2°, 2'	0	
		3°, 4°, of other side	0	
C45	.46	2'*	45,360	55,490
		2", 4°, 5°	0	
		1°, 2°, 3°: gone		
C42		4°*	44,320	49,600
		3°, 5°	0	
C51	.51	1'*	225,900	320,700
		2", 3', 4°, 5°	0	
		1°, 2°, 2', 3°: gone		
C40	.55	4°*	0	
		3°, 2', 2", 5°	0	

Table 10, cont.

Plant	d	frond	activity in apical scimitar	max. activity
C48	.60	5^{o}*	26,300	47,790
		4^{o}, 2", 2^{x}, 6^{o}	0	
		1^{o}, 2^{o}, 2', 3^{o}: gone		
C41	.61	3^{o}*	61,280	
		2', 5^{o}, 4^{o}	0	
C44	.66	2^{o}*	108,600	132,900
		1^{o}	0	
		3^{o}: abortive	0	
		3^{o} (of other side)	0	
C49	.74	2"*	11,210	14,970
		5^{o}, 6^{o}, 3'	0	
		1^{o}, 2^{o}, 2', 3^{o}, 4^{o}: gone		
C50	.90	2'*	59,280	67,530
		2", 3', 4^{o}, 5^{o}	0	
		1^{o}, 2^{o}, 3^{o}: gone		
C53	1.03	2'*	24,460	
		2", 5^{o}	0	
		1^{o}, 2^{o}, 3^{o}, 4^{o}: gone		
C46	1.32	3'*	581	1,109
		3", 5^{o}, 2"', 2^{x}	0	
		1^{o}, 2', 2", 2^{o}, 4^{o}, 3^{o}: gone		

Table 10, cont.

Plant	d	frond	activity in apical scimitar	max. activity
C43	1.37	2^{o}*	31,480	32,250
		2'	180	890
		4^{o}	650	969
		3^{o}	0	

Table 11. Results of translocation experiments on Macrocystis at Santa Barbara, November 4-7, 1974.

Plant	d (m)	frond	length (m)	activity in apiscim	max. activ.
C66	.43	x^{o}*		0	0
C55	.44	x^{o}*		2,700	5,965
		x-2', $x-1^{o}$		0	0
C59	.75	x^{o}*		1,736	3,235
		$x-1^{o}$		n.a.	863(Note 1
C60	.75	$x+1^{o}$*		1,152	1,888
		$x+3^{o}$, $x-1^{o}$, x+2'		0	0
C67	1.22	x^{o}*		0	0
		x'		0	0
C56	1.52	2"*		16,230	19,910
		2', 3', 5^{o}		0	0
C72	1.68	x^{o}*		n.a.	1,750(Note 1)
		$x+1^{o}$		1,377	1,682
C73	1.80	x^{o}*		15,050	15,690
		$x+1^{o}$		0	0
C57	1.94	3^{o}*		9,946	12,150
		4^{o}, 2'		0	0
C61	2.35	4^{o}		22,450	25,360
		5^{o}, 2"		0	0

Table 11, cont.

Plant	d (m)	frond	length (m)	activity in apiscim	max. activ.
C63	2.72	x^{o}*		929	2,895
		$x+1^{o}$		0	0
C65	3.00	x'*		1,490	1,590
		$x+2^{o}$, $x+3^{o}$		0	0
C71	3.93	2^{o}*		0	0
		3^{o}		0	948
		4^{o}		330	-
		other 3^{o}, 4^{o}		0	0
C70	4.44	4^{o}*		3,862	3,862
		5^{o}, 3', 2"		0	0
C64	6.26	x'*		0	0
		x", x^{x}		0	0
C68	6.54	x^{o}*		0	0
		$x+1^{o}$		0	0
C62	6.64	x^{o}*		0	1,505 (Note 1)
		$x+1^{o}$		131	321
		$x+2^{o}$		452	-
C54	7.90	x^{o}*		0	2,929 (Note 1)
		x^{x}		2,000	3,264
		x'		1,564	1,897
		x"		1,728	3,146

Notes. 1. Activity in base of frond only.