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On the ecology of sorediate lichens in Italy

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Abstract: The distribution of sorediate lichens in different ecological scenarios is depicted on the basis of data obtained from ITALIC, an on-line database on the lichens of Italy. Sorediate species are ca. 15% of the Italian flora. They are most frequent under humid-shaded conditions, and – limited to certain types of substrata – under moderate to high levels of eutrophication. Most of the sorediate species of Italy are relatively rare, only a few are abundant in anthropized habitats. It is suggested that the presence of sorediate species is highest under the same conditions which favour the proliferation of free-living algae.

Introduction

One of the least-known events in a lichen's life is the crucial moment when a newborn fungal hypha encounters a free-living photosynthetic partner. Most of the lichenised fungi - in the Italian flora they are 79% of the total - reproduce sexually, by means of ascospores. Once a spore falls in a suitable habitat it germinates, producing a delicate mycelium which eagerly looks for a photosynthetic partner to re-build the lichen symbiosis before being destroyed by a hostile environment (PYATT 1973, OTT 1987). Many lichens however notoriously dwell in sites which are not favourable to free-living algae (BECK 2000). In fact, it is often claimed that the lichen symbiosis permits to both partners to thrive under conditions in which none of them could thrive alone (BOWLER & RUNDEL 1975). The probability for a germinating spore to find a suitable alga has been estimated to be one in a million (SCOTT 1971), and it has been even questioned whether the most widespread photobionts do actually occur in the free state (AHMADJAN 1988).

Some lichens have elegantly solved this problem by discharging the ascospores together with strongly modified, smaller morphs of their photobiont. Such a mechanism, however, is restricted to a few genera (e.g. *Endocarpon*, *Staurothele*) and - judging from the small number of species involved and their overall scarcity - this has not resulted in greater fitness. Other lichens mainly spread through fragments of thallus (ULLRICH 1954, HEINKEN 1999). In some cases this is a rather rough mechanism, as in some Cladonias of the subgenus *Cladina*: once trampled in the dry state, the delicately branched thallus breaks into a myriad of fragments which are readily transported by wind (AHTI 1961). In other cases the process of fragmentation is more organised: the lichen produces thin, finger-like, corticated outgrowths, called isidia, which host some photobionts and which are prone to fall and to be carried away by water or by wind (see e.g. KÄRNEFELT

1990). Isidiate lichens as well constitute a small minority (e.g. they make up only 3.5% of the Italian flora), and their ecology still awaits further study. "Parasitic" lichens, i.e. those regularly starting the life-cycle on other lichens, could be of interest in the context of this paper. Such lichens literally "steal" the photobiont from other species, and represent an original solution to the problem of finding photobionts in hostile environments (FRIEDL 1987, RAMBOLD & TRIEBEL 1992, RICHARDSON 1999).

The most sophisticated and most successful system of spreading the lichen symbiosis as a whole is the production of soredia. These are small bundles of hyphae surrounding a few cells of the photobiont, which are readily dispersed by wind (ARMSTRONG 1994), water (BAILEY 1968), invertebrates (BAILEY 1970, STUBBS 1995, LORENTSSON & MATTSSON 1999) or even by birds (BAILEY & JAMES 1979). They normally generate from an active proliferation of the photobiont cells, which are readily surrounded by hyphae proliferating from the medulla (HONEGGER 1996). A soredium is the smallest form of a miniaturised lichen, and sorediate lichens are apparently the most successful way to ensure a rapid meeting between myco- and photobiont in a new site. It should be added that the term "soredia" is often applied for a wide array of morphologically and ontogenetically different propagules (POELT 1993).

Sorediate lichens occur in widely different taxonomic groups, and they involve several different photobionts, from cyanobacteria to trentepohlioid algae. Such a clever way of propagation has however its drawbacks. With notable exceptions, most of the sorediate lichen-forming fungi have lost the capacity of reproducing sexually, and there is evidence that this has resulted in a much lower degree of genetic variability (FAHSELT 1989, 1995; HAGEMAN & FAHSELT 1990). This however could not be a real drawback. Seen from another perspective, sex just seems to be not important for sorediate lichens. But why?

The production of soredia is thus a biologically interesting phenomenon: it is apparently a way of facilitating the re-synthesis of the lichen symbiosis, and at the same time it often implies the loss of sexual reproduction by the fungus.

This paper tries to explore some aspects of the biology of soredial reproduction on the basis of data on the incidence of sorediate species in different ecological scenarios. These were retrieved from a complex database on the lichens of Italy, a biogeographically diverse country, encompassing several biomes - from the nival belt of the Alps to the semi-deserts of the south - whose lichen flora is one of the best-known worldwide.

Data and methods

The data derive from ITALIC (NIMIS 2000), an information system that originated from the transformation of the checklist of Italian lichens by NIMIS (1993) into a database published in the internet (http://dbiodbs.univ.trieste.it). More information on ITALIC is given by NIMIS & MARTELLOS (2002); here we shall briefly mention only the characters used in this study to define ecological scenarios, which are:

1) Substrates: The characters are: "epiphytic", "lignicolous", saxicolous", and "terricolous". Several substrates can be attributed to a single species.

2) Ecological indicator values: Those adopted in ITALIC specify, for each factor and for each species, a range on a 5-class ordinal scale (NIMIS & MARTELLOS 2002b). The pH value, ranging from 1 (very acid) to 5 (basic), was used in combination with the "saxicolous" substrate to define siliceous (1-2) and calcareous (4-5) substrata;. The aridity value mainly referring to the degree of air humidity (from 1, very humid to 5, very dry), the light value (from 1, low solar radiation to 5 very high radiation), and the eutrophication value (from 1, no eutrophication to 5, very high eutrophication) were used to explore the incidence of sorediate species along ecological gradients.

3) Bioclimatic subdivisions of Italy: Eight Operational Geographic Units (OGUs) were used to explore the incidence of sorediate species in climatically different parts of the country. They are: a) Alpine: above treeline in the Alps and in Abruzzi; b) Subalpine: forming treeline in the Alps (dominated by *Larix* and *Picea*); c) Oromediterranean: above treeline outside the Alps; d) Montane: areas potentially covered by beech forests; e) Submediterranean: areas with mixed deciduous woodlands dominated by *Quercus*, except the following OGU; f) Humid submediterranean (Tyrrhenian): as before, but in areas with a warm-humid climate, mostly along the W side of the Peninsula; g) Humid Mediterranean: areas with Mediterranean vegetation under humid maritime conditions; h) Dry Mediterranean: as before, under dry conditions. A map of the OGUs is in NIMIS & MARTELLOS (2002), and can be retrieved on-line from ITALIC.

4) Commoness-rarity: In ITALIC - as a first approximation - commoness-rarity of each species was calculated for each OGU on the basis of three main criteria: a) number of samples in the TSB lichen herbarium (% on the total for each OGU, total nr. of samples, ca. 40.000), b) number of literature records (% of total for each OGU), c) expert judgement. The first step has grouped the species into 4 commoness-rarity classes, on the basis of the percentile distribution of the TSB samples in each OGU, as follows: A): very/ extremely rare, B): rare, C): common, D): very/extremely common. Expert assessments were used to overcome the obvious faults deriving from the fact that TSB samples were not collected at random. These were based mainly - but not only - on a similar analysis of literature data. Responsible of the expert assessment is the senior author of this paper. To create a certain degree of liberty for the expert, the classes were doubled from 4 to 8, as follows: A): er: extremely rare, vr: very rare; B): r: rare, rr: rather rare; C): rc: rather common, c: common; D): vc: very common, ec: extremely common. The main constraint for the expert was of not moving outside the four main classes (A-C) defined by the analysis of the TSB samples.

5) Other parameters: a) "pioneer" species: weak competitors colonizing newly exposed habitats (young twigs, disturbed surfaces etc.); b) "oceanic-suboceanic": species, most frequent in western Europe, and absent from continental areas; c) special requirements for water: i) in underhangs rarely wetted by rain, ii) on otherwise dry surfaces with short periods of water seepage after rain, iii) periodically submerged (e.g. in creeks); d) "parasitic": lichens starting the life-cycle on other lichens, normally of a different species; e) species restricted to metal-rich substrata.

A matrix reporting the numbers of sorediate species in the OGUs and in habitat-types retrieved from ITALIC was submitted to reciprocal ordering ordination using the package of WILDI & ORLOCI (1984). The occupancy by sorediate species in an ecological space defined by the indicator values of aridity and eutrophication was illustrated by processing the respective matrices with program SURFER (Golden inc., Colorado).

Results

The lichen flora of Italy consists of 2315 infrageneric taxa. Of these, only 347 (15%) mainly reproduce by soredia. The share of sorediate species is low in the crustose and squamulose forms (8-9%), much higher in the foliose and fruticose forms (31.9 and 36.9%, respectively); it is also much higher in lichens with green algae other than *Trentepohlia* (17.6%) than in those with filamentous cyanobacteria (8.2%) and with *Trentepohlia* (5.4%). The lichens with coccaceous cyanobacteria (mostly of the family Lichinaceae) almost never produce true soredia in Italy. On rock and soil sorediate lichens are ca. 12% of the respective totals, while on bark and on lignum they are ca. 25%. Irrespectively of growth-form and substrate, the percents of sorediate vs. non-sorediate species does not change much with altitude: from the mediterranean to the subalpine belt sorediate species make up 14-18% of the respective totals, but in the alpine belt they are only 9%. The percent incidence of sorediate species varies more dramatically along ecological gradients, with higher values in humid habitats (Fig. 1a), and in those with moderate to high eutrophication (Fig. 1c), while light intensity seems to be less important (Fig. 1b). However, the sheer number of sorediate species along the same gradients shows a different trend, with higher diversity in humid to mesic (Fig.1d), well-illuminated (Fig. 1e), not very eutrophicated situations (Fig.1f). This means that only a small number of taxa is involved in the high incidence of sorediate species in very humid and eutrophicated situations. Sorediate species are also prominent among lichens with an oceanic-suboceanic distribution (24%), and among those restricted to underhangs (23%), i.e. in humid habitats with little or no availability of liquid water. They are exceptionally numerous (38%) among the lichens which are specialised on metal-rich substrata such as iron-rich rocks and mine-spoil heaps. On the contrary, sorediate species make up only 7.2% of the lichens which are restricted to dry sites with periodical percolation of liquid water, and 7.2% of the "pioneer" lichens, those which colonize recently-exposed surfaces such as young twigs and disturbed habitats.

Almost no endolithic lichen is able to produce soredia, like those which are perennially or frequently submerged in water.

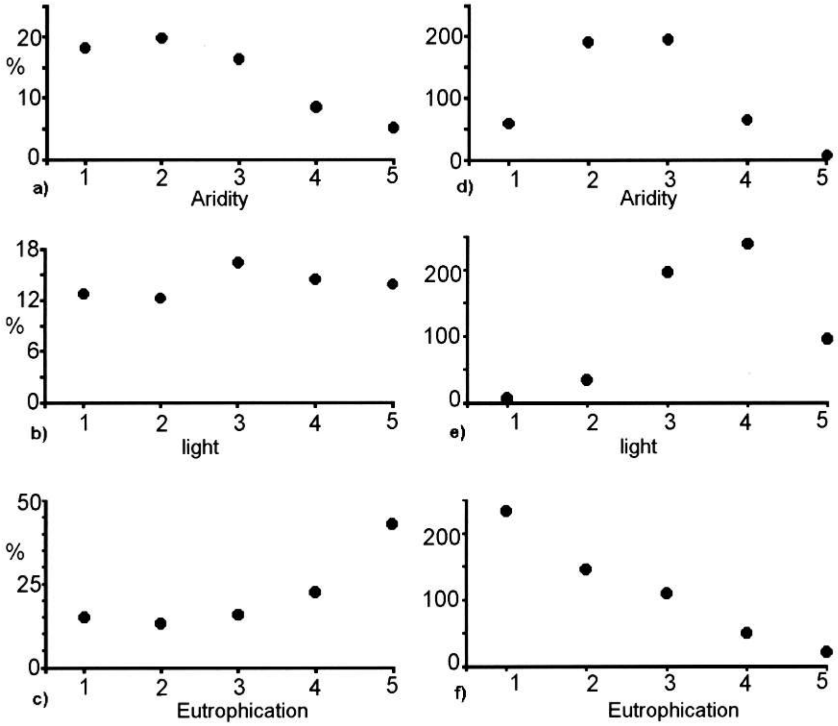


Fig. 1 a-c: Percents of sorediate vs. non-sorediate species of the Italian flora along three gradients defined by the indicator values of aridity (a, from 1, very humid to 5 - very dry), light (b, from 1, very low to 5, very high solar radiation), and eutrophication (c, from 1, no eutrophication to 5, very high eutrophication). **Fig. 1 d-f**: absolute numbers of sorediate species along the same gradients.

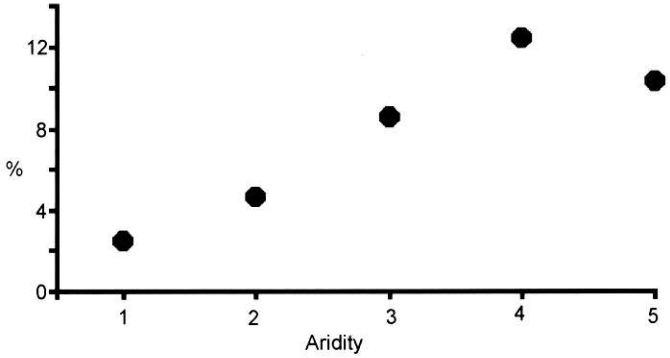


Fig. 2: Percents of "parasitic" species of the Italian flora along a gradient defined by the indicator values of aridity, from 1 (very humid) to 5 (very dry situations).

Fig. 2 shows the incidence of "parasitic" lichens in the flora of Italy along a gradient of increasing aridity: their optimum clearly lies in arid environments, contrasting with that of sorediate species (Fig. 1a). The incidence of sorediate species among "parasitic" lichens - by the way - is extremely low (1.2%).

Tab. 1: Number of saxicolous sorediate species on calcareous (C) and siliceous (S) rocks in ecological scenarios with different degrees of eutrophication (from E1, no eutrophication to E5, very high eutrophication) in 8 main phytoclimatical subdivision of Italy. For further explanations see text.

	S(E1)	S(E2)	S(E3)	S(E4)	S(E5)	C(E1)	C(E2)	C(E3)	C(E4)	C(E5)
Alpine (Ap)	14	14	9	5	2	1	3	4	6	4
Subalpine (Sa)	45	31	16	7	3	2	4	7	11	9
Oromediterranean (Om)	10	10	8	6	2	1	4	6	9	7
Montane (Mn)	53	31	18	10	4	7	10	17	19	13
Submediterranean (Ds)	19	11	8	9	4	6	10	18	21	13
Humid submedit. (Hs)	27	14	10	9	4	7	10	16	20	11
Dry mediterranean (Dm)	4	5	7	6	3	7	10	13	13	8
Humid mediterranean (Hm)	20	14	11	8	4	10	14	19	19	10

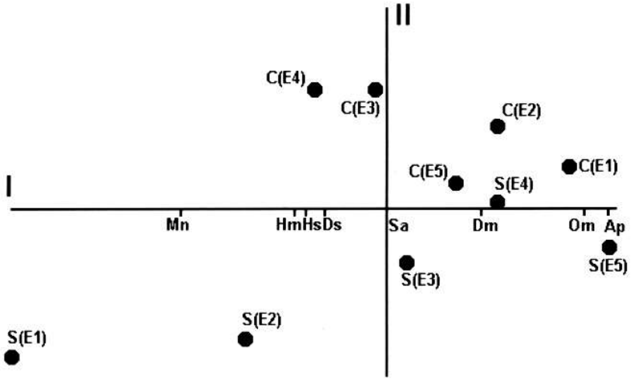


Fig. 3: Ordination of saxicolous habitat types (S=acid siliceous rocks, C=calciferous rocks), with different degrees of eutrophication (from E1 - no eutrophication - to E5, very high eutrophication) based on the data of Tab.1. The position along the first axis of the Operational Geographic Units (OGUs) in their ordination (not shown) is also reported. The OGUs are abbreviated as in Tab. 1.

The next analysis concerns saxicolous lichens only, because it involves some OGUs above treeline (Alpine, Oromediterranean) in which epiphytic lichens are by definition scarcely represented. There is a remarkable difference between calcareous and siliceous substrata in the incidence of sorediate species. While 18.5% of the silicicolous lichens are sorediate, only 8.6% of those dwelling on calciferous rocks do reproduce by soredia. This difference was considered as worthy of a more detailed analysis. Tab. 1 reports the numbers of saxicolous sorediate species in 10 habitat types defined by different degrees of eutrophication in the 8 phytoclimatic OGUs, on calcareous and on siliceous substrata.

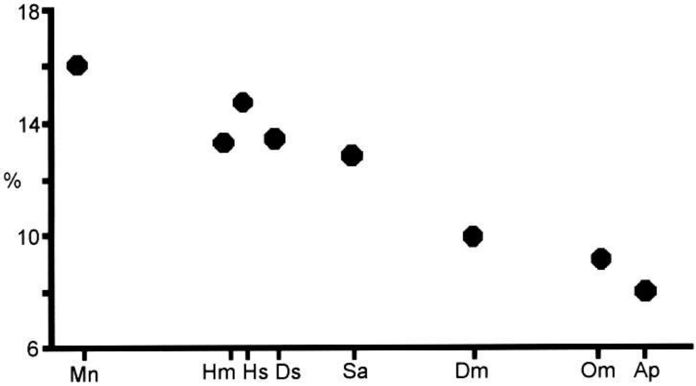


Fig. 4: Percent occurrence of sorediate species in the 8 main phytoclimatical OGUs of Italy, arranged according to their sequence on the first axis of the ordination (Fig. 3). The OGUs are abbreviated as in Tab.1.

The first axis of the reciprocal ordination of OGUs and habitat-types (Fig. 3), based on the data of Tab. 1, explains more than 55% of the total variance. Fig. 3 shows the arrangement of OGUs along the first axis, and the ordination of habitat-types. The percent of sorediate species in the OGUs, arranged as along the first axis of Fig. 3, is shown in Fig. 4. A clear trend is evident in Fig. 4, from "humid" OGUs with higher incidence of sorediate species (negative scores) to dry-continental OGUs where sorediate species are less important (positive scores). In the ordination of habitat-types (Fig. 3), the second axis neatly separates calcareous (positive scores) from siliceous substrata (negative scores). The gradients of eutrophication along the first axis are opposite for the two types of substrata: whereas on calcareous rocks the incidence of sorediate species tends to increase with increasing eutrophication, on siliceous rocks sorediate species are most frequent in non-eutrophicated habitats. Fig. 5 depicts the occupancy of sorediate species in an ecological space of 25 cells, defined by the indicator values of eutrophication and aridity, on bark (Fig. 5a), siliceous (Fig. 5b), and calcareous rocks (Fig. 5c). On bark and on siliceous rocks sorediate species are most numerous under conditions of high air humidity and no or very weak eutrophication, while on calcareous substrata they are most numerous under mesic to relatively dry conditions of high to very high eutrophication.

One interesting question concerns the commoness-rarity of sorediate species in the Italian flora. Fig. 6 compares the percents of sorediate vs. non-sorediate calcicolous, silicicolous and epiphytic lichens in the 8 classes of the commoness-rarity scale, in humid submediterranean (Tyrrhenian) Italy. On bark, and in a lesser degree on calcareous rocks the percent of sorediate lichens tends to increase with commoness. With absolute numbers (Fig. 7) the trend is the same in saxicolous habitats, while on bark the number of sorediate species tends to decrease with commoness. Again, eutrophication seems to favour only a few sorediate species, which are able to spread in anthropised habitats.

Discussion and Conclusion

Soredia are a mean of reproducing the lichen symbiosis "in toto". One would therefore expect that soredia were of selective advantage in situations where free-living algae are rare (see e.g. LAWREY 1980). On the contrary, in such habitats - e.g. in dry conditions - sorediate species are few, being much more numerous and abundant in sheltered-humid habitats, and abundant but less numerous in disturbed sites with moderate to high eutrophication.

The high incidence of sorediate lichens in humid-shaded situatons, and their scarcity in dry habitats, were mentioned by several authors, e.g. by DIETRICH & SCHEIDEGGER (1996, 1997) for Switzerland, by TØNSBERG (1992) for Norway, and by FAHSELT et al. (1989) for the Canadian high-Arctic. On the other hand, the importance of sorediate species in disturbed habitats was also underlined several times. They were reported to be prominent during early stages of successional processes (KISS 1988), and even under accumulation of dust, or in polluted situations, esp. by sulphur dioxide (PASICH 1973, 1974).

Reproduction by soredia often implies the loss of sexuality. This is often a selective advantage in the "ruderal" strategy, such as in apomictic higher plants of disturbed habitats (POELT 1994). Reproduction by soredia was regarded as an advantageous propagation strategy of r-selected species by ROGERS (1990), and according to GILBERT (1990) in the lichen flora of urban wastelands many species can be accomodated within the strategy group of stress-tolerant ruderals (see also JAHNS & OTT 1997).

The low incidence of sorediate lichens among "pioneer" species of the Italian flora somehow contrasts with these views. On a broader geographical and temporal scale, a similar assumption underlies the famour "species pair theory" of POELT (1970), who suggested that the more northern distribution of sorediate species with respect to their sexual counterparts could be related to the recent colonization of formerly glaciated areas. However, at northern Boreal latitudes sorediate species are so scarce as to lead NIMIS (1999) to speculate that - being soredia being much heavier than ascospores - the prevalence of sexual species in the Arctic could reflect a selective advantage in the rapid colonization of formerly ice-

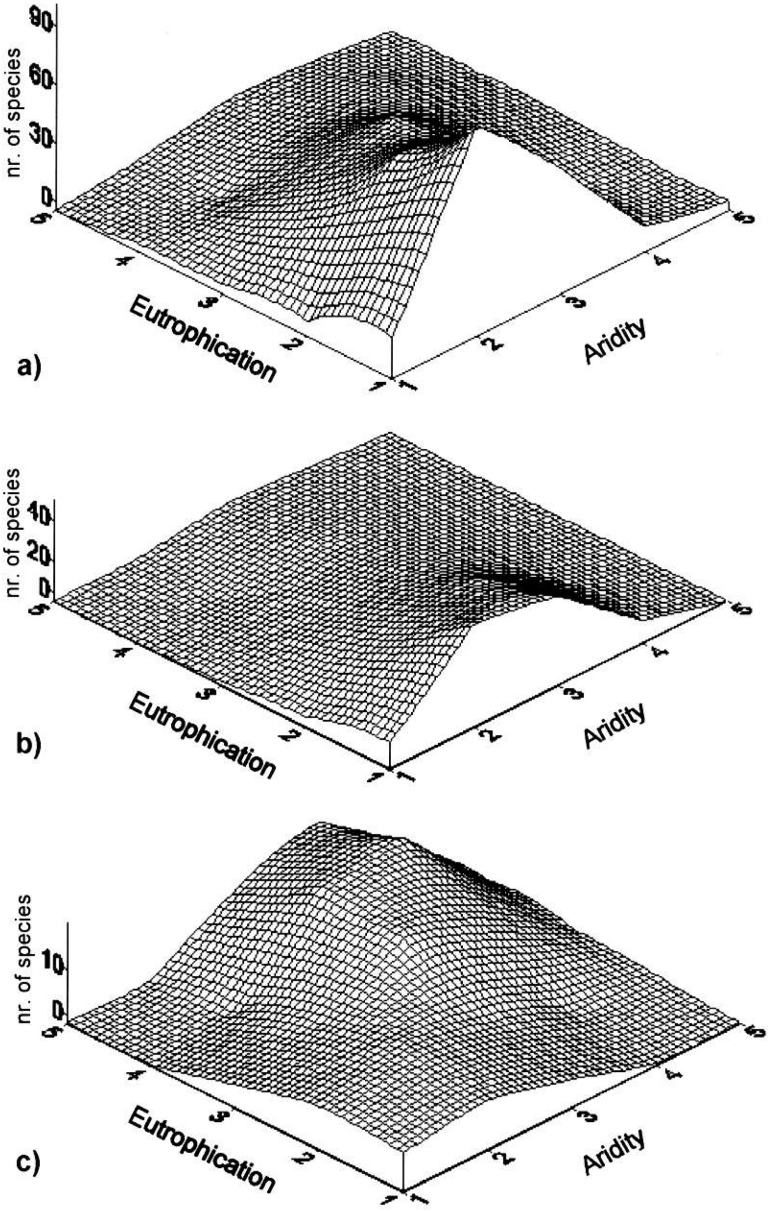
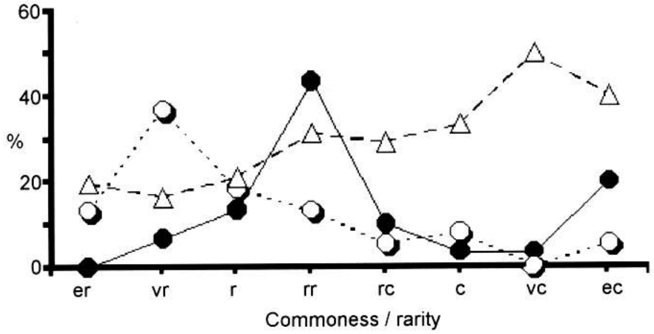


Fig. 5: Occupancy of sorediate species of an ecological space defined by the indicator values of eutrophication and aridity on bark (a), on acid siliceous rocks (b), and on calcareous rocks (c).



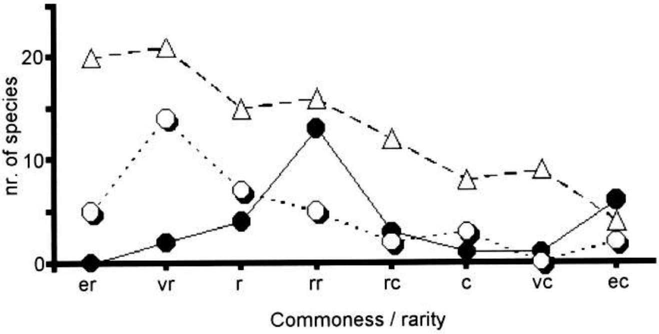


Fig. 6 (upper): Percent distribution of sorediate epiphytic (triangles) silicicolous (empty circles), and calcicolous (full circles) species among eight commoness-rarity classes, from extremely rare (er) to extremely common (ec), in humid submediterranean Italy.
Fig. 7 (lower): Number of sorediate epiphytic (triangles) silicicolous (empty circles), and calcicolous (full circles) species among eight commoness-rarity classes, from extremely rare (er) to extremely common (ec), in humid submediterranean Italy.

covered areas. Some authors actually claim that sorediate lichens tend to have broader distributional ranges than their non-sorediate counterparts (BOWLER & RUNDEL 1975, see also TOPHAM 1977 and LAWREY 1980). In any case, the hypothesis of the "ruderal" role of soredial reproduction is easier to corroborate on the basis of present than of past evidence. As a matter of fact in Italy, especially on bark and on calcareous substrata several sorediate species are bound to disturbed-eutrophicated situations. Some of them are so abundant in anthropised habitats as to induce even the authors of this paper to intuitively overestimate the incidence of sorediate species in the Italian flora. The most common sorediate species are ubiquitous in the urban floras on rocks (e.g. *Caloplaca citrina*, *C. teicholyta*, *Diploicia canescens*, *Phaeophyscia orbicularis*) and on bark, also in rather polluted situations (e.g. *Candelariella reflexa*, *Hyperphyscia adglutinata*, *Parmelia sulcata*, *Phaeophyscia orbicularis*, *Physcia adscendens*, *Physconia grisea*). However, the abundance of sorediate lichens in "ruderal" environments involves only a few, mostly foliose species. In sheer number, they are only less than 1% of the total flora of Italy. Thus, the intepretation of soredial reproduction as a "ruderal" strategy cannot be excluded, but also cannot be generalised and, at least in the Italian flora, it applies only to a minority of common species, whose biology is well worthy of further study.

In Italy - as elsewhere – sorediate lichens mostly dwell in more or less "natural" habitats, and especially in humid-shaded situations. Most of the earlier tentative explanations give more weight to humidity, others to light intensity, two factors which are obviously related through evapotranspiration, and which are difficult to disentangle. According to DIETRICH & SCHEIDEGGER (1996) a leprose-sorediose thallus with its hydrophobic surface can be regarded as an adaptation to the absorption of water vapour. JAHNS (1984) related the smaller water storage capacity of a sorediate foliose lichen to the higher frequency of sorediate thalli in humid conditions. NIMIS (1999) hypothesised that the scarcity of sorediate species in Arctic-Alpine habitats could be due to a lower survival rate of soredia in cold-dry than in warm-humid situations. HENSSEN & JAHNS (1974), however, claimed that the prevalence of sorediate lichens on shaded-humid rocks may be due in first line to the low solar radiation. Our data (Fig. 1) suggest that humidity could be more important than light in influencing the ecological distribution of sorediate species.

Perhaps however sorediate lichens are just most frequent under the same conditions which favour the proliferation of free-living photobionts. Little is known on the physiological mechanisms underlying the production of soredia (RAINERI & MODENESI 1986, 1988; GALUN & GARTY 1988), but an active proliferation of the photobiont cells is clearly indispensable for the production of these propagules (HENSSEN & JAHNS 1974). Free-living terrestrial algae are notoriously more abundant under conditions of high humidity (e.g. see GUILLITTE 1993). Eutrophication as well can have dramatic effects on the proliferation of algal patinas on bark and rock (e.g. see BARKMAN 1958). Dry, non-eutrophicated habitats could render the proliferation of the photobiont cells - and hence the formation of soredia - very difficult. If this were true, soredia were a luxus that most lichens cannot afford.

Much remains to be done for fully understanding the biology of lichen propagation through soredia. Its "ruderal" character cannot be generalized, and probably involves only a small number of species. No selective advantage seems to be related to the scarcity of free-living photobionts. Soredia are mostly produced where free-living algae are abundant, and "parasitism" is perhaps the main mechanism for acquiring photobionts where they are scarce. Thus, soredia do not circumvent the problem of the delicate mycelium looking for a photosynthetic partner to re-build a symbiosis. There should be other reasons for their widespread occurrence.

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