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Phytogeography of seaweeds of the Azores*

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ABSTRACT: 189 species of seaweeds have been recorded for the Atlantic archipelago of the Azores (114 Rhodophyceae, 41 Phaeophyceae and 34 Chlorophyceae). Ten of these have been described as endemic algae. The taxonomic status of these "endemics" is far from clear, however. Studies on the relatedness of this seaweed flora to seaweed floras of surrounding areas using clustering methods indicate its intermediary position between the seaweed floras of the subtropical Macaronesian Islands (Canaries, Madeira and Salvages) on the one side and those of the warm temperate Eurafrican coasts on the other side. The geographic position of the Azores is NW of the other Macaronesian Archipelagos and thus nearer to the American coast. The Gulf stream may easily transport seaweeds from the Carribean to the Azores. Nevertheless, the number of species of these islands in common with the American Atlantic coast is much lower than with, for example, the W. Mediterranean. Of one group of seaweeds, viz. algae with a strictly warm temperate distribution, not a single species occurs likewise on American coasts. This absence is probably explicable because of the narrow temperature range for survival of these seaweeds. Temperatures of surface waters around the Azores during pleistocene glaciations were not much lower than they are at present. Nevertheless, it can be supposed that a number of seaweeds now occurring in the Azores have become extinct during the last glaciation.

INTRODUCTION

In his paper dealing with the marine flora of Atlantic islands, Feldmann (1946) characterized the seaweed flora of the Azores as boreal, poor in species, and without any of the species that occur on the Atlantic coasts of N. America but that are absent from the E. Atlantic. According to Feldmann (l.c.), the Azores form part of the Lusitano-African region, like the other Macaronesian islands (except the Cape Verde Islands). In recent phytogeographic studies, the position of the Azores is rarely discussed, but they have been incorporated in the list of benthic marine algae of the North Atlantic Ocean (South & Tittley, 1986), and Van den Hoek (1984) included the Azorean archipelago in the Warm temperate NE Atlantic Region.

The purpose of the present study is to explore further the biogeographic position of the Azores using new floristic data in addition to older ones. The new floristic data were collected during the CANAP-V-Expedition (1981) of the Netherlands Council of Sea Research (NRZ).

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MATERIALS AND METHODS

Lists of species of seaweeds recorded from the Azores (Schmidt, 1931; Pryor, 1967; Ardré et al., 1973, 1974, and unpublished records from CANCAP-V) have been compared with lists prepared for a number of selected geographic areas (cf. Fig. 1, Tables 1 and 2, and Prud'homme van Reine & Van den Hoek, 1988).

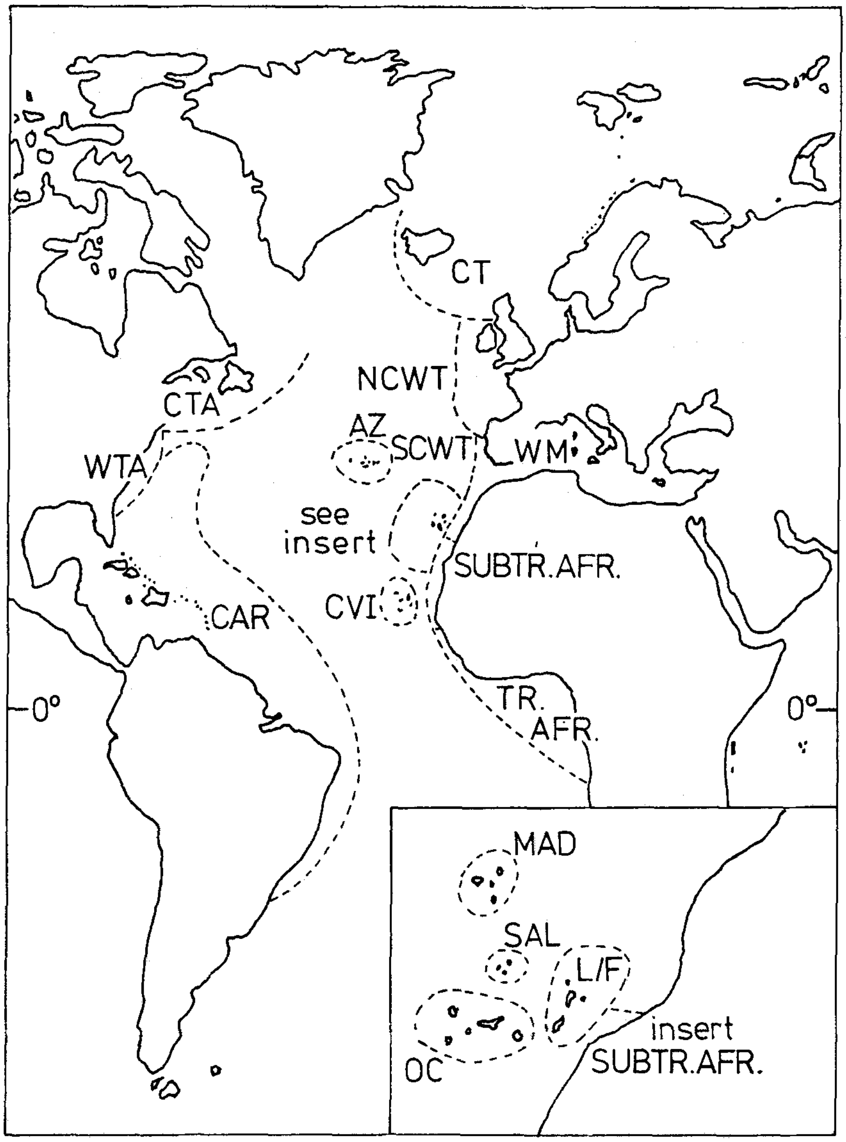


Fig. 1. The areas taken for the comparison of their seaweed flora with that of the Azores. For abbreviations denoting geographic areas see Table 1

The designation "assembled seaweed flora" is used for the total of the floras of red, brown, and green seaweeds altogether. However, in this paper this will generally be shortened as a "given area's (seaweed) flora" (for instance, the Azorean flora). If, however, the designation "seaweed floras of a given area" is used, it refers to the separate floras of red, brown, and green seaweeds.

Table 1. List of abbreviations denoting geographic areas (coasts). For delimination of these areas see Fig. 1 and Prud'homme van Reine & Van den Hoek (1988)

AZ	Azores
CAR	Caribbean
CT	Europe: Scotland, Norway and the countries around North Sea and Baltic
CTA	NE America, north of Cape Cod
CVI	Cape Verde Islands
L/F	Lanzarote, Fuerteventura and surrounding islets
MAD	Madeira Archipelago
Macar.s.s.	Macaronesia sensu stricto (L/F, MAD, OC and SAL)
NCWT	NE Spain, Atlantic France, S, SW and NW England, Wales, Ireland
OC	Canary Islands except L/F
SAL	Salvage Islands
SCWT	Morocco (excl. former Spanish Sahara), Atlantic SW Spain, Portugal
Subtr. Afr.	NW Senegal (North of Gambia), Mauretania, former Spanish Sahara
Tr. Afr.	From Gambia to the Congo River
WM	Western Mediterranean (see text)
WTA	NE America between Cape Canaveral and Cape Cod

In the present study, the very broad warm temperate NE Atlantic Region (Van den Hoek, 1984) has been divided into three subregions in the same way as described by Prud'homme van Reine & Van den Hoek (l.c.; see also my present Table 3). The Azorean seaweed flora can be expected potentially to encompass species of the following climatic distribution groups (or distribution types): tropical-to-southern cooler warm temperate (SCWT), tropical-to-northern cooler warm temperate (NCWT), tropical-to-cold temperate, tropical-to-arctic, subtropical-to-SCWT, subtropical-to-NCWT, subtropical-to-cold temperate (here including tropical-to-arctic), SCWT proper, SCWT-to-NCWT and SCWT-to-cold temperate (here including SCWT-to-arctic) (cf. also Table 4). For discussion about the delimitation of the areas, see Prud'homme van Reine & Van den Hoek (1988); for the concept "climatic distribution group" see Van den Hoek (1979, 1982b, 1982c).

To analyse the data the same methods have been used as described in Prud'homme van Reine & Van den Hoek (1988).

RESULTS

189 of the 1505 species of seaweed included in the data matrix (921 Rhodophytes, 329 Phaeophytes and 255 Chlorophytes) have been recorded from the Azores. For numbers of species shared with other areas, see Table 5.

Results of Group clustering of, respectively, the Rhodophycean, Phaeophycean, Chlorophycean, and assembled (= total) seaweed floras using the Preston dissimilarity

Table 2. References consulted to list the species compositions of seaweed floras in the various regions. For abbreviations denoting geographic areas (first column) see Table 1

CAR	Collins & Hervey (1917), Van den Hoek (1982a), Taylor (1960), Wynne (1986)
CVI	Askenasy (1886), Bailey & Harvey (1862), Feldmann (1935), John et al. (1979), Lawson & Price (1969), Lemoine (1964), Price et al. (1978, 1986), Prud'homme van Reine (1984), Prud'homme van Reine et al. (1984), Reinbold (1908)
Tr. Afr.	John et al. (1979), Lawson & John (1982), Lawson & Price (1969), Price et al. (1978, 1986)
Subtr. Afr.	Bodard & Mollion (1974), Dangeard (1952), Hariot (1911), John et al. (1979), Lawson & John (1977), Lawson & Price (1969), Naegelé (1960), Price et al. (1978, 1986), Primo (1953), Seoane-Camba (1960), Sourie (1954a, 1954b)
OC	Afonso-Carrillo (1984), Afonso-Carrillo & Gil-Rodríguez (1982), Afonso-Carrillo et al. (1984, 1985), Audiffred (1985), Gil-Rodríguez & Afonso-Carrillo (1980, 1982), Gil-Rodríguez et al. (1984, 1985), Haroun-Tabraue et al. (1984), Prud'homme van Reine et al. (1984)
L/F	Afonso-Carrillo (1984), Afonso-Carrillo & Gil-Rodríguez (1980), Afonso-Carrillo et al. (1984, 1985), Gil-Rodríguez & Afonso-Carrillo (1980, 1982), Gil-Rodríguez et al. (1984, 1985), Prud'homme van Reine et al. (1984)
SAL	Audiffred & Weisscher (1984)
MAD	Audiffred & Prud'homme van Reine (1985), Cabioch (1974), Levring (1974), Pedersen (1983), Prud'homme van Reine et al. (1984)
AZ	André et al. (1973, 1974), Schmidt (1931), South & Tittley (1986)
WM	Boudouresque & Perret (1977), Boudouresque et al. (1984), Codomier (1971), Coppejans (1977, 1979, 1983), Coppejans & Boudouresque (1983), Feldmann-Mazoyer (1940), Funk (1927, 1955), Furnari & Scammacca (1973), Gallardo et al. (1985), Giaccone (1969), Hamel (1924–31, 1924–36, 1931–39), Hamel & Lemoine (1952), Van den Hoek (1963), Koster (1941), Lauret (1968, 1970), Meñez & Mathieson (1981), Ollivier (1929), Preda (1908), Sauvageau (1912), Schotter (1968), Verlaque (1981), Verlaque & Boudouresque (1981), Verlaque & Tine (1981), Verlaque et al. (1977)
NCWT	South & Tittley (1986)
SCWT	Bornet (1892), Dangeard (1949), Debray (1897), Gayral (1958, 1960, 1961), Hamel (1924-31, 1924-36, 1931-1939), Hamel & Lemoine (1952), South & Tittley (1986)
CT	South & Tittley (1986)
CTA	Van den Hoek (1982a), South & Tittley (1986), Taylor (1957)
WTA	Van den Hoek (1982a), South & Tittley (1986), Taylor (1957, 1960), Wynne (1986)
General:	Denizot (1968), Falkenberg (1901), Kuckuck (1964), Prud'homme van Reine (1982), Silva (1960)

Table 3. Delimitation of regions and subregions along the NE Atlantic coasts

Latitudinal boundaries between (sub)regions	Boundary on or halfway between		Boundary on yearly isotherm
	winter isotherm	summer isotherm	
Tropical E Atlantic region and subtropical subregion	20 °C	25 °C	22.5 °C
Subtropical subregion and southern cooler warm temperate subregion	16.5 °C	21.5 °C	18.5 °C
Southern cooler warm temperate subregion and northern cooler warm temperate subregion	12.5 °C	18.5 °C	15.5 °C
Northern cooler warm temperate subregion and cold temperate region	10 °C	15 °C	12.5 °C

Table 4. List of abbreviations denoting climatic distribution groups. For delimitation see Van den Hoek (1984) and Table 3

CT	Cold Temperate
NCWT	Northern Cooler Warm Temperate
SCWT	Southern Cooler Warm Temperate
Subtr.	Subtropical
Tr.	Tropical
WT	Warm Temperate

Table 5. Azorean seaweeds shared with other areas. For abbreviations denoting geographic areas see Table 1

	Number of species of seaweeds				
	Red	Brown	Green	Sum total	
Total numbers in the Azores	114	41	34	189	
N. of these in the Atlantic, restricted to the Azores	8	0	2	10	
N. of endemics	4	–	2	6	
Species also recorded from outside the areas studied	4	–	0	4	
Also found in:					Total number of seaweeds in the seaweed floras of the separate areas:
SCWT	92	33	25	150	560
NCWT	82	31	23	136	754
WM	93	32	27	152	828
Subtr. Afr.	51	18	15	84	296
Tr. Afr.	39	10	19	68	301
CVI	34	17	11	62	223
OC	76	29	26	131	402
L/F	52	27	17	96	244
SAL	40	22	17	79	193
MAD	66	24	23	113	292

coefficient displays different clusters of the Azores seaweed floras with either the seaweed floras of the warm temperate Eurafrican coasts, or with those of Macaronesia sensu stricto (cf. Table 1), or with both clusters together (thus excluding only the Cape Verde Islands, Tropical Africa and Subtropical Africa). In Figure 2 the result of clustering assembled seaweed floras is given.

The Cumulative Minimal Spanning Subtrees also showed differences in the way the Azorean seaweed flora could be linked to other seaweed floras. In Figure 3 the result for the green seaweeds is given: in Figure 4 the result for the assembled seaweed floras.

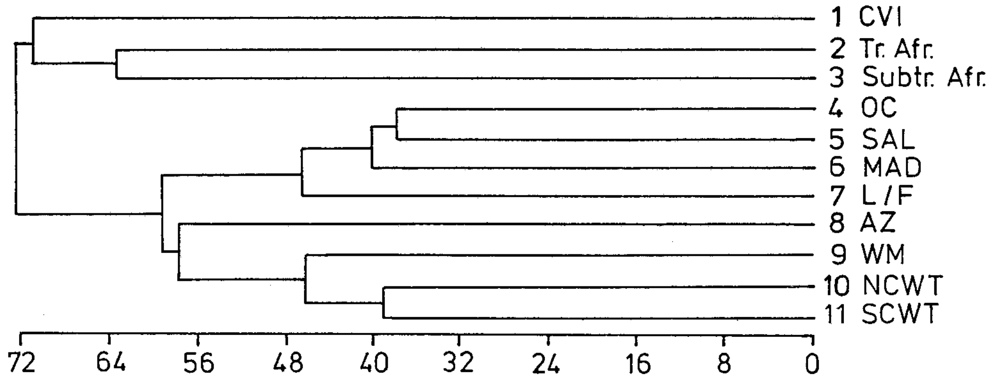


Fig. 2. Dendrogram of a Group cluster analysis of the assembled seaweed floras compared according to Preston's dissimilarity coefficient. For abbreviations denoting geographic areas see Table 1

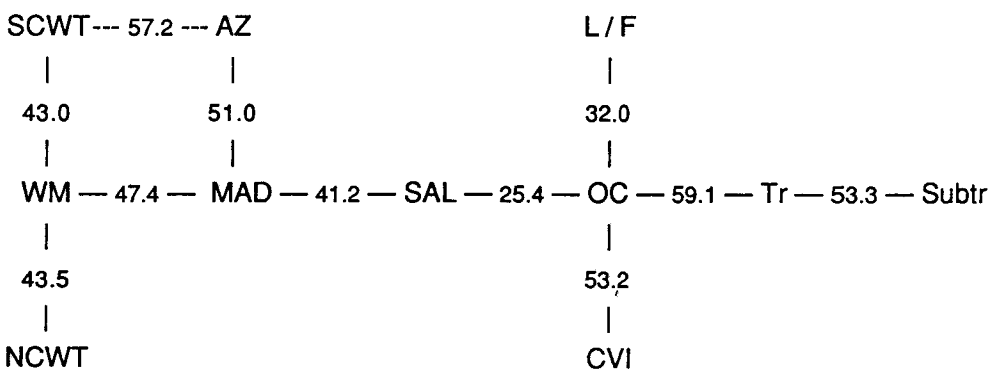


Fig. 3. Cumulative Minimal Spanning Subtree of the green seaweed floras when compared according to Preston's dissimilarity coefficient. For abbreviations denoting geographic areas see Table 1. Dissimilarity is given as percentage. Solid lines represent links of lowest dissimilarity. Broken lines represent another possible link, to which is added its dissimilarity value

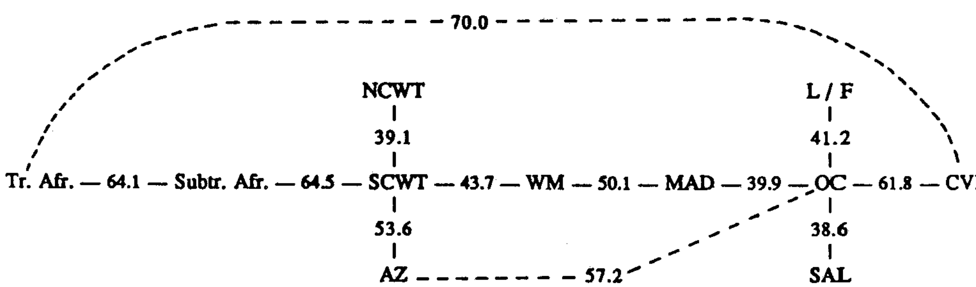


Fig. 4. Cumulative Minimal Spanning Subtree of the assembled seaweed floras when compared according to Preston's dissimilarity coefficient. For abbreviations denoting geographic areas see Table 1. Dissimilarity is given as percentage. Solid lines represent links of lowest dissimilarity. Broken lines represent other possible links, to which their dissimilarity values are added

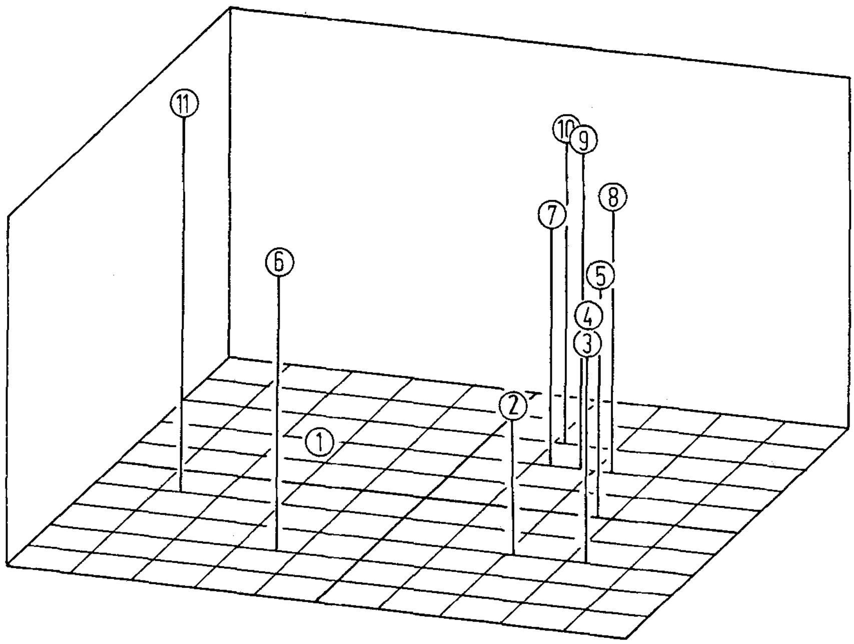


Fig. 5. Three dimensional visualization of (dis-)similarities between brown seaweed floras compared according to Preston's dissimilarity coefficient. The first principal axis (X-axis) explains 27 percent of the variation, the (Y) 21 and the third (Z) 11 percent. The meaning of the numbers denoting the geographic areas is as follows: 1 = Cape Verde Islands; 2 = Azores; 3 = NE Spain, Atlantic France, S., SW and NW England, Wales, Ireland; 4 = Morocco (excl. former Spanish Sahara), Atlantic SW Spain, Portugal; 5 = Western Mediterranean; 6 = Subtr. Afr.: NW Senegal (North of Gambia), Mauretania, former Spanish Sahara; 7 = Canary Islands except Lanzarote, Fuerteventura and surrounding islets; 8 = Madeira Archipelago; 9 = Lanzarote, Fuerteventura and surrounding islets; 10 = Salvage Islands; 11 = Tr. Afr: From Gambia to the Congo River

When a three-dimensional system is used to elucidate the (dis-)similarities of the seaweed floras of the areas, only ca 60 % of the (dis-)similarities in the n-dimensional space can be visualized. The intermediary position of the seaweed flora of the Azores can be best figured by the results for the brown seaweeds (Fig. 5). For the assembled seaweed floras, see Figure 5 in Prud'homme van Reine & Van den Hoek (1988).

In Figure 6 and Table 6 the results of the comparison of the species of the Azorean seaweed flora shared with Atlantic America on the one side and with Atlantic Eurafrica on the other side are summarized. The Azorean species shared with Macaronesia s.s. and with the western part of the Mediterranean are also indicated. One should realize that the total number of species in each climatic distribution group is only given for the Azorean flora. For other floras, only those species of each distribution type are given that are shared with this Azorean flora. Thus, the total numbers of each climatic distribution group in each flora may be larger than indicated here. For the acutal numbers of species of geographic areas in the NE Atlantic Ocean see Table 7, Figure 7, and Table 5, last column. The numbers of species shared with the Azorean seaweed flora as well as the numbers of endemics are also given.

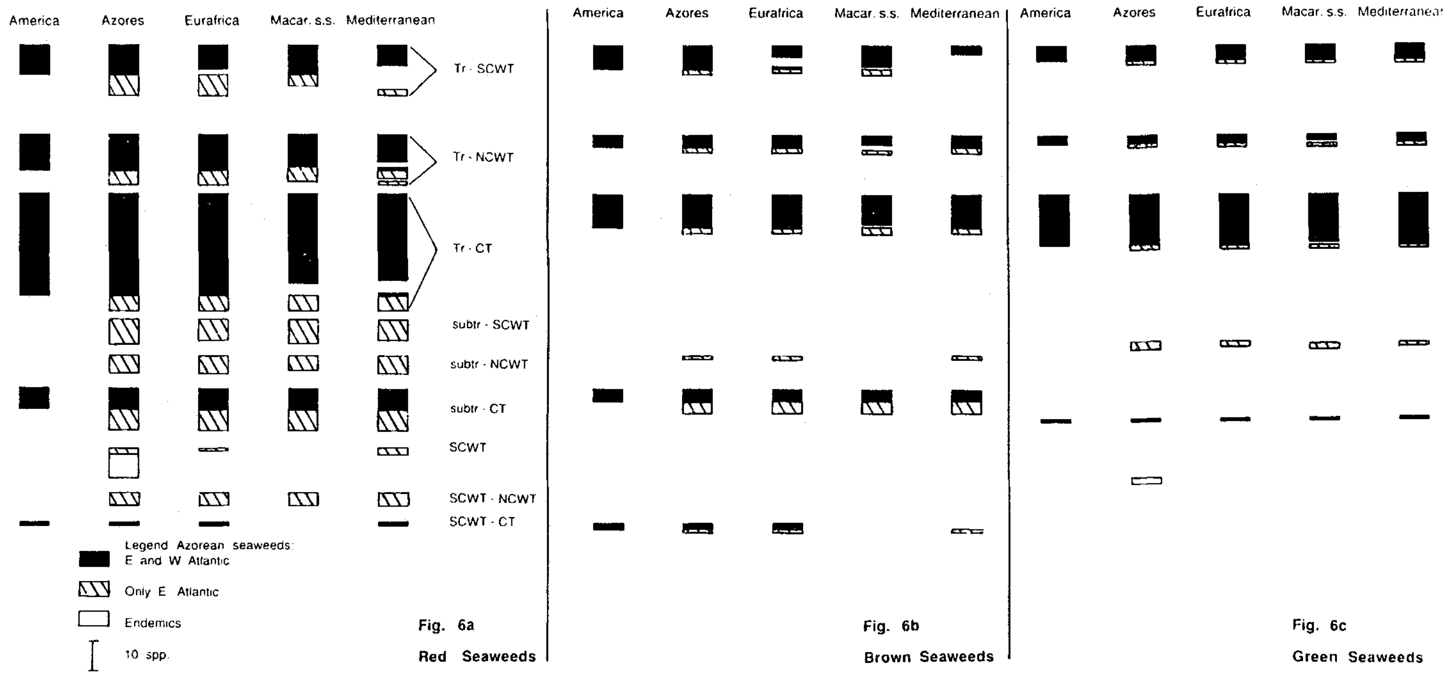


Fig. 6. Comparison of Azorean seaweeds with seaweed floras from other areas (shared species only). For abbreviations denoting distribution types see Table 4. For delimitation of regions and subregions see Table 3. a: red seaweeds; b: brown seaweeds; c: green seaweeds

Table 6. Comparison of Azorean seaweed floras with other seaweed floras (numbers of shared species only). For abbreviations denoting distribution types see Table 4. For abbreviations denoting geographic areas see Table 1. "Eurafrican coasts" stands for the warm temperate W European and NW African Atlantic coasts

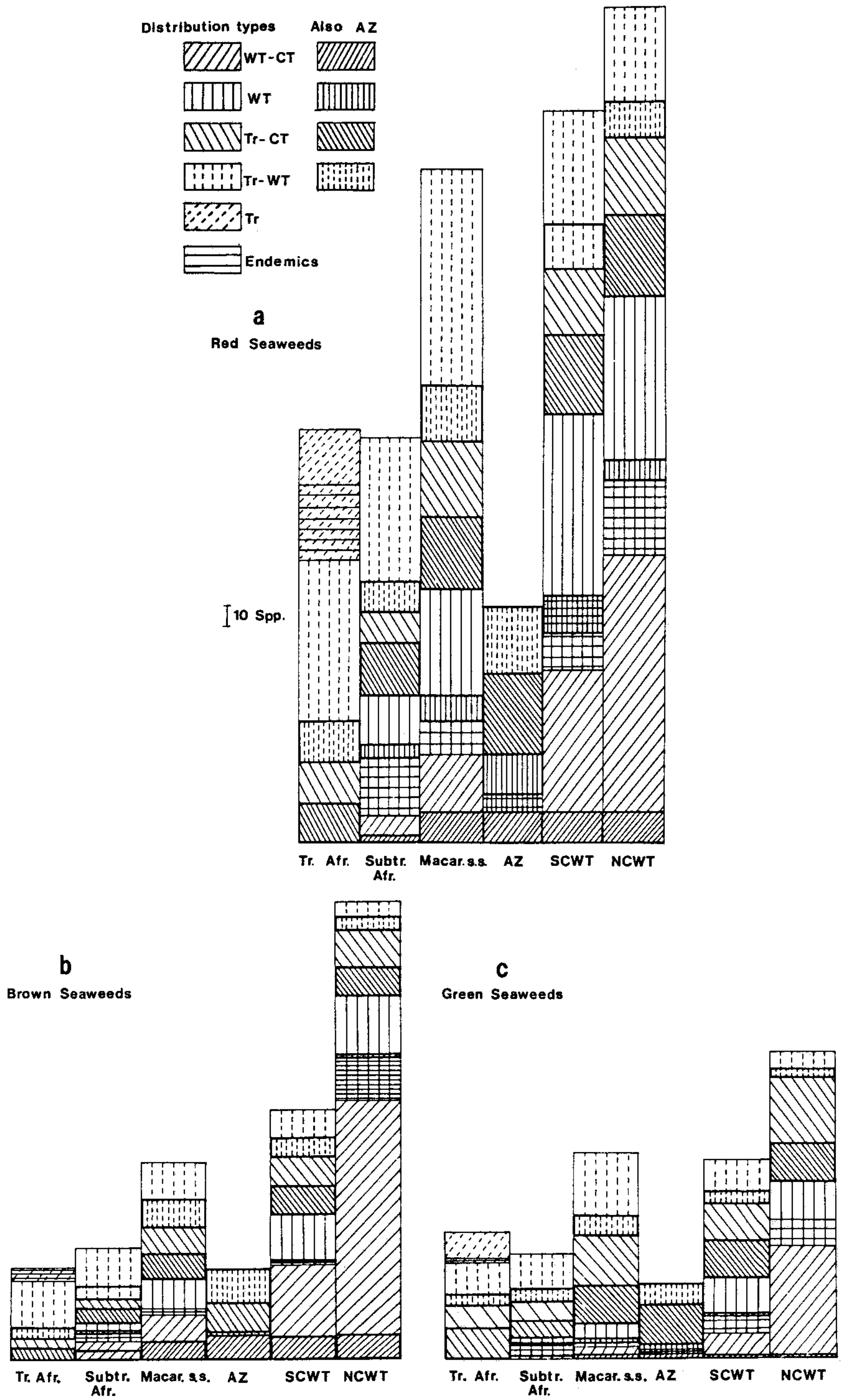
Distribution types	American coasts	AZ	Macar.s.s.	Eurafrican coasts	WM
	Red seaweeds				
Tr-WT	22	32	27	30	23
Tr-CT	34	39	35	39	37
WT	0	28	13	18	19
WT-CT	8	15	14	15	14
Total	64	114	89	102	93
	Brown seaweeds				
Tr-WT	12	16	13	12	9
Tr-CT	11	13	12	13	13
WT	0	1	0	1	1
WT-CT	6	11	8	11	9
Total	29	41	33	37	32
	Green seaweeds				
Tr-WT	8	10	9	10	7
Tr-CT	17	18	17	18	18
WT	0	5	2	2	1
WT-CT	1	1	1	1	1
Total	26	34	29	31	27
Sum Total	119	189	151	170	152

DISCUSSION

In this discussion, the "relatedness" between floras is meant as either the reciprocal of the dissimilarity (Figs 2–5) or the number of species shared (Fig. 6, Tables 5 and 6); thus roughly the floristic similarity between floras on the species level.

In all clustering exercises (Figs 2–5), the seaweed floras of the archipelagos of Macaronesia s.s. form a distinct cluster, and the floras of the cooler warm temperate Eurafrican coasts and the W Mediterranean a second distinct cluster. The floras of the Azores and the Cape Verde Islands as well as those of tropical and subtropical Africa are only distantly related to these two larger clusters.

In 8 of the total of 20 different graphs representing the inter-flora relationships based on the Preston-dissimilarity coefficients (Phaeophyceae, Rhodophyceae, Chlorophyceae, assembled [= total] flores; each processed with single-linkage, Group, Ward, minimal spanning tree, and a three-dimensional graph) the Azores seaweed floras are clustered as a separate unit with the clusters of both Macaronesia s.s. and the warm-temperate Eurafrican coasts (subtropical Africa excluded). In the other graphs the Azorean seaweed floras are either primarily clustered with those of Macaronesia s.s. and later with those of the Eurafrican coasts or primarily with Eurafrica and secundarily with Macaronesia s.s. Only four of these graphs are presented here (cf. Figs 2–5).


Distribution types
Also AZ
WT-CT
WT
Tr-CT
Tr-WT
Tr
Endemics
a
Red Seaweeds
10 Spp.
Tr. Afr.
Subtr. Afr.
Macar. s.s.
AZ
SCWT
NCWT
b
Brown Seaweeds
Tr. Afr.
Subtr. Afr.
Macar. s.s.
AZ
SCWT
NCWT
c
Green Seaweeds
Tr. Afr.
Subtr. Afr.
Macar. s.s.
AZ
SCWT
NCWT

In Figure 2 the assembled seaweed flora of the Azores occupies a separate and individual position, quite distantly related to floras of the warm temperate Eurafrican coasts (excluding the very dissimilar seaweed flora of subtropical Africa, however). The three Eurafrican warm temperate areas are mutually more closely related and a similarly close relatedness can be deduced for the Macaronesian islands sensu stricto. Minimal Spanning Subtrees may also show this close relationship to Eurafrican warm temperate areas (Fig. 4) while in other seaweed groups (Fig. 3) a closer relatedness to Macaronesian islands (s.s.) can be observed. The two larger clusters together with the seaweed flora of the Azores would agree with the Lusitano-African region as proposed by Feldmann (1946).

Figures 6 and 7, and Tables 6 and 7 give information about the nature of this individual and intermediate position of the Azorean seaweed flora. It is striking that all Azorean seaweeds that have been recorded from the Atlantic coasts of N America can also be found in the E Atlantic. Feldmann (1946) also perceived this. Thus the situation for the seaweed flora of the Azores is different from that of the Cape Verde Islands. In the latter flora several of these "American" species occur (Prud'homme van Reine & Van den Hoek, 1988), although both geographic position and the direction of ocean currents suggest relatively easy transport routes for seaweeds from tropical America to the Azores and difficult routes to the Cape Verde Islands.

The prevailing ocean current in the Azores is the N Atlantic Current, the oceanic continuation of the Gulf Stream. Seaweeds that have the ability to survive a several months-long journey may have been dispersed from the N American coasts to the Azores. For E Atlantic and Macaronesian seaweeds the direction of the surface ocean currents is opposite to the direction of the proposed transport. Nevertheless for all species restricted to the E Atlantic and also occurring at the Azores, transport from the Eurafrican coast or from Macaronesian islands must be supposed. There is no reason to suppose ocean currents to have changed their direction during the time the Azores exist (Sarnthein et al., 1982).

Endemics

The relative number of strictly warm temperate seaweeds in the Azorean floras is low as compared to the numbers in Macaronesia s.s. and those on Eurafrican temperate coasts (Table 7). The number of endemics, however, is not very different from that in other areas except the W Mediterranean, the latter being an area with high endemism.

Some of the Azorean endemics recorded by Feldmann (1946) have since been recorded from other areas. In some cases, species recorded as Azorean endemics for the Atlantic Ocean have also been recorded from areas outside the Atlantic. In Table 5 these two groups have been separated; in the Tables 7 and 8 the broad definition of endemics is used. Feldmann (1946) listed 9 strict endemics (4 red algae and 5 green algae; cf. my

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Fig. 7. Numbers of species and the different distribution types composing the seaweed floras of six geographic areas in the NE Atlantic Ocean. For abbreviations denoting geographic areas (horizontal axis) see Table 1. The vertical axis denotes the numbers of species (see small bar in Fig. 7a). For abbreviations denoting distribution types see Table 4. The numbers of species shared with the Azores and the numbers of endemics of each geographic area are also indicated. a: red seaweeds; b: brown seaweeds; c: green seaweeds

Table 7. Distribution types as percentages of the total number of species in an area (numbers of endemics are given in brackets)

	AZ		Subtr. Afr.		Macar.s.s		WM		SCWT		NCWT	
	n	%	n	%	n	%	n	%	n	%	n	%
Red algae total	114	100	197	100	327	100	522	100	355	100	405	100
WT-CT	15	13.2	13	6.6	43	13.1	80	15.3	84	23.7	140	34.6
WT	28	24.6	58	29.4	80	24.5	268	51.3	124	34.9	125	30.9
(Endemics)	(8)	(7.0)	(28)	(14.2)	(16)	(4.9)	(151)	(28.9)	(18)	(5.1)	36	(8.9)
Tr-CT	39	34.2	41	20.8	72	22.0	75	14.4	70	19.7	77	19.0
Tr-WT	32	28.0	85	43.1	132	40.4	99	19.0	77	21.7	63	15.6
Brown algae total	41	100	51	100	91	100	165	100	114	100	209	100
WT-CT	11	26.8	8	15.7	20	22.0	42	25.5	43	37.7	118	56.5
WT	1	2.4	8	15.7	17	18.7	78	47.3	23	20.2	48	23.0
(Endemics)	(0)	(–)	(4)	(7.8)	(4)	(4.4)	(52)	(31.5)	(1)	(0.7)	(20)	(9.6)
Tr-CT	13	31.7	11	21.6	24	26.4	27	16.4	26	22.8	30	14.3
Tr-WT	16	39.0	24	47.1	30	33.0	18	10.9	22	19.3	13	6.2
Green algae total	34	100	48	100	94	100	141	100	91	100	140	100
WT-CT	1	2.9	1	2.1	5	5.3	22	15.6	11	12.1	51	36.4
WT	5	14.7	8	16.6	11	11.7	44	31.2	25	27.5	29	20.7
(Endemics)	(2)	(5.9)	(5)	(10.4)	(2)	(2.1)	(22)	(15.6)	(8)	(8.8)	(12)	(8.6)
Tr-CT	18	52.9	17	35.4	40	42.5	47	33.3	34	37.4	48	34.3
Tr-WT	10	29.4	22	45.8	38	40.4	28	19.9	21	23.1	12	8.6
Sum total	189	100	296	100	512	100	828	100	560	100	754	100
WT-CT	27	14.3	22	7.4	68	13.3	144	17.4	138	24.6	309	41.0
WT	34	18.0	74	25.0	102	21.0	390	47.1	172	30.7	202	26.8
(Endemics)	10	(5.3)	(37)	(12.5)	(22)	(4.3)	(225)	(27.2)	(27)	(4.8)	(68)	(9.0)
Tr-CT	70	37.0	69	23.3	136	26.6	149	18.0	130	23.2	155	20.6
Tr-WT	58	30.7	131	44.3	200	39.1	145	17.5	120	21.4	88	11.7

Table 8. Supposed endemic seaweeds of the Azores. × = strictly endemic; + = relatively endemic, in the Atlantic restricted to the Azores, but also occurring in other oceans; – = not endemic, but recorded as such by Feldmann

Species	In Feldmann (1946)	Remarks	Found outside the Azores
Red seaweeds			
+ *Liagora divaricata* Tseng	no	det. I. A. Abbott	Pacific Ocean
× *Lithophyllum azorum* Lemoine	yes		
× *Lithophylum bipartitum* Lemoine	yes		
× *Polysiphonia azorica* Schmidt	yes		
× *Polysiphonia hochstetteriana* Schmidt	yes		
+ *Schizymenia obovata* J. Ag.	no	doubted by Schmidt (1931)	S. Africa
+ *Schizymenia undulata* J. Ag. = *Grateloupia longifolia* Kylin 1938	no	doubted by Schmidt (1931)	S. Africa
+ *Symphyocladia marchantioides* (Harvey) Falkenberg	no	Ardré et al. (1974)	Pacific Ocean
Green seaweeds			
– *Bryopsis penicillata* Suhr	yes	A form of *Bryopsis plumosa* acc. to Koster (1941)	Mediterranean
× *Cladophora michaelensis* Schmidt	yes		
– *Cladophora theotoni* Schmidt	yes		Senegal
× *Cladophora weizenbauri* Schmidt	yes		
– *Codium elisabethae* Schmidt	yes	det. P. C. Silva	Porto Santo (Madeira arch.)

Table 8). In his comments he stressed the uncertain taxonomic position of these endemics. It is very probable that several of these are not separate taxa (Van den Hoek, pers. comm. for *Cladophora*) but as long as no new information is available they cannot be discarded. Detailed taxonomic research is needed as well for the relative (Atlantic) endemics, i.e. species that are restricted to one area (e.g. the Azores) in the Atlantic, but which occur also in other oceans (see also Tables 5 and 8).

The Eurafrican coast

The species of the Azorean seaweed floras are almost all shared by the Eurafrican mainland seaweed floras (Fig. 6). Most of these Azorean seaweeds occur on the Atlantic coasts as well as in the Mediterranean. Of most distribution groups large numbers of species are amphiatlantic, but in the warm-temperate distribution groups (Subtr.-SCWT, Subtr.-NCWT, SCWT proper and SCWT-NCWT in Fig. 6 and WT in Table 6) not a single amphiatlantic species occurs. Thus a distinct E American imprint, so characteristic for the Cape Verdean seaweed flora (Prud'homme van Reine & Van den Hoek, 1988) and possibly also present in Macaronesia s.s., is not present in the Azores.

In view of the relative geographic proximity of the Azores to the Eurafrican and Macaronesian coasts one would expect unimpeded seaweed dissemination between these coasts. This would result in seaweed floras being different as a result of differences in environmental regimes, particularly temperature regimes. However, the temperature regime of the Azores is similar to that of Madeira, and only slightly different from those of the oceanic Canary Islands (OC) and the warmer part of the Southern Cooler Warm Temperate area (Table 9). Nevertheless, dissimilarities between the Azorean seaweed floras and these other seaweed floras are at the 50 %-level. Apparently other, non-environmental, possibly historical, factors are responsible for the separate and individual position of the Azorean seaweed floras. If this is true, the implication is that unimpeded seaweed dissemination between the Azores and other coasts is not possible.

Table 9. Mean surface temperatures of the sea in °C. For details see Prell et al. (1976), Crowley (1981), Sarnthein et al. (1982) and McIntyre & Kipp (1976). For abbreviations of area designations see Table 1. LG = Last glaciation (ca 18 000 years ago)

Area / Season	Subtr. Afr.		AZ		MAD		OC		SCWT	
	LG	Recent	LG	Recent	LG	Recent	LG	Recent	LG	Recent
Summer	19–24	21–26	18–20	21–23	22–23	21.5–23	19–22	21.5–22.5	12–19	17.5–21.5
Winter	12–17	17.5–20.5	12–15	15–17.5	14–16	16–18	12–14	18–19.5	4–12	12.5–18

North America

The absence of strictly warm temperate American species can be explained on the basis of differences in temperature regimes. The relationships between distribution boundaries and temperature responses of seaweeds have been experimentally determined for several species of the NE American tropical-to-temperate distribution group, the warm temperate Mediterranean-Atlantic distribution group, the amphiatlantic tropical-to-warm temperate distribution group and the amphiatlantic temperate distribution group (Yarish et al., 1984, 1986; see also Breeman, 1988). The warm temperate Mediterranean-Atlantic seaweeds have rather narrow growth and survival potentials at temperatures lower than 5 °C or higher than 20 °C. These E Atlantic endemic species cannot grow along NE American shores, because the seasonal temperature range (>20 °C) at any point along the NE American coast exceeds their temperature ranges. This is most probably also the explanation of the absence of amphiatlantic strictly warm temperate seaweeds in the seaweed floras of the Azores.

The warm temperate NE American coast algae, however, need high seawater temperatures in summer for growth and reproduction. These high seawater temperatures do not occur in the Azores and thus the few warm-temperate American seaweeds that have also been recorded from E Atlantic coasts cannot grow at the Azorean coasts.

Table 10. Species of Azorean seaweeds that may have become extinct during the last glaciation. 1 = also in warm temperate America; 2 = also in the western part of the Mediterranean; 3 = also recorded from outside the N and central Atlantic

Amphiatlantic species	
Red algae	
Amphiroa fragilissima (L.) Lamour.	1.2
Audouinella barbadensis (Vick.) Woelk.	
Heterosiphonia crispellata (C. Ag.) Wynne	2
Jania adhaerens Lamour.	1.2
Platoma cyclocolpa (Mont.) Schmitz	2
Polysiphonia havanensis Mont.	1
Porolithon onkodes (Heydr.) Fosl.	3
Brown algae	
Dictyota adnata Zanard.	3
Dictyota menstrualis (Hoyt) Schnet. et al.	1
Lobophora variegata (Lamour.) Wom.	1.2.3
Sargassum cymosum C. Ag.	
Sargassum desfontainesii (Turn.) C. Ag.	
Spatoglossum schroederi (Mert.) Kütz.	1
Green algae	
Chaetomorpha pachynema Mont.	
Dasycladus vermicularis (Scop.) Krass.	2
Derbesia furcellata (Zanard.) Ardiss.	2
Rhizoclonium ambiguum (Hook. & Harv.) Kütz	1
Struvea anastomosans (Harv.) Picc.	
East Atlantic species	
Red algae	
Griffithsia phyllamphora J. Ag.	2
Halichrysis depressa (Mont.) Born.	2
Jania crassa Lamour.	3
Lithothamnion philipii Fosl.	2
Neogoniolithon orotavicum (Fosl.) Lemoine	
Peyssonnelia rosa-marina Boud. & Deniz.	2
Polysiphonia sertularioides (Grat.) J. Ag.	2
Pseudolithophyllum esperi Lemoine	
Brown algae	
Cystoseira abies-marina (Gmel.) C. Ag.	
Green algae	
Cladophora theotonii Schmidt	
Macaronesian species	
Red algae	
Gelidium canariense (Grun.) Seoane-C.	
Brown algae	
Dictyota liturata J. Ag.	3
Green algae	
Codium elisabethae Schmidt	

On the other hand, several species of seaweeds which are confined to the tropics in America can also be found on Azorean coasts (Table 10). In that table all amphiatlantic seaweeds not recorded for Warm Temperate America are examples of the phenomenon. Upon the assumption that the Caribbean and Azorean populations of one and the same species have the same temperature response (an assumption that has to be tested first), it can be supposed that these algae meet at the Warm Temperate American coast with conditions which do not permit their survival. These conditions are possibly an adverse combination of temperature, light and/or photoperiod (Van den Hoek, pers. comm.). This combination of conditions evidently does not occur in at least parts of the Azorean (and other warm E Atlantic) coasts and thus a detailed study of these conditions as well as of the tolerances of the seaweeds occurring there can possibly elucidate this distributional difference.

Cold spells

For a number of Azorean seaweeds the last glacial period and probably also earlier cold periods in Pliocene and Pleistocene could have been crucial. During the last glacial period (ca 18 000 years ago) surface temperatures of the seawater around the Azores were a few degrees centigrade lower than nowadays (Table 9). This table shows that mean surface temperatures of the sea around the Azores are within the values given for recent mean surface temperatures in the Southern Cooler Warm Temperate subregion (= SCWT): Azorean seawater temperatures during the last glaciation were near the lowest temperatures of recent SCWT seawater, while recent Azorean seawater temperatures are, especially in summer, just a few degrees higher than recent SCWT seawater. On the basis of the results of Yarish et al. (1984, 1986), it is clear that these slight differences in seawater temperatures may have been sufficient for some warm temperate and tropical-to-warm temperate species to pass the lethal northern boundary. This means that only those seaweeds that nowadays occur in the warmer parts of SCWT as well as on the Azores may have suffered from the lower seawater temperatures occurring during the last glaciation. Only these algae can therefore be expected to have become extinct during that cold period, while all other seaweeds could have survived that period. Of the 44 recorded species of which the distribution type is Tropical-to-SCWT, Subtropical-to-SCWT or strictly SCWT (endemics excluded) the 33 species not recorded from European coasts (summer isotherms below 21 °C, winter isotherms below 15 °C) may have become extinct according to the above assumptions (see Table 10). Several of these species, however, occur in the western part of the Mediterranean or along the Warm Temperate American coasts and thus can survive lower winter temperatures.

Furthermore, the hypothesis that strictly tropical species are restricted to the tropics on the basis of their temperature responses has been tested for three strictly tropical species (Prud'homme van Reine & Van den Hoek, 1988). The tests demonstrated that these tropical seaweeds are potentially capable of surviving much lower temperatures than those occurring in the area where these seaweeds can be found nowadays. This may also be the case for some of these Azorean warm water seaweeds.

If, however, the supposed extinction took place during the last glacial maximum, these species, then extinct, must have reached the islands later and thus within the last 18 000 years. Thus, most of the seaweeds now occurring in the Azores might have taken 1–5 million years to reach this archipelago, but the seaweeds that need higher seawater temperatures must have reached the Azores within the relatively short period of 18 000 years. For the Cape Verde Islands (Prud'homme van Reine & Van den Hoek, 1988) and for the archipelagos of Macaronesia s.s., a different origin could be suggested for several of the warm-water species as opposed to species from colder waters, but for Azorean seaweeds this is not possible. They could have come from African coasts, from American coasts or from other Macaronesian islands. These suggestions, however, do not differ from suggestions based on recent distribution and recent routes of transport as discussed above. Of the 33 species discussed above (see Table 10), a total of 19 species are of amphiatlantic occurrence and 13 are E Atlantic endemics.

Alternative theories

For a number of species of the Cape Verde Islands it could be suggested, as an alternative theory, that they represent remnants of a formerly continuous Tethyan seaweed flora (Prud'homme van Reine & Van den Hoek, 1988). A suggestion like this can be tested by using the methods of vicariance biogeography (see Garbary, 1987). The Azores emerged less than 5 million years ago (Schmincke, 1982), although the oldest submarine parts probably originated in the early Miocene (Mitchell-Thomé, 1976). Thus, the Azores emerged much later than the closure of Tethys and Paratethys and no survivors of an original Tethyan tropical early miocene seaweed flora can be suggested for the Azorean seaweed floras.

CONCLUSIONS

The number of species of seaweeds found in the Azores is low compared to other Macaronesian archipelagos and is even smaller than the number of species recorded from the tiny Salvage Islands (Table 5). Reasons for this paucity may be the well-known extinction rule for island biota, especially for islands which are located at considerable distance from other shores (see Mac Arthur & Wilson, 1967).

The long migration route for seaweeds from the American coasts to the Azores as well as from the Eurafrican and Macaronesian coasts to the Azores, and the small dimensions of the islands and thus of the length of their coasts are possible reasons for the paucity of the assembled seaweed flora of the Azores. The seaweeds of the Azores can therefore be characterized as chance survivors of chance invasions by long-range dispersal (see Van den Hoek, 1987).

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