THE MARINE ALGAL FLORA OF THE AZORES AND ITS BIOGEOGRAPHICAL AFFINITIES

By IAN TITTLEY [1] & ANA I. NETO [2]

With 9 figures and 3 tables

ABSTRACT. Studies on the marine algae of the Azores go back just over half a century. Although in comparison to mainland European Atlantic coasts the Azores flora is less well-known, its isolated geographical position has encouraged a recent resurgence of algal interest resulting in many new algal records. Currently 274 species are listed, comprising 45 Chlorophyta, 52 Phaeophyta and 177 Rhodophyta. Ten species appear to be endemic (5 Chlorophyta, 5 Rhodophyta) but most are of taxonomically difficult groups (*Cladophora, Corallinaceae, Polysiphonia*) and their status is questionable. Several hypotheses have been proposed as to the floristic relationships of the Azores marine flora; some point to affinities with West Africa and Macaronesia, others to the Mediterranean or America. The situation is complex with different algal classes showing different affinities. A mix of southern and northern elements is present in the flora together with those that show transatlantic (Mediterranean-Caribbean) links. A few species are known only through drift specimens. Results of new analyses using numerical methods and a more complete data set generally support these conclusions. Ordination of individual island floras suggests some separation of algal floras according to geographic grouping.

INTRODUCTION

The study of the marine algal flora of the Azores goes back over 150 years. Neto (1992) reviewed the relatively small number of studies undertaken and noted the change in direction of research from initially taxonomic to ecological studies, with recently an emphasis on understanding zonation and community structure and the factors governing these. Although in comparison to European Atlantic coasts the Azores marine flora is less well-known, its isolated geographical position has encouraged a recent increase of algal interest and has resulted in many new species records. The more important of these recent field studies include

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* Contribution No. 19 of the "Expedition Azores 1989".

Bol. Mus. Mun. Funchal, Sup. no. 4: 747-766, 1995 ISSN 0870-3876

those of NETO (1989, 1992), NETO & AZEVEDO (1990), NETO & BALDWIN (1990) and the sublittoral survey by FREDERICQ *et al.* (1992); the "Expedição Açores 1989" (MARTINS *et al.*, 1992; NETO & TITTLEY, 1996 in press; TITTLEY & NETO, 1994) undertook intensive littoral and sublittoral studies on the island of Faial. The main aim of the present paper is to report new data and to re-evaluate the biogeographical affinities of the Azores marine algal flora using these data.

BIOGEOGRAPHICAL AFFINITIES: PREVIOUS STUDIES

The floristic affinities of the Azores marine flora have long been the subject of debate. SCHMIDT (1931) compared the Azores flora with locations in Africa and Europe (Table 1) and noted that very similar numbers of species were shared with France, Spain, Portugal, the Western Mediterranean and Northwest Africa although component species differed in each case. A slightly smaller number of species was shared with Britain and the Canary Islands. More recently PRUD'HOMME VAN REINE & VAN DEN HOEK (1988, 1990) in a comprehensive review of the Cape Verde and Macaronesian algal floras noted that the Azores shared 151 species in common with Macaronesia and 59 species in common with tropical America. They also analysed Atlantic algal data using a clustering method and showed (Fig. 1) the Azores flora to be associated with a northern group of floras (Morocco to Britain) and separate from the tropical west African and Cape Verde Islands floras. SOUTH & TITTLEY (1986) listed 1116 species of Chlorophyta, Phaeophyta and Rhodophyta from 33 areas (Fig. 2) in the North Atlantic Ocean (north of latitude 39°) 190 species were listed for the Azores.

Subsequently TITTLEY *et al.* (1990) used these data to test the concept of biogeographical provinces in the North Atlantic. Ecocladistic analysis for the Phaeophyta associated the Azores flora with the Iberian flora and the American flora (TITTLEY *et al.*, 1990, Figs 3a-c); ordination placed the Azores brown algal flora at the end of a linear arrangement of European algal floras which met a similar arrangement of American floras through a cluster of Arctic sites (TITTLEY *et al.*, 1990, Fig. 6a). Ordination of the Chlorophyta in contrast separated the Azores from a main cluster (TITTLEY *et al.*, 1990, Fig. 6b). Ecocladistic analysis placed the Azores Chlorophyta (TITTLEY *et al.* 1990, Figs 3d-f) near the base of the ecocladogram, between the Arctic Jan Mayen-Spitzbergen floras and a group of American floras. Ecocladistic analysis of Rhodophyta data suggested a closer relationship of the Azores flora to those of Virginia (TITTLEY *et al.*, 1990, Figs. 4a-e); the Azores-America link was repeated in both random and systematic subsets of the data (TITTLEY *et al*, 1990, Figs 4a-b, 5a-b). Ordination of these data in one case placed the Azores flora at the end of linear arrangement of European sites but in the second subset of the data was widely separated from the European arrangement, and situated midway between European and American groupings (TITTLEY *et al.*, 1990, Figs 6c-d).

METHODS

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METHODS

New taxonomic, nomenclatural and distributional information was added to the database of SOUTH & TITTLEY (1986). Complete checklists for the Azores including new records are given in NETO (1994) and TITTLEY & NETO (1994). The corrected databases of North Atlantic benthic marine algae and their distributions were re-analysed using the same methods as used by TITTLEY *et al.*, 1990 to ascertain whether or not the floristic affinities of the Azores flora identified previously still stand. Three numerical methods were used, (i) an ecocladistic Wagner-tree method (PAUP programme, SWAFFORD 1985) which expresses floristic relationships in the form of an ecocladogram branches of which represent individual floras or groups of floras; (ii) an ordination method (DECORANA, Detrended Correspondence Analysis, part of the Vespan suite, MALLOCH, 1993) which produces an ordination plot which is a scattergram of sites whose positions relative to one another indicate floristic similarity or dissimilarity; (iii) a classificatory method based on ordination (TWINSPAN, Two Way Indicator Species Analysis, part of the Vespan suite, MALLOCH, 1993) the output of which is a dendrogram, branches of which and relative cut-off levels represent floristic relationships. These methods are fully reviewed in TITTLEY *et al.* (1990). A second analysis was performed on the database of seaweed floras of the individual islands of the Azores archipelago to identify inter-island floristic relationships.

RESULTS

Overall Atlantic flora

New data has increased the 1116 species listed by SOUTH & TITTLEY (1986) for the North Atlantic to 1155. Similarly, the 190 and 256 species listed for the Azores by SOUTH & TITTLEY (1986) and NETO (1994) respectivley has now increased to 274. This represents 24% of the North Atlantic flora. The Azores flora is generally less species rich than those of Iberia, France and England (a 'hot-spot' of algal biodiversity in the North Atlantic) but richer than the species impoverished cold-water floras in the northern North Atlantic (totals for selected floras are given in Table 2). The Azores flora is less species-rich than other parts of Macaronesia, the Canary Islands support over 600 species. The Azores shares species in common with all the 33 floras listed in SOUTH & TITTLEY (1986); greater numbers were shared with Iberia, France and England (Table 3) than with the species poor floras of the North Atlantic and of America.

New algal records for the Azores

Examples of new algal records for the Azores include *Rhodymenia holmesii* (nomenclature follows SOUTH & TITTLEY, 1986, and NETO (1994) a diminutive red alga inhabiting shaded crevices and niches, widespread in the northern North Atlantic Ocean but

hitherto absent from Portugal thus making the Azores its southern limit of distribution. The discovery of three new species records of *Polysiphonia* (*P. atlantica, P.opaca and P. urceolata*) for the Azores must be treated with caution because of taxonmomic difficulties in the genus; several *Polysiphonia* spp. could not be identified for certain (TITTLEY & NETO, 1994). Of the ten new records listed by FREDERICQ *et al.* (1992), most were warmer water species attaining their northern limits on the Azores; examples included *Corynomorpha prismatica* previously known from the Mediterranean, Canary Islands and Madeira; exceptions were *Scinaia turgida*, which occurs in the northern Atlantic and Mediterranean and *Schimmelmannia ornata* which was only previously known in France in the North Atlantic. FRALICK & HEHRE (1990) listed the Azores green algae and incorporated four new species records (*Ernodesmis verticillata, Halimeda tuna, Microdictyon colacodictyon*, and *Rhizoclonium hookeri*) all of which are warm water species not previously recorded in the North Atlantic.

ATHANASIADIS & TITTLEY (1994) also report new records for the Azores detected during the "Expedição Açores 1989" all of which were deemed to be introductions to the archipelago. These were red algae, all members of the Antithamniae, diminutive forms occurring among the algal turf. *Scageliopsis patens* was only previously known from Western Australia; *Antithamnion diminuatum*, originally from South Australia was detected in South Africa prior to its discovery on Faial. *Antithamnion pectinatum* also originally described from the southern hemisphere (New Zealand) and widespread in the warm temperate Pacific Ocean, has been found on Faial following its earlier discovery on the north American coast in 1985 and Mediterranean France in 1989. Other notable aliens in the Azores marine flora include the small red alga *Symphyocladia marchantioides* discovered by ARDRÉ *et al.* (1974) in the early 1970s, and the tetrasporophyte stage of *Bonnemaisonia hamifera* found during the "Expedição Acores 1989" (an alien long established in the Atlantic Ocean which originates from Japan). The small brown alga *Endarachne binghamiae* which closely resembles *Petalonia fascia* (widespread in the North Atlantic), has also now been confirmed for the Azores. This genus and species was first described from the coast of California has been recently discovered in Brazil and on the mid Atlantic island of St. Helena, and the Azores represents its northern limit in the Atlantic.

Some species records have been discounted; these include *Ascophyllum nodosum* which occurs commonly only as drift material, and *Fucus distichus* and *F. vesiculosus* which do not grow on the islands.

Numerical analysis

Ecocladistic analysis of the revised database for subset 1 of the Rhodophyta produced a large number of equally parsimonious cladograms one of which is illustrated here (Fig. 3); the branch representing the Azores flora was positioned at the base of the ecocladogram with the Virginia, Delaware and Maryland floras as nearest neighbours. Subsequent higher

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branches represented mainly arctic floras, followed by branch and branchlets representing American floras. A combe-like series of ultimate branches represented European floras in geographical order, from northern Norway (lower down) to northern and southern Spain (apically). This result is very similar to the previous analysis of TITTLEY *et al.* (1990).

Ordination analysis also produced very similar results to the previous analyses; in data subset 1 south to north linear arrangements of separated American and European floras merged in a cluster representing Arctic floras (Fig. 4). The Azores flora was positioned at the end of the European chain of sites. In the second data subset the linear arrangements of American and European floras was truncated (Fig. 5) and as in the previous analysis the Azores flora was positioned in the plot away from both American and European groupings. Two way indicator species analysis of data subset 1 classified Atlantic floras into two main groupings (Fig. 6), (i) those from the Azores to Shetland, (ii) the remainder (northern European, Arctic and American floras). A second dichotomy in the dendrogram linked the Azores and Southern Spain/Portugal floras but separated these from the Northern Spain to Shetland floras.

. Ecocladistic analysis of the revised Phaeophyta data produced eight ecocladograms one of which is illustrated (Fig. 7); the Azores branch was one of a small apical group comprising also Northern Spain and Southern Spain/Portugal and sister to a branch and branchlets representing Virginia, New Jersey, Connecticut, Rhode Island and Maine. There followed a combe series of species-poor Delaware, Maryland and Arctic floras. A major branch representing European floras occurred near the base of the ecocladogram; two branches representing American floras were positioned at the base. This result is very similar to that of the previous analysis.

Ordination anlysis of Chlorophyta data (Fig. 8) gave a plot with a single cluster of points with two outliers (Spitzbergen, Azores). The ordination of sites was more spread out than in the previous analysis of Chlorophyta, and closer inspection revealed a spread of European sites along axis 1, from the Azores on the right side of the plot to Northern Norway on the left. This pattern resembled those in the plots of Rhodophyta and Phaeophyta in TITTLEY *et al.* (1990). The corresponding species ordination (not illustrated) shows 14 species (including *Chaetomorpha pachynema, Cladophora coelothrix* and *Valonia utricularis* and the new records of FRALICK & HEHRE (1990)) to be responsible for separating the Azores from the main cluster of sites.

Analysis of the individual island floras of the Azores archipelago by Decorana ordination (Fig. 9) revealed a single cluster of sites with a maximum separation of two standard deviations along both axes 1 and 2. The central islands group of floras were spread apart from the eastern islands group along the first axis; western islands group were spread along the second axis. Although the result suggests significant differences at the extremes of the ordination, individual islands within the cluster are spread less than one deviation apart suggesting no strong differences between adjacently ordinated island floras but a gradual

change between the extremes. Twinspan (not illustrated here) separated the central islands floras of Faial, Pico and Terceira from the remainder.

DISCUSSION & CONCLUSIONS

The many new species records detected recently for the Azores have increased its total flora to 274; this number will be further increased when undetermined material held by the authors is resolved especially that of taxomically difficult groups such as the crustose corallinaceae and *Polysiphonia*. Further careful investigation of subtidal habitats will probably also add to the total. The isolated mid-Atlantic position of the archipelago and its recent geological age suggests that the flora should be relatively poor; however, recent investigations have revealed a moderately rich flora. The Azores support a species richer flora than do the isolated north Atlantic islands of Iceland, Jan Mayen and Spitzbergen, and the less isolated Faroes group. Species paucity on these northern islands relates to their arctic-subarctic positions where also continental algal diversity is low. Mid Atlantic islands to the south of the Azores such as Ascension, St. Helena, Tristan da Cunha and South Georgia support only relatively species poor floras with respectively 120, 61, 115 and 101 species recorded (PRICE & JOHN, 1978; LAWSON *et al.*, 1993; BAARDSETH, 1941; JOHN *et al.*, 1994). Low species numbers on isolated islands also reflect incomplete study due to difficulty of access and the restricted habitat range available as most of the examples cited are single islands. The Azores in contrast comprises many islands with a wider range of habitats available for algal colonisation. The well-worked Macaronesian Canary Islands which lie in close proximity to the African continent, and in warmer waters to the south of the Azores, are species-rich with over 600 recorded (Haroun pers. comm.).

The Azores probabbly support no endemic species; those suggested as being endemic are mostly members of taxonomically difficult groups and require reassessment. The Chlorophyte *Codium elisabethae* (distinguishable from *C. bursa* only on microscopic characters) and until recently thought to be endemic has been discovered on Porto Santo, Madeira (AUDIFFRED & PRUD'HOMME VAN REINE, 1985). There are 42 species whose distributions in the North Atlantic Ocean as defined by SOUTH & TITTLEY (1986) are restricted to the Azores but which occur outside the region. These include the green algae *Ernodesmis verticillata*, *Halimeda tuna*, *Microdictyon calodictyon*, the brown algae *Cystoseira abies-marina*, *Dilophus menstrualis*, *Lobophora variegata*, and the red algae *Balliella cladoderma*, *Erythrocystis montagnei*, *Griffithsia phyllamphora*, *Halichrysis depressa* and *Wrangelia argus*.

The recent discovery of introduced species may reflect the Azores important position in transatlantic communications; while the evidence for introductions is strong some species may have been always present but overlooked or confused with others.

Reanalysis of the North Atlantic database reveals the robustness of the previous

results. Despite the addition of over 80 new species records for the Azores and additions to and deletions from floras elsewhere in the North Atlantic, the same overall floristic relationships emerged. Ecocladistic analysis pointed to strong links with the Iberian flora but also to affinities with the temperate American flora. The latter is a little surprising in view of the small number of shared species. Ordinations now present a more consistent picture of distributional relationships for all three algal classes with the Azores positioned terminally in a chain of European floras with one exception (Rhodophyta data subset 2) where the ordination suggested a stronger link to the American flora.

The classificatory approach using Twinspan underlined the strong link with Iberia and floras only as far north as Shetland. Other studies have also examined the relationships between the Azores marine algal flora and those of Macaronesia and the Mediterranean (PRUD'HOMME VAN REINE & VAN DEN HOEK, 1988, 1990) and there are affinities with those regions as well as tropical America. The Azores algal flora show affinties with floras to the north, south, east and west, with 151 species shared with both southern Spain/Portugal and the Canary Islands. Future work should examine the Azores flora in a wider context. Incorporation of additional data for northern west African, Macaronesia and the south eastern United States into the North Atlantic database and its reanalysis may help clarify floristic relationships.

Within the 500km spread of the Archipelago no strong floristic and biogeographical differences emerged between individual islands or island groups; the western islands Corvo and Flores were placed at the opposite end of the ordination from the eastern islands of Santa Maria and São Miguel.

Parts of the Azores archipelago still remain phycologically uninvestigated and future work should therefore focus on lesser known areas, especially subtidal habitats where with a single exception (NETO & TITTLEY, 1995) most investigations have been only superficial. Future studies will also focus on investigating the unexamined but important Azores algal collections held at institutions outside the Azores and Portugal.

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TABLE 1 - Azores species shared with other areas (from SCHMIDT., 1931).

	Britain	France	Spain	Port.	Medit.	NWAfr.	Canary I.
Rhodophyta	47	52	57	59	60	61	43
Phaeophyta	22	25	22	22	20	23	22
Chlorophyta	17	19	17	18	22	17	17
Total	86	96	96	99	102	101	82

TABLE 2 - Species totals fo

Azores
Southern Spain-P
Northen Spain
France
Low countries
West Baltic
Southern Norway
Northern Norway
Ireland
England & Wales
Scotland
Shetland
Newfoundland
Maritime Provinc
Maine

TABLE 3 - Azores species s

1	Ss	Soutl
2	Ns	Nort
3	Fr	Franc
4	Lc	Low
5	Wb	West
6	Eb	East
7	Sn	Soutl
8	Nn	Nort
9	Ir	Irela
10	EW	Engl
11	Sc	Scot
12	Sh	Shetl
13	Fa	Faro
14	Jm	Jan M
15	Sp	Spitz
16	Ic	Icela
17	Eg	Easte
18	Wg	West
19	Ac	Arcti
20	La	Labr
21	Nf	New
22	Qu	Queb
23	Mp	Mari
24	Ma	Main
25	Nh	New
26	Ms	Mass
27	Ri	Rhoc
28	Co	Conn
29	Nj	New
30	De	Dela
31	My	Mary
32	Vi	Virgi

TABLE 2 - Species totals for selected North Atlantic areas

	Rhodophyta	Phaeophyta	Chlorophyta	Total
Azores	177	52	45	274
Southern Spain-Portugal	250	102	71	423
Northen Spain	252	112	83	447
France	365	198	140	703
Low countries	164	129	96	389
West Baltic	153	134	93	380
Southern Norway	185	140	80	405
Northern Norway	95	97	54	246
Ireland	269	145	83	497
England & Wales	304	182	94	580
Scotland	205	141	72	418
Shetland	131	99	52	282
Newfoundland	82	87	61	230
Maritime Provinces	118	102	73	293
Maine	79	61	51	191

TABLE 3 - Azores species shared with other floras in the North Atlantic

			Rhodophyta	Phaeophyta	Chlorophyta
1	Ss	Southern Spain-Portugal	90	38	23
2	Ns	Northern Spain	76	34	20
3	Fr	France	88	40	23
4	Lc	Low Countries 30	30	24	13
5	Wb	West Baltic	28	12	13
6	Eb	East Baltic			
7	Sn	Southern Norway	37	18	12
8	Nn	Northern Norway	14	13	5
9	Ir	Ireland	68	32	20
10	EW	England & Wales	73	35	20
11	Sc	Scotland	56	28	15
12	Sh	Shetland	35	18	13
13	Fa	Faroes	26	15	9
14	Jm	Jan Mayen & Bear I.	1	2	2
15	Sp	Spitzbergen	7	2	4
16	Ic	Iceland	21	11	8
17	Eg	Eastern Greenland	4	5	5
18	Wg	Western Greenland	10	6	8
19	Ac	Arctic Canada	14	8	9
20	La	Labrador	10	7	11
21	Nf	Newfoundland	17	12	9
22	Qu	Quebec	15	15	10
23	Mp	Maritime Provinces	26	18	11
24	Ma	Maine	18	10	8
25	Nh	New Hampshire	22	12	10
26	Ms	Massachusetts	31	11	10
27	Ri	Rhode Island	27	9	4
28	Co	Connecticut & Long I. 26	26	13	9
29	Nj	New Jersey	19	8	8
30	De	Delaware	10	7	8
31	My	Maryland	5	5	8
32	Vi	Virginia	15	10	9

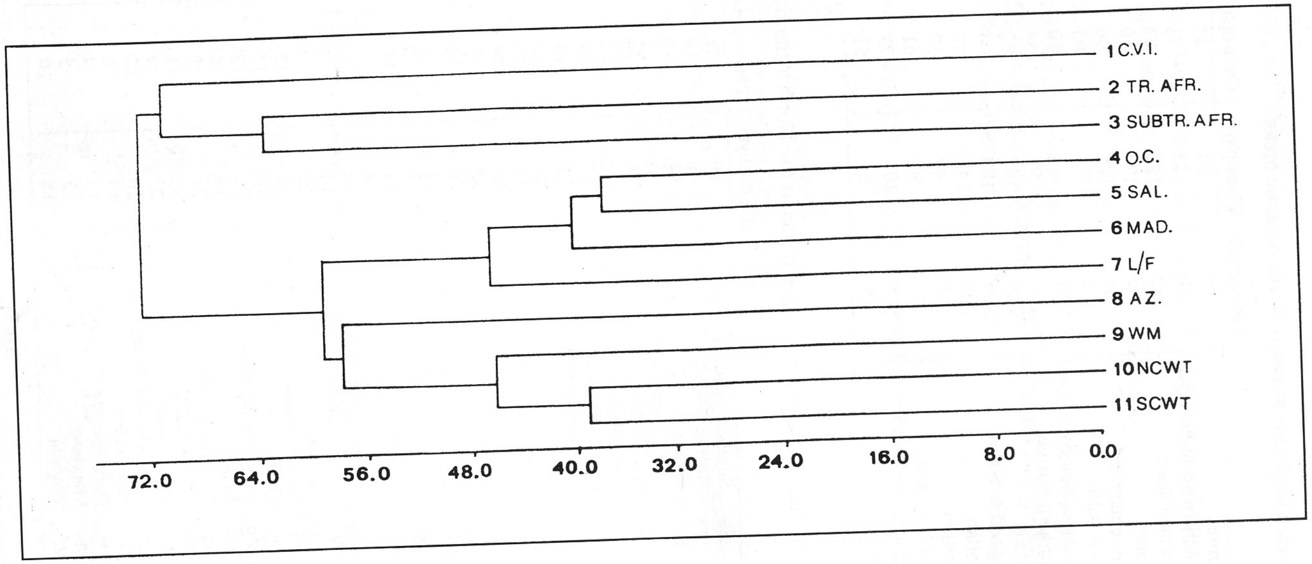

Figure 1 - Dendrogram of floristic relationships from PRUD'HOMME VAN REINE & VAN DEN HOEK (1988) (CVI = Cape Verde Is.; TR. AFR. = Tropical Africa; SUBTR AFR = Subtropical Africa; O.C. = Canary Is. except L/F; SAL. Salvage Is.; MAD. = Madeira; L/F = Lanzarote & Fuerteventura; AZ. = Azores; WM = Western Mediterranean; NCWT = Norther cooler warm temperate area; SCWT = Southern cooler warm temperate area).

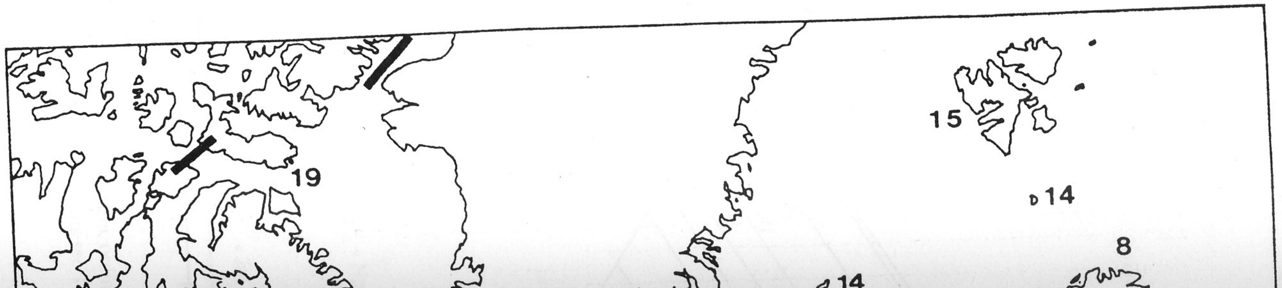

Figure 1 - Dendrogram of floristic relationships from PRUD'HOMME VAN REINE & VAN DEN HOEK (1988) (CVI = Cape Verde Is.; TR. AFR. = Tropical Africa; SUBTR AFR = Subtropical Africa; O.C. = Canary Is. except L/F; SAL. Salvage Is.; MAD. = Madeira; L/F = Lanzarote & Fuerteventura; AZ. = Azores; WM = Western Mediterranean; NCWT = Norther cooler warm temperate area; SCWT = Southern cooler warm temperate area).

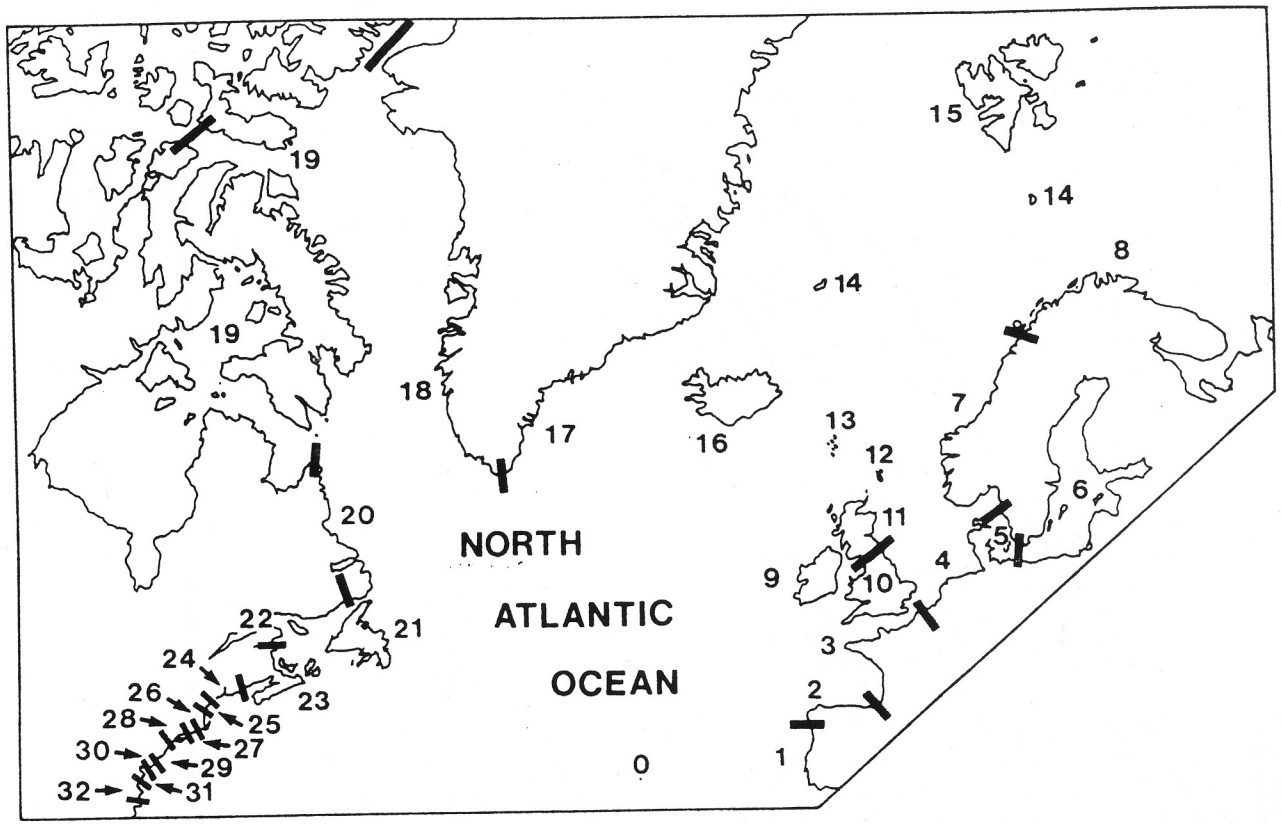

Figure 2 - 33 North Atlantic Floras from SOUTH & TITTLEY (1986).
For key to numbers see Table 3.

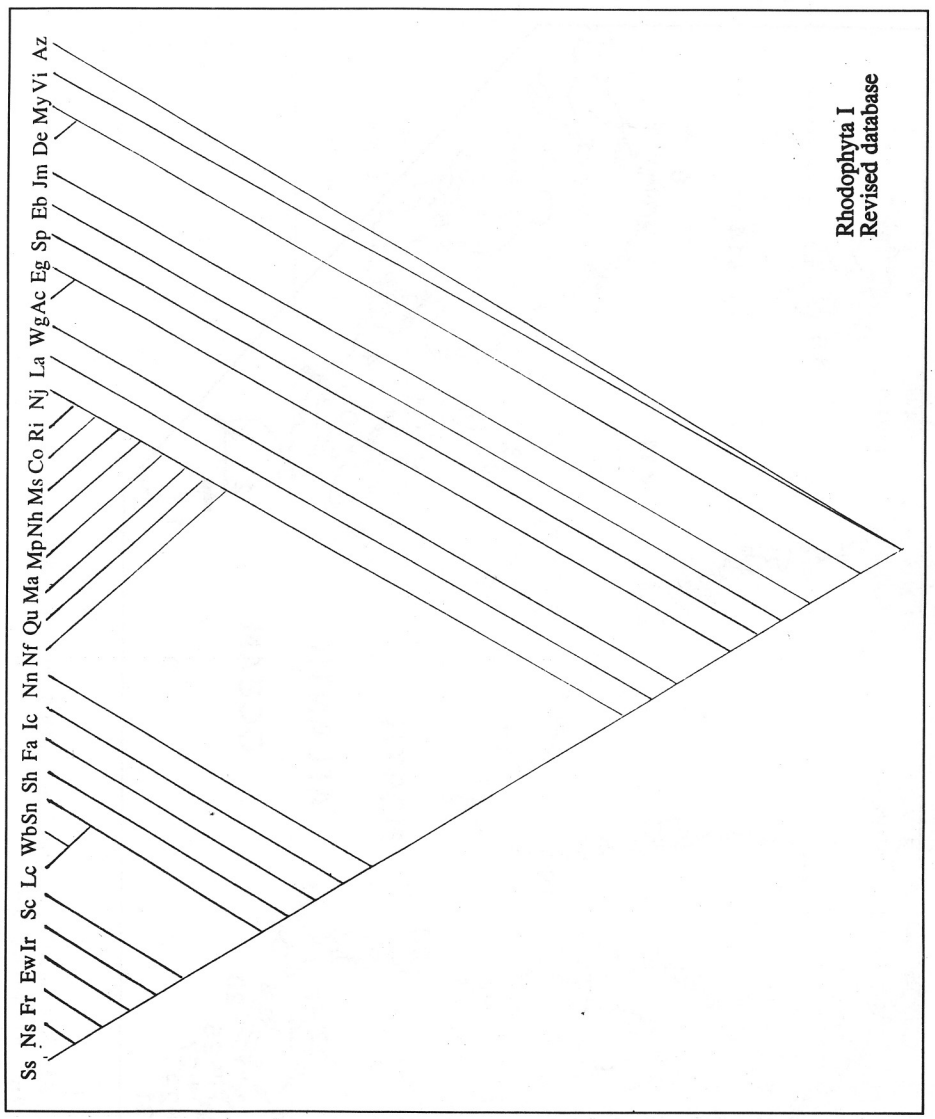

Figure 3 - Area ecocladogram for the North Atlantic: Rhodophyta I revised database.
For key to abbreviations see Table 3.

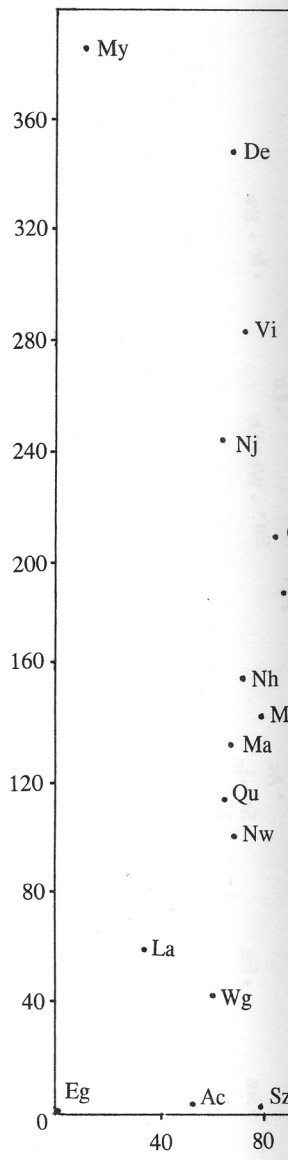

Figure 4 - North Atlant
For key to abbreviation

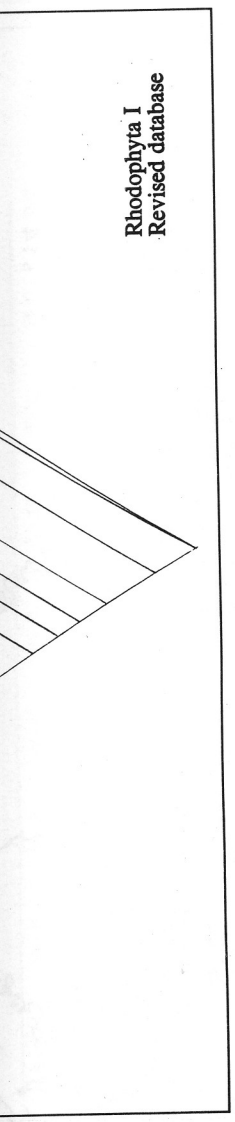

Figure 3 - Area ecocladogram for the North Atlantic: Rhodophyta I revised database.
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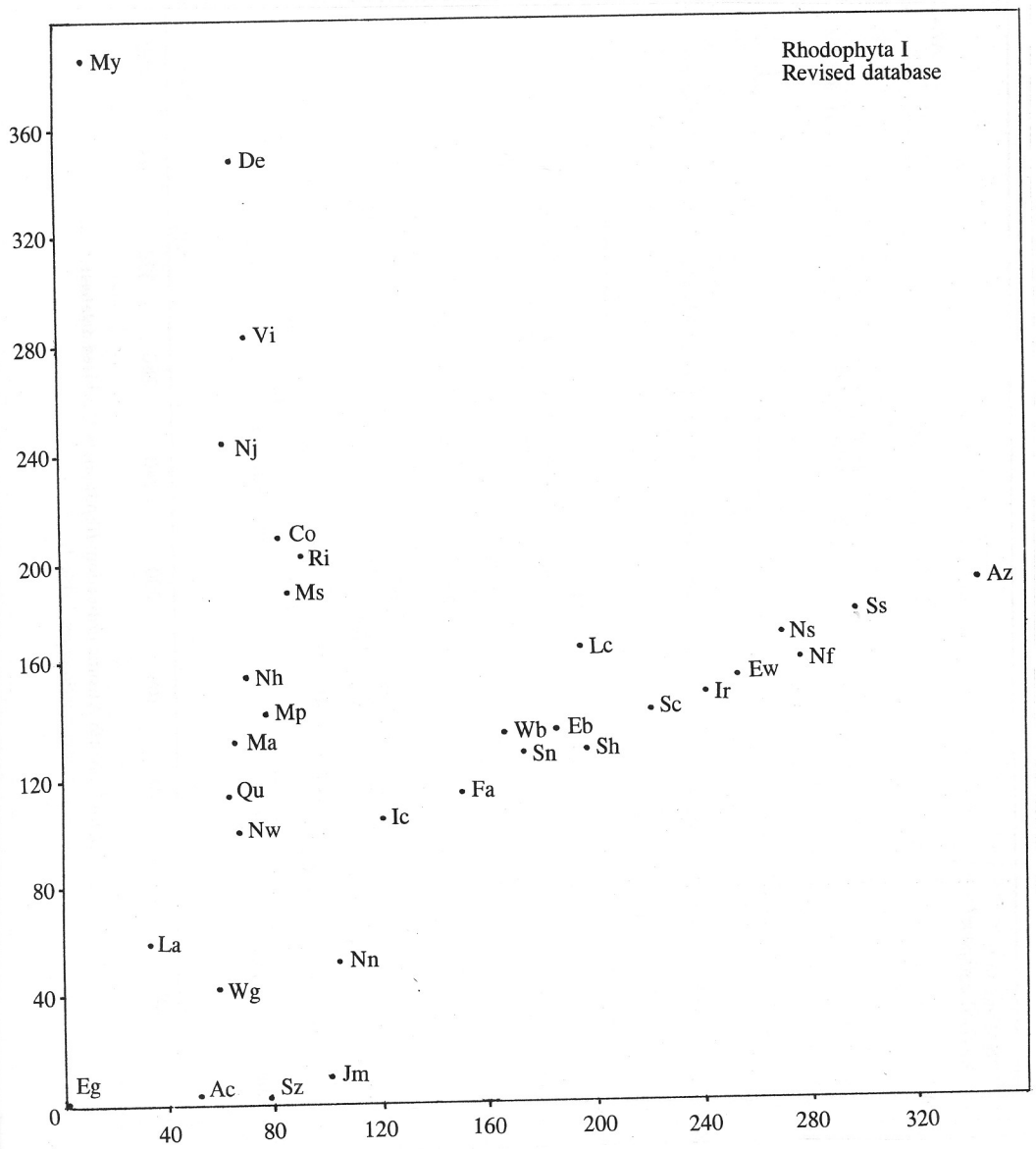


Figure 4 - North Atlantic ordination: Rhodophyta I revised database.
For key to abbreviations see Table 3.

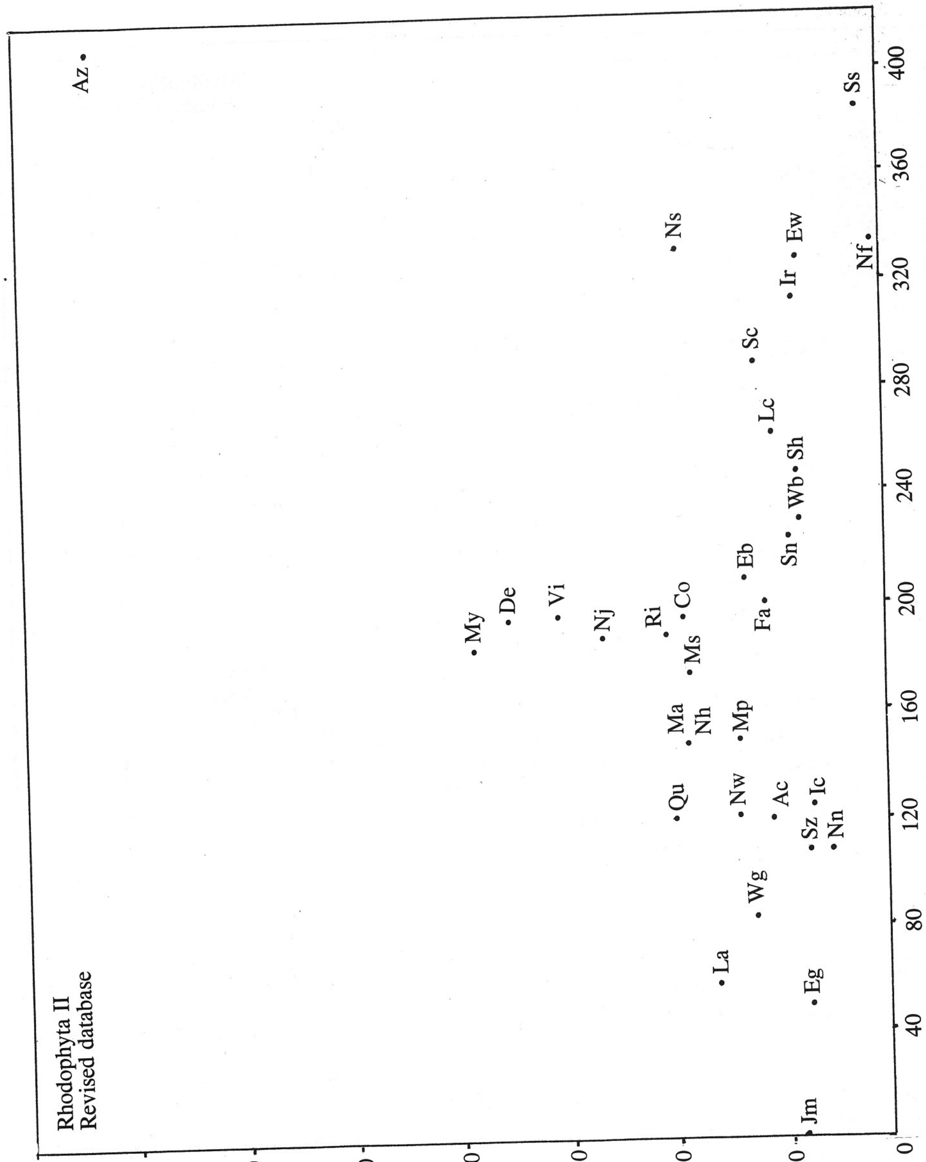


Figure 5 - North Atlantic ordination: Rhodophyta II revised database.
For key to abbreviations see Table 3.

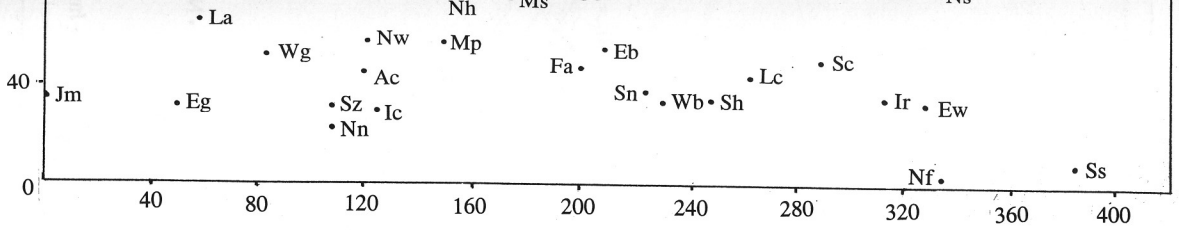


Figure 5 - North Atlantic ordination: Rhodophyta II revised database.
For key to abbreviations see Table 3.

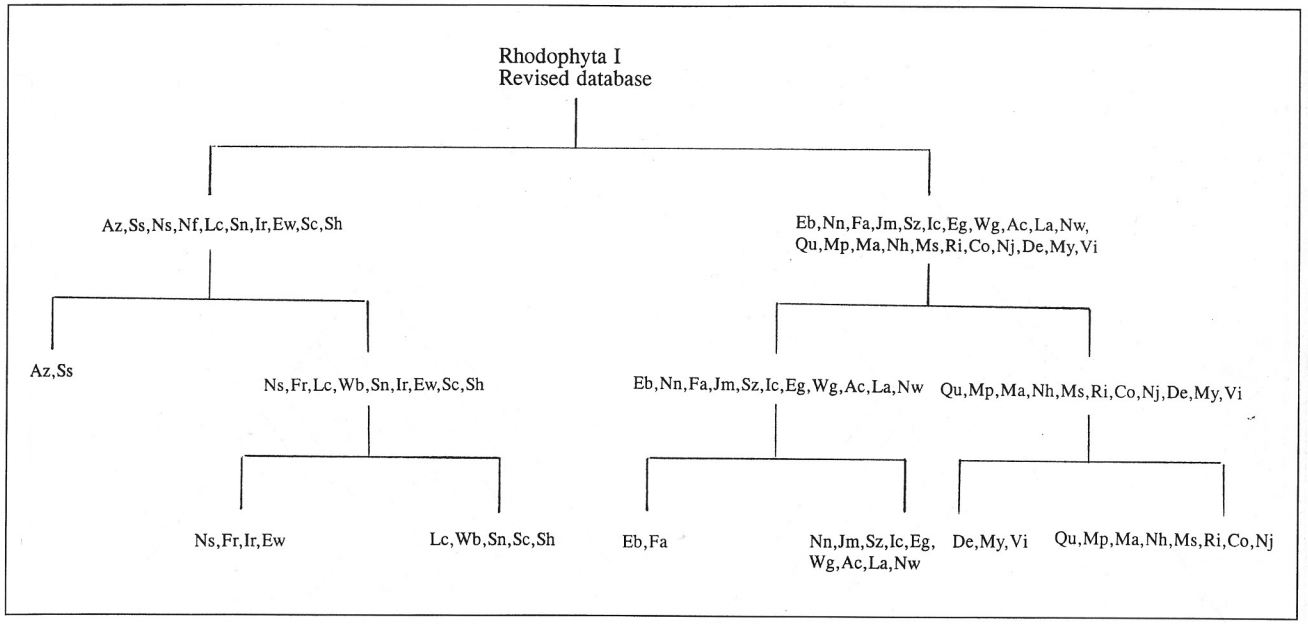


Figure 6 - Twinspan classification of North Atlantic floras: Rhodophyta I revised database.
For key to abbreviations see Table 3.

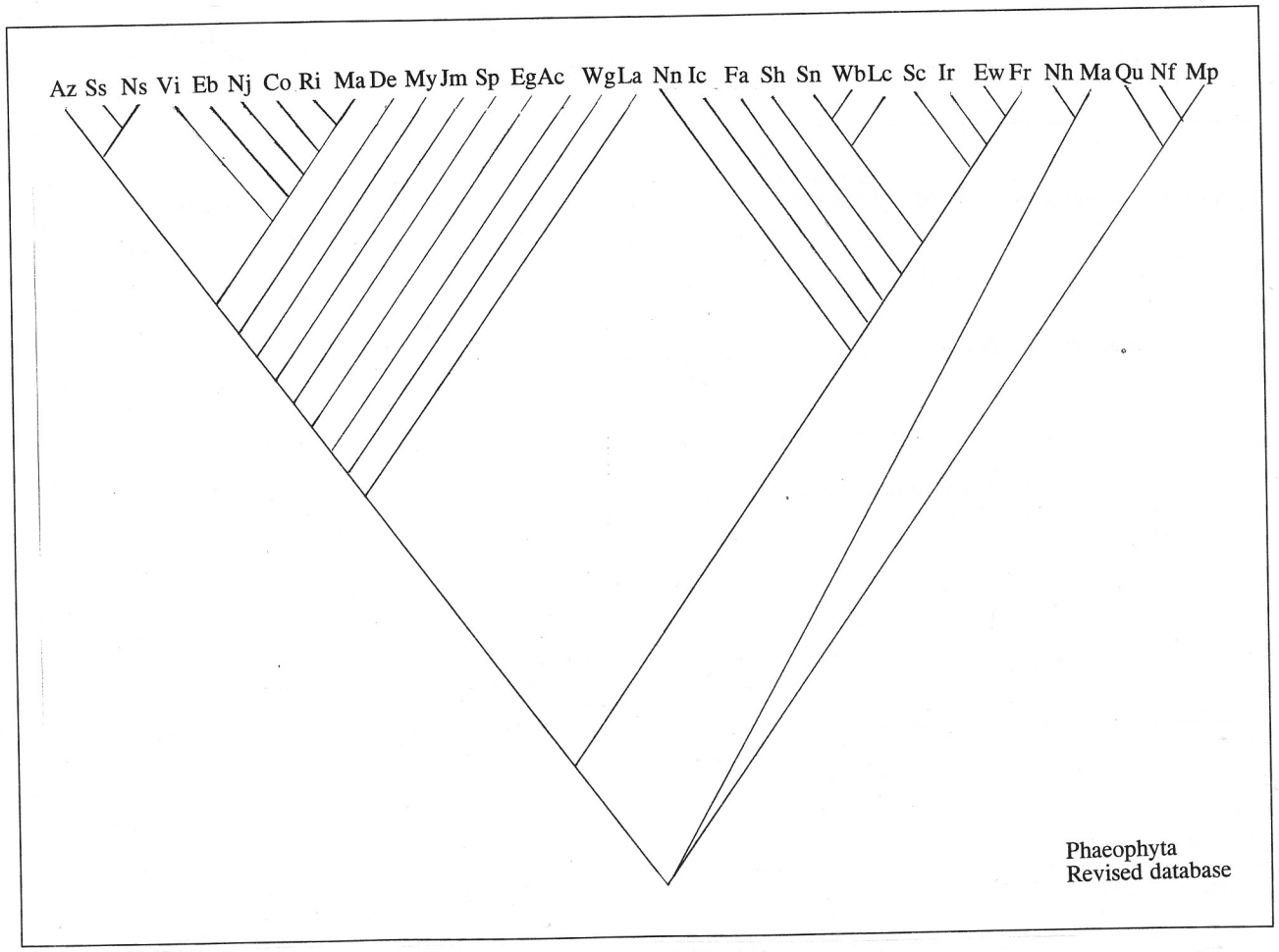
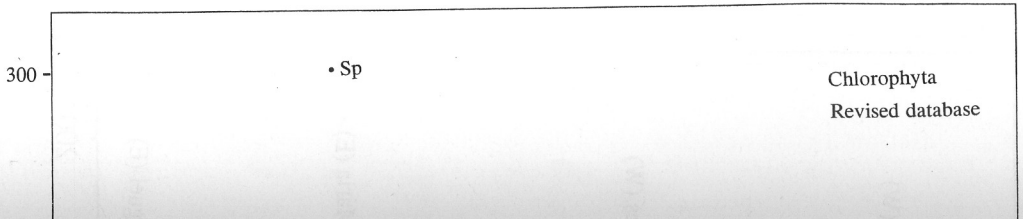


Figure 7 - Area ecocladogram for the North Atlantic: Phaeophyta revised database.
For key to abbreviations see Table 3.



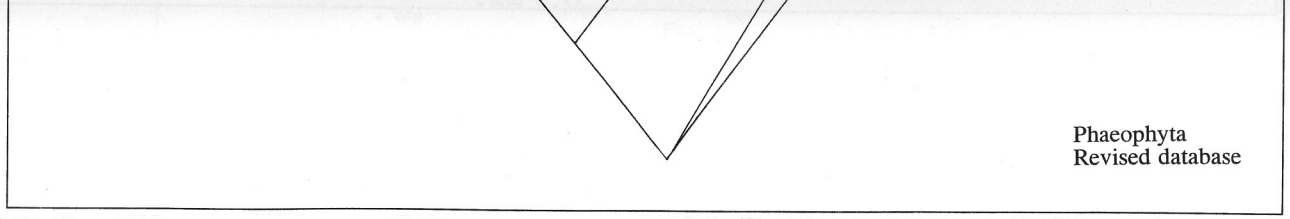


Figure 7 - Area ecocladogram for the North Atlantic: Phaeophyta revised database.
For key to abbreviations see Table 3.

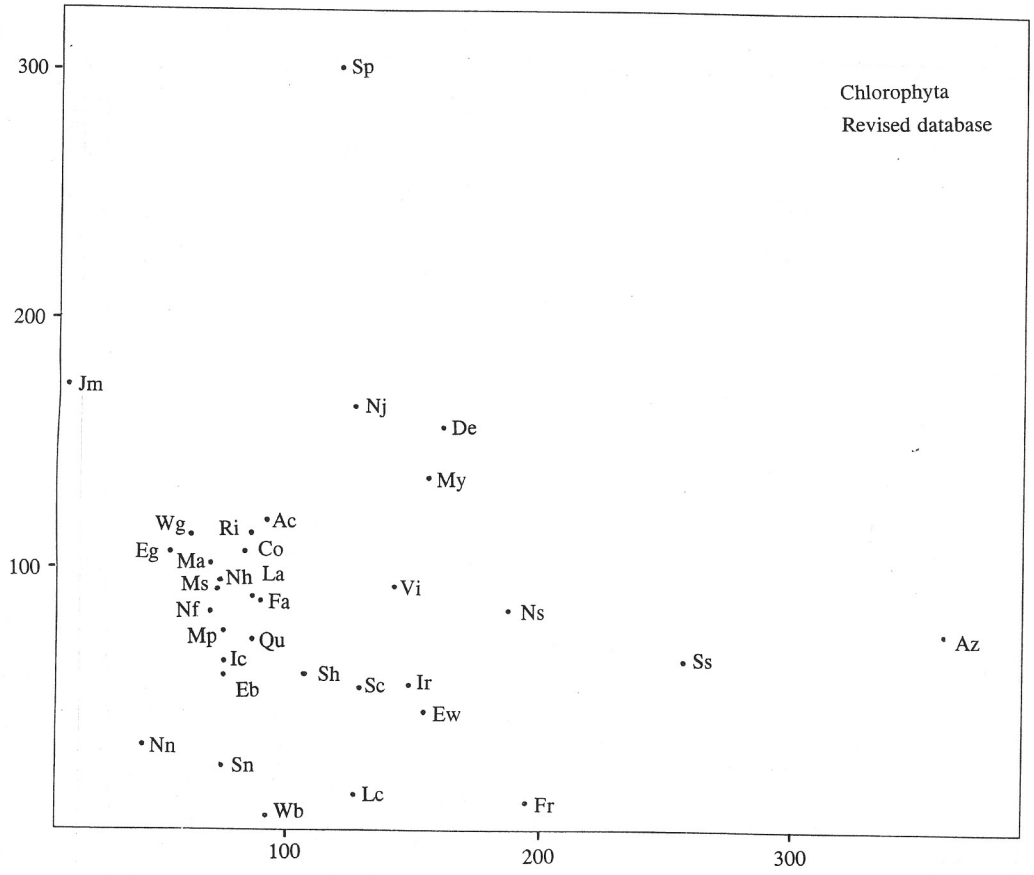


Figure 8 - North Atlantic ordination: Chlorophyta revised database.
For key to abbreviations.

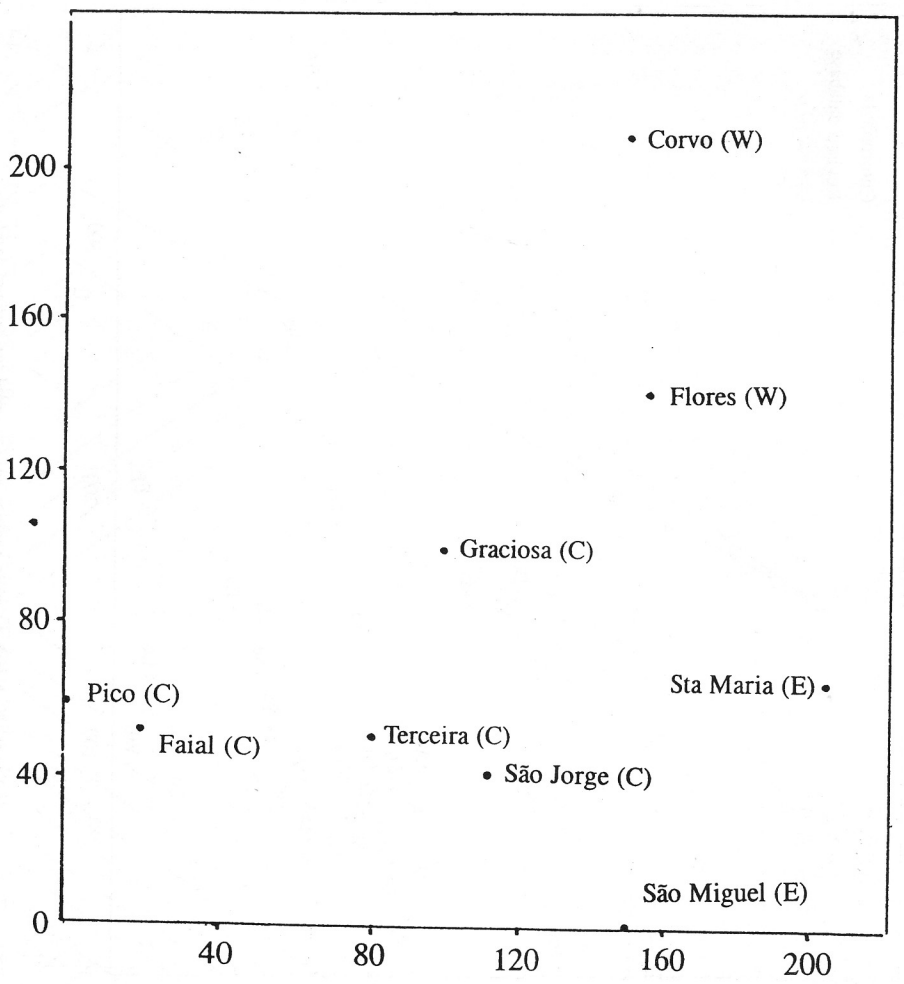


Figure 9 - Azores islands floras ordination.