We hypothesise that marine algae and various common microbes of the atmosphere (spora) use chemical induction of water condensation to enable or increase their wind dispersal between their aquatic, terrestrial or epiphytic growth sites. Biogenic chemical cloud condensation nuclei (CCN) and ice nuclei (IN), sometimes co-occurring in single species (e.g. *Pseudomonas syringae*), release heat energy of phase change, thus contributing to local air movements that can be used both for lofting and for lateral dispersal of their producers. The phase-change catalysis may occur on the microbial surface (e.g. *P. syringae*) or may happen more distantly through the release of chemical precursors for suitable ions (e.g. plankton-derived dimethylsulphide [DMS] forming atmospheric sulphate). Small phytoplankton and bacteria take off from water through bubble-burst processes especially in ‘white-caps’, these often themselves caused by convective winds.

Selection for local induction of wind is likely to be most effective at the level of clonal microbial patches. Algal blooms having high DMS emission may represent attempts to create winds for dispersal; if so, algal cell changes occurring in such blooms may have features convergent to terrestrial dispersal cyclomorphoses of aphids, locusts, subcortical insects and others. It is already established that biogenic cloud formation occurs on a scale fully capable of affecting world climate. This fact features prominently in the Gaia Hypothesis. However, in contrast to the evolutionary scenario for microbe dispersal that we present, the claim of an adaptive function at the world level still lacks an explanatory mechanism.

**KEY WORDS:** Gaia, aerobiology, cumulus cloud, condensation nuclei, ice nuclei, DMS, plankton blooms, cyclomorphosis, dispersal.

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INTRODUCTION

Herrings falling with rain miles inland in Scotland, frogs and a juvenile turtle being found in American hailstones (Gislén 1948), and live bacteria and fungal spores collected by rocket more than 50 km from the Earth’s surface (Imshenetsky et al. 1978) all demonstrate that both terrestrial and marine organisms are sometimes raised very high by extreme atmospheric events. Allergies and airborne diseases further prove the troposphere to be, in most places, a dilute suspension, or ‘spora’, of microbes, viruses and pollen (Gregory 1967). All these organisms owe their presence in the air to atmospheric instabilities. The basic principles are physical but some of the details may be biological. In particular the seeding of condensation either to water or to ice, which greatly adds to the local energy of convection, has for a quarter century been suggested to be, even for the world as a whole, mainly biogenic (Schnell & Vally 1972, Lovelock 1997). Whether causative organisms adaptively evolved (Lovelock 1988) their propensity to seed cloud formation remains controversial (Lenton 1997), there being grave problems with all the selection scenarios so far proposed (Dawkins 1982; Caldeira 1989, 1991). Here, based upon the universal imperative of organisms to disperse, which applies even if new habitat is never better than old (Hamilton & May 1977) we suggest a new hypothesis that some microbes have evolved to seed cloud formation to create local dispersal vehicles for themselves, winds and clouds.

LOFTING MICROBES FROM WATER: BUBBLE BURSTS AND CONVECTION

When wind over an expanse of water reaches a velocity of about 20 km/hr, wave tops start to break. Rising bubbles in the ‘white caps’ concentrate planktonic microbes at their lower surface; when the bubbles break these microbes, sometimes aided by cell-surface hydrophobicity (Blanchard 1983), are tossed into the air within minute droplets formed from the burst surface film. Their concentration in such drops is almost always elevated over that in the surface sea water, sometimes by more than two orders of magnitude (Woodcock 1948, Blanchard & Syzdek 1970, Baylor et al. 1977, Blanchard 1983). The bubble-burst mechanism of take off which has been principally investigated for bacteria (Blanchard 1983) must also work for microalgae that are significantly smaller than the bubbles. Since the size range of bubbles in breaking sea water is 20 µm to over 1 cm in diameter, with peak concentration at about 100 µm (Blanchard 1983), there is scope for lofting small algae, although they will not be concentrated or ejected to the same degree as bacteria. Direct evidence for algal take-off seems lacking but various studies suggest it is common. Working with inshore and oceanic sea water from latitudes
Spora and Gaia: how microbes fly with their clouds

between about 42° and 32° in the Atlantic, including in the Sargasso Sea, WALLACE & DUCE (1978) found about half the organic matter in surface water was transported to surface froth by induced bubbles. Conditions for white caps on the sea are also conditions for air turbulence above it and the updraughts must catch some of the algae thrown from bubbles and lift them higher. In another study 20% of the particulate organic matter in air 15-20 m above the Sargasso was found to be different from the rest. Firstly, its carbon was sea-derived, and, secondly, its particles were larger, the diameters ranging upwards from about 0.75 µm (CHESSELET et al. 1981). The fall rate for a 20 µm spore or pollen grain is only 0.5 cm/sec (HIRST et al. 1967) and microplankton cells important for our argument (see below) are mostly smaller (e.g. Emiliana huxleyi: 5 µm while eucaryotic picoplankton range down to about 0.5 µm). Since pollen grains of small anemophilous weeds such as Plantago coronopus, with a 20 µm diameter, liberated from only a few centimetres above ground level, are found in high spora (GREGORY 1967), it is no surprise that microplankton are also present there (STEVENSON & COLLIER 1962, SCHNELL & VALI 1975) with potential to be carried for long distances (PEDGELEY 1982, 1991). Actual wind transport of marine algae (SCHLICHTING 1969) is most striking when toxic dinophytes in marine aerosols blowing onto land cause severe skin and respiratory problems to humans (WOODCOCK 1948, HART 1966) and even occasionally cause death to livestock (MACHADO 1979). However, turbulence forced by wind over an uneven surface is not the only lifting mechanism. Surface plankton that intercept sunlight warm their water layer and transfer heat quickly to the air above (MAZUMDER et al. 1990, SATHYENDRANATH et al. 1991). Hence even in initially still air, surface plankton patches tend to cause thermals to form above them. Rising like huge bubbles (SCHLICHTING 1964, ROGERS & YAU 1989) or columns (MALKUS 1953, PEDGELEY 1991), and seemingly, again, with a propensity to concentrate spora at their lower margins when these exist (HEISE & HEISE 1948, GREGORY 1967), thermals lift spora high in the troposphere. They initiate clouds (HEISE & HEISE 1948, SCHLICHTING 1964, GREGORY 1967, HIRST et al. 1967, JAYAWEERA & FLANAGAN 1982) and in the process release latent heat, so drawing more air from below. If the atmosphere over a warmed sea happens to be metastable on a large scale, the effects of condensation may be very dramatic: tropical storms, waterspouts, even monsoons, may be started (SATHYENDRANATH et al. 1991). Above the storms, convective cloud tops may go as high as 15 km and inject spora well into the stratosphere.

The crucial effect in our evolutionary interpretation, however, does not require extreme events or high altitudes. It relies on the fact that thermals and cumulus clouds almost never rise vertically and that air generally has lateral motion (MALKUS 1949, 1953). A tiny organism or group which could cause a thermal, be launched into it, and which could later help to seed its condensation (SNIDER et al. 1985) so as not only to release more lofting power for its vehicle (via latent heat) but also to provide itself UV shelter and eventually to begin the aggregative condensation that may return the organism to the planet's surface (SNIDER et al. 1985), would be very effectively dispersed. Whether or not adaptive causation of this kind is believable, the literature in plant epidemiology (DAVIS & MAIN 1986) and entomology (PEDGELEY 1982) abundantly attests that spores are distantly and successfully transported. Sometimes spores even survive transit across oceans (PEDGELEY 1991), but that is clearly exceptional. From here on we expand only the hypothesis that certain classes of microbes may have evolved to add to the effectiveness of atmospheric transport, most commonly with effects ranging from a few tens of metres to tens of kilometres.
Consider the marine examples again and the controversy about 'adaptive' dimethyl sulphide (DMS). LOVELOCK and co-workers suggested that emissions of this gas by various marine algae, especially the abundant bloom-forming microplankton in the unrelated groups Haptophyta and Dinophyta (VAN DEN HOEK et al. 1995), might seed cloud formation on a planetary scale and thus affect world climate (CHARLSON et al. 1987). Correlations between marine DMS emissions and the concentration of cloud condensation nuclei (CCN) over parts of the South Atlantic and the Southern Ocean support the first part of this proposal (AYERS & GRAS 1991, ANDREAE et al. 1995). However, fundamental gaps remain in our understanding of this biosphere-climate interaction (ANDREAE & CRUTZEN 1997), not least concerning its biological basis. The precursor to DMS in marine algal cells, dimethylsulphoniopropionate (DMSP), is plausibly evolved as an osmolyte buffering plankton cells against salt concentration changes and sometimes ice damage (VAIRAVAMURTHY et al. 1985, KARSTEN et al. 1996). However, the step of claiming that an initial side effect of DMSP synthesis — namely DMS production — was adaptively seized on in some way to regulate the climate of the planet, is controversial. Indeed in the claim's simplest form a darwinian mechanism for additional expenditure for such an end can be excluded: a benefit that increases the welfare of an entire group considered in isolation does not increase the frequency of a causative element (HALDANE 1932, WRIGHT 1948 [1961 printing], FISHER 1958). Worse, if creating the benefit had a cost, the gene causing the group benefit definitely declines (HAMilton 1963, 1975). We thus need a selection process at a lower level, although not necessarily at that of the individual.

Before DMS emitted by an alga can release the latent heat energy of condensation various processes must occur including sea-air transfer, oxidation to sulphate, nucleation to form aerosol, growth into condensation nuclei (CN) or the larger CCN, and finally advection of these nuclei into supersaturated air (FEVEK et al. 1986). The potential for an alteration of wind speed in the region of the responsible organism seems at first to be small because the oxidation of DMS alone is widely thought to require a period of the order of a day (ANDREAE 1986) and this must be followed by the other processes, estimated to take a total of over 3 days (RAES 1995). During this time an air parcel may typically have travelled hundreds of kilometres. However these figures refer to means and the earliest formation of CCNs could be much sooner. Moreover, much faster routes have been conjectured with a first and highest peak of $\text{H}_2\text{SO}_4$ in only 6 hr (LIN & CHAMEIDES 1993). The simultaneous measurements of ANDREAE et al. (1995) over the tropical South Atlantic show a strong correlation between sea-to-air DMS flux (as also atmospheric DMS concentration) and CN concentration, with over 60% of the variance of CN attributable to the DMS. As mentioned by these authors (and later reiterated by ANDREAE & CRUTZEN 1997), this adds weight to various proposals that DMS oxidation, aerosol formation, and particle growth can sometimes occur much faster than had been assumed. Especially on sunny days with their high midday peak of radicals in the air, just when local convection is strongest, there seems a good chance for some situations in which convection due to algal DMS emissions generate a local increase of wind speed in a matter of hours. If white tops are augmented or initiated by this increase, then the take-off process already described can potentially pay back to a DMS-emitting alga at the individual or clonal patch level of selec-
tion (or to individuals via inclusive fitness) an extra possibility for causative genes to become airborne (Schlichting 1969, Van den Hoek et al. 1995), and to disperse rapidly away (Woodcock 1948, Stevenson & Collier 1962).

**DISPERSAL AND CYCLOMORPHOSIS**

Dispersal is extremely important to life, indeed for self or progeny it can be considered an organism’s third priority after survival and reproduction. It remains a crucial necessity even if growth conditions at the point of landing are never better than at the point of takeoff (Hamilton & May 1977), although if they are sometimes better the incentive is of course all the stronger (Comins et al. 1980). With data on algal relatedness in plankton patches and also on the scale of the biophysical effects, the very adverse calculations presented by Caldeira (1989) referring to adaptive alteration of climate by DMS might be modified to seem much less hostile, at least as applied to adaptive cloud formation of some kind. The selection at the individual or patch level would not be strong (Hamilton 1964, 1975) but assuming several hundred million repetitions (that is counting algal blooms in both spring and autumn) to have occurred since, say, coccolithophores formed chalk in the Cretaceous period (while a still higher figure could be suggested for the dinophytes whose record extends to the Archaean) (Paerl 1988, Van den Hoek et al. 1995), weak positive selection could easily accomplish what is found.

Under such a scenario other facts concerning algal DMS emission fall into line. Various workers have expressed perplexity at the rather low and variable correlations in blooms between DMS production and chlorophyll concentration (Andreae 1986, Leck et al. 1990, Andreae & Crutzen 1997); algae, it seems, are sometimes not forming DMSP or else are storing it. Andreae (1986) in particular has noted the puzzlingly high emissions from tropical oligotrophic seas where there are few algae. The Emiliana huxleyi strain from the Sargasso Sea proves innately a higher DMS producer than strains from temperate seas (Andreae 1986, Wolfe et al. 1997). Algae in such warm sunlit water with low mean wind velocity may have both special needs and extra chances for seeding local convective disturbances. Air samples collected during a cruise in the South Equatorial Current of the Pacific captured nitrate ions and particulate matter believed to be of planktonic origin in much higher concentrations at 1200 and at 1400 than at 1000 hr during the day (Rosinski et al. 1986). This would accord with both a convective dependence on wind and also with possible wind causation. Sulphur compound emissions from the sea were believed (but not tested) to be peaking in parallel. These facts further support the suggestion above of rapid processing of DMS to form CN and CCN. For comparison, similar samples from the same cruise collected in latitudes 40°S and 60°S showed only slight midday nitrate ion increases.

Regarding the combination of bloom formation with the toxicity often accompanying in the set of DMS emitting algae, we note that (i) blooms commonly occur in marine frontal systems where nutrient rich and poor waters mix, conditions encouraging immense multiplication and, probably, clonal patch formation (Pingree et al. 1975), (ii) again given such clonal conditions, which even unicells might be able to recognise (Beale 1990), local resources may be further adaptively exploited through group predation (Burkholder et al. 1992) or dASMmophy (Estep & MacIntyre 1989), thus increasing the chance that a communal emission will be
powerful enough to trigger a dispersal event, (iii) differing temperatures of frontal 
waters may help create local tropospheric quasi-instabilities that will be responsive 
to seeding, (iv) plankton in blooms concentrate especially in the extreme surface 
layers, as appropriate for take-off (Pingree et al. 1975, Fudge 1977, Pærl 1988, 
Malin et al. 1994), (v) as plankton exhaust local nutrients they may switch from 
using nitrogen-based osmolytes to DMSP (Turner et al. 1988, Leck et al. 1990, Liss 
et al. 1994, Macdonald et al. 1996) and thus, via DMS, to the chance to initiate or 
augment convective events. Findings that DMS release greatly increases when phy-
toplankton blooms are ceasing growth (Nguyen et al. 1988, Turner et al. 1988) or 
are being grazed by zooplankton (Dacey & Wakeham 1986, Wolfe et al. 1997) are 
consistent with a dispersal function. In the case of predation the emission increase 
may represent not so much a direct effect of ingestion by zooplankton (Leck et al. 
1990) as an adaptive reaction by the phytoplankton to a perception of predation, 
bacterial attack (Leck et al. 1990, Wolfe et al. 1997), or virus presence (Malin et 
et al. 1994, Bratbak et al. 1995) in their environment, indicating a time ripe for dis-
persal. Many fast-breeding organisms of other habitats use cues of adverse factors 
to initiate production of their defensive, dispersive or resting forms, or to begin 
other facultative changes (e.g. to induce wings in aphids; Dixon 1985). Cyclomor-
phosis induced by predators and grazers is known (Roff 1996) in Insecta (Hershey 
& Dodson 1987), Cirripedia, Cladocera, Rotifera, Bryozoa and in both zoo- (Kuhl-
mann & Heckmann 1985) and phytoplankton (Trainor 1992, Fialkowska & Pajda-
stos 1997). (In phytoplankton successions of morphs or ‘phases’ are indeed gener-
al; Kudo 1966, Van Den Hoek et al. 1995). Predator induced change also occurs in 
higher plants (Gibson et al. 1993). Tests like those used to prove these cases to be 
facultative over a series of generations could demonstrate the suggested chemical 
‘cyclomorphosis’ of phytoplankton, or at least show individual changes in DMS pro-
duction. If aggregations are largely clonal, selection of altruistic DMS-specialising 
morphs are a further possibility. More generally, chemical morph differences do 
indeed sometimes affect chances of microbe take off, as shown by Blanchard & 
Syzdek (1978) with the bacterium Serratia marcescens A red strain was several hun-
dreds times more concentrated in bubble drops due to its higher hydrophobicity 
than a white strain while a pink strain was intermediate. This suggested a single 
compound mediating both effects but instead, in later work, redness and hydropho-
bicity were proved separable and not to depend on the same molecular pathway 
(Barness & Rosenberg 1989, Vanderme et al. 1992). Thus, as in actually more 
likely for the different features of an adaptive morph, they appear to be due to 
some general switch occurring under conditions hostile to growth (Razantsvea et 
al. 1994). On this view the redness (due to the pyrrole, prodigiosin) may, as with 
various other organic pigmentations (Swain 1978, Harborne 1991) be for UV pro-
tection for cells destined for exposure to sunlight. The same explanation for colour 
change might apply to ‘red tide’ blooms generally (Wyatt & Horwood 1973).

At least two of the above characters revealed by bloom-forming algae (toxin 
production and rise to the water surface in suitable weather conditions) apply also 
to blooms of cyanophytes. Procaroytes of this group seem to be fairly common in 
spora over land (Brown et al. 1964, Schlichting 1969), but, rather surprisingly not 
over the sea. Although on the whole rather few have yet been tested (Maki et al. 
seem to show little production of CN-potentiating sulphur compounds (Bechard & 
Rayburn 1979, Richard et al. 1996). However, a set of freshwater species belonging 
to genera well-known in the aerial spora (Schlichting 1969) are indeed producers
(JENKINS et al. 1967, BECHARD & RAYBURN 1979). Generally it further fits to our theme that small ('ultra-') plankton, including seemingly some cyanobacteria, are greater DMS emitters than large plankton. Thus the highest DMSP concentrations recorded for dinophytes in the list of KELLER et al. (1989) come from small species (in Amphidinium and Pro-rocentrum) and the two most negligible concentrations are from two large species (in Ceratium and Pyrocystis). With < 50 µm and > 100 µm given respectively for maximum dimensions in these two pairs (KUDO 1966), the two former genera provide subjects obviously more suited for lofting in bubble droplets (BLANCHARD 1983).

TERRESTRIAL CLOUD FORMATION, ICE NUCLEATION AND DESCENT

Little evidence exists for important natural sulphur emissions over land and fresh water apart from that just mentioned for some cyanobacteria (JENKINS et al. 1967, BECHARD & RAYBURN 1979). Sulphur on land is generally scarcer and in any case DMSP as an osmolyte must be relatively unneeded except possibly in salty habitats (DACEY et al. 1987). However, a rapidly expanding theme of terrestrial microbiology, ice-nucleation (IN) (WOLBER 1993, WARRREN 1994, SZYRMER & ZAWADZKI 1997) suggests alternative adaptations for cloud transport and especially for its termination (SNIDER et al. 1985). Although IN and CN properties sometimes coexist in the same organisms (SNIDER et al. 1985), ice nucleation is usually more important as the trigger for precipitation than for forming clouds. This is because the minute water droplets in cloud grow too slowly by aggregation to form rain. However, if seeded by minute ice crystals (or particles capable of initiating them), the disparity of the equilibrium vapour pressures of ice and water causes the ice crystals to grow rapidly at the expense of evaporation of neighbouring cloud droplets. The resulting crystals soon achieve substantial fall rates and then accrete more droplets by collision. If at lower altitudes ice crystals melt, their fall and further enlargement continues as rain.

Spora may often be in danger of remaining airborne too long and consequently being damaged by radiation and freeze drying (SNIDER et al. 1985). The danger will be most acute for very small organisms like bacteria. Although some spora collected at 48-77 km altitude by the Russian rocket were still alive (IMSHENETSKY et al. 1978) germination percentage generally falls with altitude of collection (GREGORY 1967). Thus the smaller the species, the greater is its likely advantage from CC and IN abilities. Most recent research on biogenic ice nucleation refers to a few species in three genera of bacteria (Pseudomonas, Xanthomonas, and Erwinia) with the first and last presenting CC ability too (SNIDER et al. 1985). However, a few species (both saprophytic and pathogenic) in the hypomycete fungal form genera Fusarium (POULEUR et al. 1992, RICHARD et al. 1996) and Penicillium (JAYAWEERA & FLANAGAN 1982) have revealed similar ability. The IN temperatures for the best strains of these various cases range up to −2 or −1 °C making them amongst the best IN agents of any kind, organic or inorganic. If IN ability is not adaptive it has to be a very unusual chance coincidence that all five last-mentioned genera are well known in high air spora (GREGORY 1967). Their IN (JAYAWEERA & FLANAGAN 1982, SCHNELL 1982, BAKER 1997) and in some cases CN (SNIDER et al. 1985) properties, presumed to be maintained during transport, have already been speculated to be important in causing rain or snow; protection during flight and return to earth
have been adaptive riders to the suggestion (Snider et al. 1985). However, as with DMSP in the sea, there is a more individualistic explanation for IN in these terrestrial examples than through events in the troposphere. All five of the mentioned genera are also known (through at least some members) as blight, fungal-spot and superficial root-rot pathogens on plants. When these species attack living plant surfaces, a means of initiating frost damage at high sub-zero temperatures may aid subsequent exploitation. In the high aerial stages too the case for immediate benefit is stronger and more 'individual' than it is for DMSP because the ice-nucleation is by molecules seemingly inseparable from the cell surface, perhaps even facultatively exposed there (Caple et al. 1986). (DNA sequence analysis suggests that in the bacteria the proteinaceous IN products derive from a single origin [Wolber 1993] but the compounds used by Fusarium appear to be different [Hasegawa et al. 1994]). Each cell possessing IN molecules could help itself, first (if in a frost-prone situation) to obtain nutrients and grow on its plant; second (especially where cloud seeding may occur direct into the ice phase) to gain a cloud-cover when dispersing; and, third, to be rained, snowed or hailed back to earth (Schnell & Vali 1972, 1975; Mandrioli et al. 1973; Snider et al. 1985; Baker 1997), where, fourth, it is likely to encounter suitably damp and rain-cleared leaf habitat on which to grow (Lindemann & Upper 1985).  

Ice-nucleating bacteria are also present in the sea, often mixed with DMSP emitting algae (Schnell & Vali 1975, 1976; Schnell 1982; Fall & Schnell 1985). Algae from an inshore bloom were particularly effective ice-nucleators (Schnell & Vali 1976), perhaps suggesting bacteria originating from land (Fall & Schnell 1985). In summary, putting together terrestrial and marine data, many but not all hints in the literature support a hypothesis that biogenic IN can adaptively aid aerial transport and descent of spora. More speculatively, the highly variable and possibly facultative expressions of CCN and IN abilities of spora (Caple et al. 1986) (which, in fact, for IN abilities of leaf-surface bacteria is observed changeable over a period a few hours [Hirano & Upper 1989]), may be connected with the puzzle that the ascending columns that form cumulus "... do not, always, have a fixed source at the ground, but must often carry their energy supply with them as they move" (Malkus 1949); that energy supply might be latent heat of water phase change facultatively released by microbes.  

So far Cladosporium, the terrestrial genus whose spores are usually most common in collections over both land and sea (Pady & Kapica 1955, Gregory 1967, Mandrioli et al. 1973, Jayaweera & Flanagan 1982, Hjelmroos 1993) have only revealed a rather marginal IN ability (Jayaweera & Flanagan 1982) while the next most common genus, Alternaria, has not yet shown any. However it is not clear that tests have yet been done on conidiospores rather than on vegetative mycelium. Perhaps significantly, IN ability was noted rising in older cultures of Fusarium (Pouleur et al. 1992, Richard et al. 1996), and also was only found weakly in one replicate of one sample of some tropical isolates tested (Richard et al. 1996). Since the mainly saprophytic forms such as C. herbarum (anamorph of Mycosphaerella tassiana, a common secondary agent of leaf decay, and the most commonly reported species in spora) might gain no advantage from ice-nucleating in already dead leaves, it is important to test spores directly.  

Back at earth level and once again considering take off, we note that many observations suggest moulds and fungal pathogens of genera found in the tropospheric spora release spores just when thermals are likely (Schlichting 1964, Pady 1971, Li & Kendrick 1994). Trees appear the most typical sources and even at herb
level, sporulation in a 'canopy' is reported best for take off (LINDEMANN et al. 1982). The situation for bacteria may be similar (SCHNELL & VALI 1972, GROSS et al. 1983, LINDEMANN & UPPER 1985, HIRANO & UPPER 1989); some, together with yeasts, seem to favour and perhaps cause foggy conditions. This may give low-level dispersal directly (FUZZI et al. 1997) or, in the case of nocturnal and morning radiation mists, it may hold spora in readiness for more distant convective dispersal later in the day (LINDEMANN et al. 1982, FUZZI et al. 1997).

CO-DISPERSAL

So far we have related facts relevant to both individual and group dispersal strategies within a species. Polymorphism suggesting either individual facultative changes, altruism or parasitic adaptation is indicated by bacterial species having IN ability only in a small minority of the individuals in cultures (MAKI et al. 1974, HIRANO et al. 1978, LINDOW et al. 1982). In such diffuse dispersal enterprises as we are suggesting much literal 'free-riding' is unavoidable. Physical linkage to co-clonal cells is a dubious way to combat a 'parasite load' in passively wind-dispersed organisms because of the increased settling rate of larger units, but one haptophyte alga, Phaeocystis pouchetii, best known of all plankton for its DMS production, has a special bloom phase where it is colonial in a gelatinous and often foamy matrix. This phase seems well adapted to blow low across the often windy oceans were it occurs and it certainly does so (LISS et al. 1994, VAN DEN HOEK et al. 1995). In conditions appropriate to our theory many algae form slime (JENKINSON 1986). Some eukaryotes like P. pouchetii as well as some cyanobacteria form gelatinous colonies and of these some (e.g. diatoms, WILSON 1967) are known to increase foam. Suspicion of similar causes extends to oceanic foam generally (WILSON 1959). Marine wet aerosols blowing on land may contain higher plankton biomass than the surface water from which they derive (DEAN 1963).

More interesting, however, is to consider whether several species might contribute in different roles to an event of convective dispersal. Thus, in the mixtures of algae and proaryotes in the sea which SCHNELL & VALI (1975) have documented, we might imagine the microalgae providing the winds and the accompanying IN bacteria travelling with them providing the ice nuclei that get the team back to the sea after dispersal. This sets up an unlikely but not impossible scenario, its key necessity being that the mixed-species 'team' normally remains together throughout the journey. The reason is best seen by looking at alternatives. If due to differential settling by size, two species that were emitted together by a patch tend to land separately, then DMS-emitting algae will often have lofted bacteria that fail to assist the return by rain, indeed which abandon them to slowly lose even their own within-species correlation. Likewise good IN genotypes of bacteria will often be rained into the sea along with algae that had not been good lofters and who will not serve them in the next dispersal episode (in the case of our conjecture for DMS, sites a little downwind of an actively emitting patch are presumably best for take off). Because we are proposing team relations in an assemblage each member of which relies on propagule smallness for dispersal, multi-species parcels are unlikely. Thus in spite of the existence of some correlations of dispersing types in spora, as in some algal assemblages (ROSAS et al. 1989, ROY-OCTLA & CARRERA 1993) and also the very common Cladosporium-Alternaria combination, the prospect for evolving close interspecies cooperation seems generally poor.
Clear evolutionary achievements of attached dispersal, like that shown in lichen soredia and thallus fragments, which certainly can be distantly airborne (Gregory 1967, Hamata & Olech 1991), are rare. The general problem is similar to that of rationalising adaptive mutualism in the 'team' of Sphagnum species that build raised oligotrophic bogs; but whereas in the case of bogs we might invoke accidental carriage and co-planting of compatible spores on feet of moorland birds, a similar carriage of plankton by sea birds simply replaces the need for any 'team' to fly at all. The notion of a reciprocatory team (Axelrod & Hamilton 1981; Queller 1992; Frank 1994, 1995, 1997a) becomes vastly more plausible if physical linkage of the mutualists is guaranteed (Hamilton 1987, Frank 1997a). This happens most definitely when the larger party enwraps the smaller within itself. The varied affinities of the 'chloroplasts' of phytoplankton are relevant here. Some indeed seem to show cellular associations still changing at the present time (e.g. in Peridinium, Van Den Hoek et al. 1995) although the relevance of the intracellular combinations here to any issues of wind and cloud is, of course, quite unknown. However, strong ice-nucleating abilities are known in lichens (Pouleur et al. 1992, Ashworth & Kieft 1995, Richard et al. 1996, Worland et al. 1996), and it should be investigated whether this extends to their soredia. Following recent work by Queller (1992) and Frank (1994, 1995, 1997a, 1997b, 1998a, 1998b), we see the key to behaviour in such potential interspecies teams in regression predictors of allospecific social phenotypes by actor's genotype (or more precisely, by actor's breeding value; Frank 1998a); these regressions being evaluated for the associations as they occur in nature. Non-randomness in associations will be normally due to relatedness but there are other possibilities (Wilson & Dugatkin 1997). In effect we need to know how the social goods and ills dispensed by an individual are 'paid back' to causative genes by the system into which they are sent. Hence the first step in making a case for 'teams' will be to show that associations of genotypes both within and between species are non-random in appropriate ways.

Fred Campbell Meier: History and Conclusion

The idea of precipitation adaptively aiding return of spora to earth is more than 10 years old (Snyder et al. 1985), whilst the broader but not specifically evolutionary idea of bubble processes in marine whitecaps lofting living and other particles into the troposphere, where they may affect earth climate, traces back at least to the '50s (Woodcock 1957). These allusions are brief, however, and neither topic central to the paper in which it appears. This is also true of an enigmatic briefer and earlier comment that may refer to self-assisted microbial dispersal by wind and cloud. The comment is due to F.C. Meier (1936), pioneer in the study of high air spora and originator of the term 'aerobiology', who died in his forties when the plane provided for his research was lost in the Pacific Ocean in 1938 (Haskell & Barss 1939). Little other than brief summaries of the late aerobiological phase of his work have been published, but in one abstract outlining some collecting flights over the Caribbean, following a comment on clearance of air spora by rain below cloud level, Meier states: "... viable spores taken from air currents above the clouds show that dissemination of certain fungi may occur regardless of and ultimately aided by rainfall at lower levels" (OUR ITALICS) (Meier 1936). Does he imply here the energising of lofting through water condensation or more simply that rain is likely
to be the eventual agent of a safe return of spora to the earth? Whichever, the rain, ice or thermals affecting his own aircraft may have been disastrous for Meier himself and those who flew with him. During his last collecting flight on the 23rd of July 1938 the final message of the radio operator defined the dense cumulus and strato-cumulus clouds into which they were flying at 9100 ft, proceeding from San Francisco towards the equator; last words of all expressed the operator’s slight concern with a problem of “rain static”.

It is a long leap from Meier’s probably fatal clouds and from ours to planetary stability. While all facts and arguments we have brought forward remain far below that level, the potential for impact on the global system of the adaptations we have conjectured is vast. The mechanisms we describe do not directly bring us any nearer to discovering why life influences that are stabilising to the planet should be more common than destabilising ones (Hamilton 1995, 1996) and actually the slant even of the present case is somewhat equivocal (Lovelock & Kump 1994, Andreae & Crutzen 1997). But a proof that large side effects, stabilising or not, can arise from activities that are adaptive, either at patch or individual level, for thoughtless aerial and marine plankton, strengthening the expectation of large influences from similar unpromising systems (Lenton 1997), can perhaps help clear a path towards a principled theory.

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REFERENCES


Sporas and Gaia: how microbes fly with their clouds