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Growth Form and Reproductive Character of Lichens near Active Fumaroles in Japan

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Abstract

Total cover of lichens was determined at intervals across six small-scale geothermal vents in northern Japan and found to be least where soil surface temperature or vascular cover was high or in the direct path of vent gases. Individual lichen species and cover of each were documented in 20 transects across geothermally-created bare areas, some of which were large-scale volcanic features in the Japanese islands of Hokkaido and Kyushu. In many locations, lichens were the macroscopic vegetational components best able to survive near fumaroles, thus demonstrating in these symbiotic forms a superior facility for growing under highly stressed conditions. In total, 39 species of crustose, five fruticose and three foliose lichens were recorded, and on transects where rock substrate was available crustose species were usually established nearer the source of fumarolic gases than macrolichens. Of the 38 crustose species that were apotheciate in at least some quadrats, 22 produced ascospores. Macrolichens in Kyushu transects were sometimes apotheciate under heavily fumigated conditions, while those in Hokkaido rarely produced sexual structures near geothermal vents.

Keywords: lichens, geothermal gases, fumaroles, solfataras, volcanoes, reproduction, growth form

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1. Introduction

Vegetational communities can be severely affected by geothermal activity and, in the most extreme cases, are totally obscured by ash and outpourings of lava. However, when emissions consist primarily of gases, vegetation may persist in a modified form. Under severe growth-limiting conditions lichens are often more successful than higher plants, but little is known of the full range of lichens that survive in highly fumigated natural environments.

Temperatures near vents, or fumaroles, may be high, and soil and air chemistry unusual. Affected soils are often highly acidic, nutrient-poor and toxic (Yoshioka et al., 1965; Poli, 1970; Given, 1980). Emissions vary from one fumarole to another but include H_2O, along with H_2S, SO_2, CO_2, CO and H_2, depending partly on rock formations through which water passes before being vented to the surface. Sites in which gases are sulphurous by nature are often in upslope locations (Brock, 1986), and as H_2S in subterranean streams approaches the surface it is oxidized to elemental S, which is common in soil, or to the gaseous form, SO_2 (Brock, 1986; Cihacek and Bremner, 1993).

Levels of S and other elements in lichens have been correlated with the reciprocal of distance from source of emission (Saeki et al., 1977; Beckett et al., 1982), indicating that such elements originate from the atmosphere. Palomaki et al. (1992) found that, after only a few months in a high S environment, the S content may be as high as in thalli exposed for much longer times. Sensitivity is increased when humidity is high (Holopainen and Kauppi, 1989), so fumarole lichens are particularly vulnerable. Because species richness of lichens decreases near a source of urban pollution (McCune, 1988) and tolerance to atmospheric impurities differs among lichen species (Kozlowski, 1985; Nash, 1988), exposure to fumarolic gases could produce compositional changes in natural communities. Some species may be disadvantaged or eliminated and others favored as a result of competitive release (Lawrey, 1981).

In vented craters, such as that of the Usu volcano in Japan, vascular plants re-establish, but not mosses or lichens (Tsuyusaki, 1987). However, lichens grow in other volcanic areas (e.g., Yoshioka et al., 1965; Tsujimura, 1977; Given, 1980; C.W. Smith, 1981). In vent fields in Iceland, crustose occurrences were reported (Kristinsson, 1972), but most fumarole lichens known previously have been fruticose. *Cladonia crassensis* was present in *Lycopodium* communities (Yoshioka, 1968) near Japanese vents, and Poli (1970) observed fruticose lichens and mosses establishing closer than vascular plants. The ecology of six *Cladonia* species dominating Japanese fumarolic plant communities were investigated by Glime and Iwatsuki (1990), and isozyme differences were noted in *Cladina mitis* thalli growing near a vent in one of these sites (Fahselt, 1992). In Hawaii endemic *Cladonia* and *Cladina* species were the most common lichens near steam vents, while crustose species were of minor importance (Kappen and Smith, 1980; Smith, 1981). Species of *Cladonia, Cladia, Parmotrema* and *Usnea* were prominent in the two bands of vegetation nearest geothermally heated bare ground in New Zealand, but no microlichens were reported (Given, 1980).

Casual observation in volcanic areas of Japan, such as Esan and Showashinzan (Fig. 1), suggested that the absence of microlichens near geothermal vents might be related to lack of microsites suitable for establishment. Thus, one objective of the present study was to document lichen growth forms in volcanic mountains and lower elevation vent fields that were most heavily affected by fumaroles.

A variety of edaphic factors has previously been associated with the survival of vegetational elements near fumaroles and, in the case of terricolous lichens, the importance of soil temperature and pH have been clearly demonstrated (Glime and Iwatsuki, 1990). Because of the unusual chemistry of emissions from most fumaroles, a second objective was to consider lichen presence and cover in relation to the proximity of vents.

Another aspect of fumarole lichens that has been little investigated is their reproductive character. Pollutants such as SO_2 are known to affect reproduction; soredia and isidia may be damaged, and ascospore production and germination may also be reduced (Kofler et al., 1967; Lawrey, 1984; Kiss, 1988; Belandria et al., 1989). Smith (1981) noted that fertility of *Cladonia oceania* declined near active vents, but reproductive possibilities for lichens in natural geothermal environments have otherwise not been assessed. Thus, the last objective was to record the occurrence of reproductive structures on lichens that were subject to intense outgassing from fumaroles.

2. Materials and Methods

Because of the abundance of geothermal features in SE Asia, the study was conducted in Japan. A number of small vents occur near the Atosanupuri volcano, also known as Io-san or Mt. Io, where most of the common lichens belong to the genus *Cladonia* (including *Cladina*) (Glime and Iwatsuki, 1990). Vents in this region produce mostly steam, but also H_2S and CO_2 (Anonymous, 1989), and thus can be termed solfataras. At most fumaroles, the sulphur content was so high that elemental S was evident on the soil surface. Transects were set up across six of these vents.

In the Numayu area, approximately 1 km SW of Io-san, or Mt. Io (Fig. 1), solfataras were largely sheltered from prevailing winds by surrounding vegetation. The dominant vascular species growing near these small

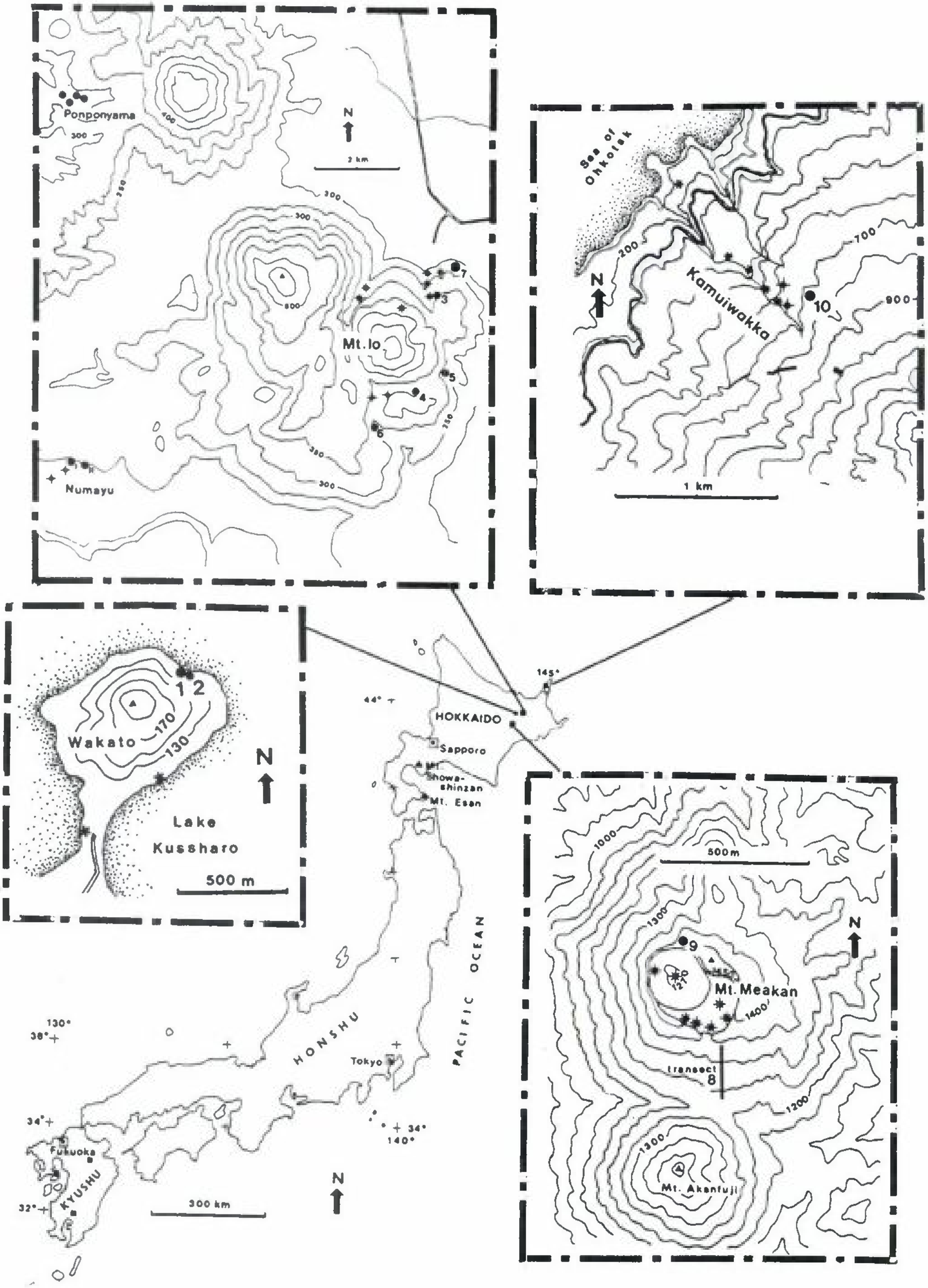

Figure 1. Location of study sites in Hokkaido, Japan. Eight-pointed stars represent large vents, four-pointed stars smaller vents, asterisks show thermal pools, and solid dots are vented areas across which transects were laid. Elevations are in m.

fumaroles was *Pinus pumila,* along with other species including *Pteridium aquilinum* and *Miscanthus chinensis,* and the substrate was of sandy mineral soil. Bare areas surrounding vents were not necessarily centered on the openings because orientation of chimneys affects the direction of delivery, especially in such protected locations. On September 10, 1989, two 6 m transects (i and ii) were centered on separate vents, each deliberately set along the path that vent gases were directed. In each case the line began above the vent in a less affected area of low pine vegetation, crossed the vent itself and extended below the point of gaseous emissions the same distance as above. At 1 m intervals, vascular and total lichen cover were estimated within 20 × 20 cm quadrats, as was cover of litter from dead vasculars. Surface soil temperature and air temperature at a height of 1 m was taken mid-day in cloudy weather, using a digital thermocouple (TC) thermometer (Westcor Inc., Logan, Utah) accurate to 0.1°C. Temperatures were expressed as means of 10 readings acquired in a rotational fashion within a one hr period.

In a geothermal area named Ponponyama about 2 km NW of Io-san (Fig. 1) numerous smaller valley vents were located in the midst of prairie-like vegetation primarily of herbs and grasses, e.g., *Miscanthus chinensis, Panicum bisulcatum, Hypericum erectum* and *Carex oxyandra,* all surrounded by forest dominated by *Quercus mongolica.* At many vents in this somewhat moister location lichens and mosses both occurred nearer to vents than vascular species. Cover values for lichens were estimated in quadrats placed at 1 m intervals across four vents, each transect oriented along the direction of gas dispersal. The mineral soils were fine-textured and soil surface temperature was measured in each quadrat, as at Numayu, and the correlation between soil temperature and lichen cover determined. Temperature and cover were thus recorded in a total of 42 quadrats in the Io-san area.

Subsequently, on 20 other transects situated in both northern and southern Japan, the full range of lichen species capable of persisting in geothermal areas was determined (Table 1); 10 transects were in the northernmost main island, Hokkaido (43–45°N) (Fig. 1) and 10 in the southern island of Kyushu (31–33°N) (Fig. 2). Several of these were across large scale or higher altitude volcanic sites, and most had rocks or boulders present, as well as soil, to provide establishment possibilities for both saxicolous and terricolous species. The chemical composition of gases emitted from only some of the vents was known, but it was clear from the yellow deposits of elemental S, which were evident near fumarolic openings in all sites but one, that emissions were sulphurous. The vent with no visible S, Io-san III, was about 300 m from others that showed strong S deposits and in a general area where sulphurous gases had been documented.

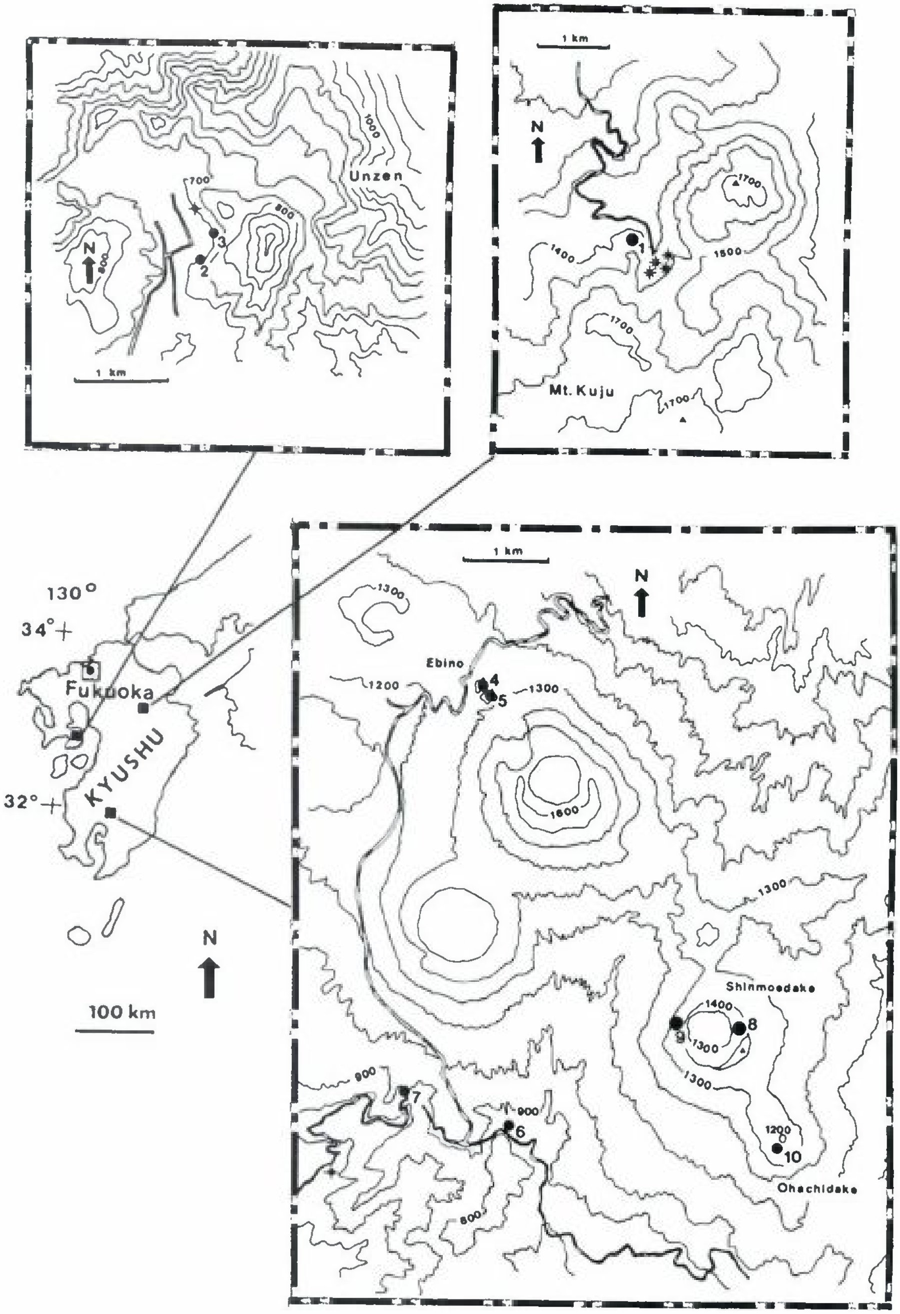

Figure 2. Location of study sites in Kyushu, Japan. Eight-pointed stars represent large vents, four-pointed stars smaller vents and solid dots are vented areas across which transects were laid. Elevations are in m.

Table 1 Locations, elevations and lengths of transects across geothermally active areas in Japan

Sites		Co-ordinates	Elevation, m	Length, m
Hokkaido				
1	Wakoto I	43°35'N, 144°19'E	110–120	18
2	Wakoto II	43°35'N, 144°19'E	110–115	9
3	Mt. Io I	43°35'N, 144°25'E	290	5
4	Mt. Io II	43°35'N, 144°25'E	330	70
5	Mt. Io III	43°35'N, 144°25'E	290	24
6	Mt. Io IV	43°35'N, 144°25'E	290	10
7	Mt. Io V	43°35'N, 144°25'E	220–230	95
8	Meakan S	43°21'N, 144°1'E	1,225–1,350	250
9	Meakan N	43°21'N, 144°0'E	1,415–1,425	25
10	Kamuiwakka	44°6'N, 145°2'E	740	35
Kyushu				
1	Mt. Kuju	33°6'N, 131°17'E	1,400–1,500	180
2	Unzen I	32°45'N, 130°8'E	700	4
3	Unzen II	32°45'N, 130°8'E	740	7
4	Ebino I	31°57'N, 130°51'E	1,280	17
5	Ebino II	31°57'N, 130°51'E	1,280	14
6	Shinyu	31°54'N, 130°51'E	840–860	18
7	Miyoban	31°54'N, 130°51'E	880–890	26
8	Shinmoedake I	31°54'N, 130°53'E	1,310–1,400	180
9	Shinmoedake II	31°54'N, 130°53'E	1,300–1,340	55
10	Ohachidake	31°53'N, 130°55'E	1,220–1,230	18

In the case of large or particularly active geothermal features, e.g., volcanoes, it was impossible and pointless to run transects through actual vents, so the initial quadrat was placed at the point where macroscopic life was first evident and the transect was extended radially toward an area of less intensive fumes. Miyoban was an exception, in that the transect did not progress steadily from a more to less exposed area because the vent field had solfataras scattered throughout. Wakoto I and Io-san V also differed somewhat, in that the substrate in both locations included vascular litter and humus, elements that were essentially lacking in other locations.

Between September 1989 and December 1989, records of occurrence of lichen species, estimated cover of each and presence of fruiting bodies were made in 20 × 20 cm quadrats along each of the 20 transects; the total length (3.5 to 250 m) and the interval between successive quadrats (consistently 0.5, 1, 2, 5, 10 or 20 m along any one line) were determined by the scale of outgassing. The positions on a transect where mosses and vasculars occurred nearest the vent were also noted.

If a quadrat at one interval included no lichens, it was moved to the closest lichenized rock surface, if such was, a) no further away than half the between-point distance and, b) measured 50 cm or more in at least one dimension. To ensure that fumarole-tolerant lichens would be properly identified, the specimens collected were the best available within an affected area, rather than larger, more well-developed and similar specimens from outside. In each site at least one collection was made of every apparently different lichen, and initially a provisional code name was used for each.

All microlichens were identified by M. Inoue of Akita University, who also distinguished among unidentified crustose forms that differed from one another. Macrolichens were determined by H. Kashiwadani of the National Science Museum, Tokyo, and K. Yoshida of the Saitama Museum of Natural History, Chichibu, Japan. Vouchers of macrolichens were retained at the University of Western Ontario, and crustose specimens were deposited in the lichen herbarium at Akita University, Japan.

3. Results

At Numayu, air temperatures over the relatively small vents were the same as near transect ends (Figs. 3 and 4). Temperatures at the surface of the soil varied, but the quadrat located at the point of emission was not necessarily hottest. Cover of vascular plants, mainly pine, was 95–100% at a distance of 3 m above vents, but dropped in the next two quadrats, both of which contained considerable litter of higher plants. In above-vent quadrats where cover of pine and other plants was low, terricolous lichens were well-represented. However, neither vasculars nor lichens occurred at the fumarole itself, a condition which persisted to 3 m below.

On Ponponyama transects, lichen cover was lowest in quadrats at the vents and the next immediately below (Fig. 5). However, establishment was more successful at 2 or 3 m below the opening. Soil surface temperature varied across the bare areas, but as at Numayu the highest readings were not always closest to a fumarole. A plot of lichen cover in both areas against mean soil surface temperature is shown in Fig. 6, and little correlation was found between them ($R^2 = 0.026$). Although the few quadrats with high temperatures supported no lichen growth, some of those with normal temperatures also had none. The highest values of lichen cover were either above vents or well below (at a distance of 3 m), and the lowest cover was at the vent itself or 1 m below. Of

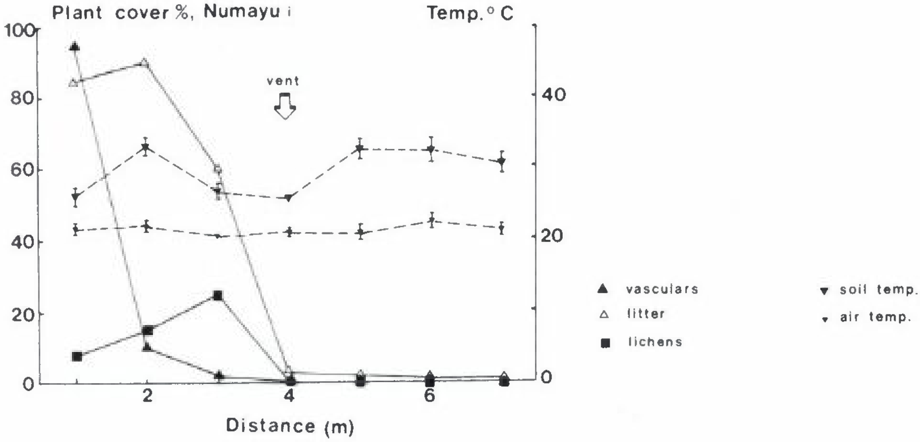

Figure 3. A plot of temperature and plant cover across solfatara **i** at Numayu, Japan. The vent is located centrally on the transect and gases are oriented toward the right.

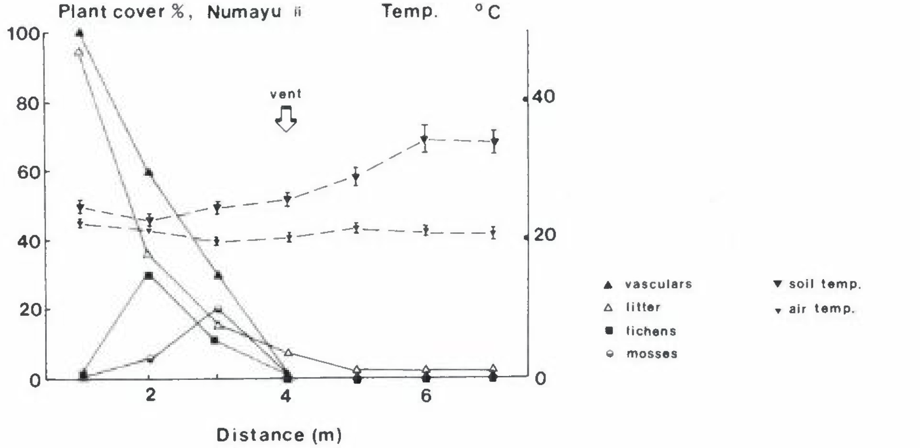

Figure 4. A plot of temperature and plant cover across solfatara **ii** at Numayu, Japan. The vent is located centrally on the transect and gases are oriented toward the right.

the quadrats above the vent, those dominated by vascular plants exhibited lowest cover of lichens.

The full complement of lichen species persisting near fumaroles along the 20 remaining transects is shown in Tables 2 and 3. Low frequency values reflect the poorly developed lichen communities of vent fields. The practice of taking lichen records on off-line rocks produced higher cover values estimates than if only quadrats set on the transect itself were considered, and it also increased the number of recorded lichen occurrences.

Table 2 Lichen frequencies (quadrats where present/total quadrats) in transects across Hokkaido fumaroles[1]

Lichen	Sites									
	1	2	3	4	5	6	7	8	9	10
Crustose species										
Acarospora asahinae H. Magn.		0.3						<0.1		0.4
Acarospora fuscata (Schrader) Th. Fr.						0.1°	0.1^{-}			
Aspicilia gibbosa (Ach.) Korb.								0.3		
Bacidia sp. 2		0.3								
Bacidia sp. 3		0.1								
Buellia cf. *aethalea* (Ach.) Th. Fr.								0.3	0.7	
Buellia indissimilis (Nyl.) B. de Lesd.										0.1°
Fuscidea submollis M. Inoue										0.4
Lecanora polytropa (Hoffm.) Mass.								0.2	0.5	0.8
Lecanora sp. 1		0.1	0.2		0.2	0.2			1.0	
Lecanora sp. 2								0.2°	0.5	
Lecanora sp. 3								<0.1		
Lecidea plana (Lahm.) Nyl.										0.3
Micarea botryoides (Nyl.) Coppins		0.1								
Rhizocarpon badioatrum (Flk.) Th. Fr.			0.1	0.5	0.5	0.6		0.3	1.0	0.8
Crustose sp. A			0.5°	0.3°	0.3°	0.2°	0.2°		0.5°	
Crustose sp. B									1.0°	
Crustose sp. C							0.1°			
Crustose sp. D							0.7^{-}			
Crustose sp. I								0.2°		

Table 2 Continued.

Lichen	Sites 1	2	3	4	5	6	7	8	9	10
Macrolichens										
Cladonia carassensis Vain.	0.1^-									
Cladonia parasitica (Hoffm.) Hoffm.							0.1^-			
Cladonia theiophila Asah.[1]	0.6°	0.4^-	0.2^-		0.1^-		0.4^-			0.6^-
Parmelia fertilis Mull. Arg.	0.1^-									
Parmelia stygia Ach.										0.1^-
Umbilicaria torrefacta (Lightf.) Schrader										0.1^-
Transect descriptors										
Number of quadrats	10	10	6	15	13	11	20	26	6	8
Total species	3	6	4	2	4	4	6	8	7	9
Crustose/macrolichen species	0	5	3	α	3	α	2	α	α	2
Observed crustose occurrences nearer than closest macrolichen	0	0	6	11	10	11	4	37	34	0

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[1] Superscripts: None = Most or all specimens in a stand apotheciate with spores; $^\circ$ = Apothecia in most or all, but no spores seen; $^-$ = Sterile, no apothecia in ≥80% of quadrats.

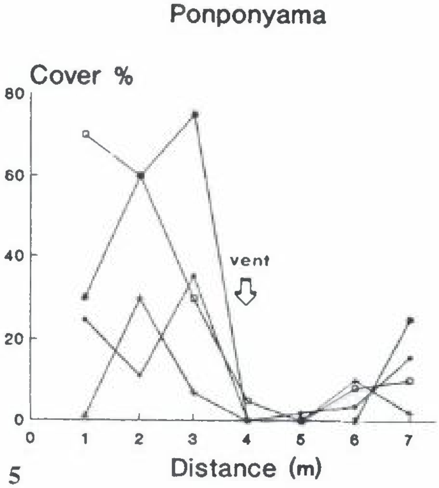
Table 3 Lichen frequencies (quadrats where present/total quadrats) in transects across Kyushu fumaroles[1]

Lichen	Sites									
	1	2	3	4	5	6	7	8	9	10
Crustose species										
Acarospora sp.		0.1	0.6	0.1	0.4	0.7	0.2	0.5	0.5	0.3
Bacidia sp. 1										0.4°
Bacidia sp. 4	0.8			0.8						
Buellia subdisciformis (Leight.) Vain.						0.3				
Fuscidea cricumflexa (Nyl.) V. Wirth & Vezda				0.7						
Fuscidea mollis (Wahlenb. V. Wirth & Vezda)		0.6				0.4	0.5^{-}			0.1°
Fuscidea submollis M. Inoue	0.6									
Huilia chungii (Zahlb.) M. Inoue		0.1			0.3		0.3	0.6		1.0
Micarea sp.	0.5									
Phyllopsora sp.							0.1°	0.4°		
Rhizocarpon cf. *polycarpon* (Hepp.) Th. Fr.					0.6			0.1		
Schaereria cinereorufa (Schaer.)	0.1									
Crustose sp. F						0.2°				
Crustose sp. G	0.1°									
Crustose sp. H		0.1^{-}	0.1							0.3^{-}
Crustose sp. J	0.1°					0.8°				
Crustose sp. K	0.3°									
Crustose sp. L	0.4°									
Crustose sp. M	0.5°			0.1°	0.1°					
Crustose sp. N							0.4^{-}			

Table 3 Continued.

Lichen	Sites 1	2	3	4	5	6	7	8	9	10
Macrolichens										
Cladonia pseduomacilenta Asah.				0.1°	0.1^{-}	0.1^{-}	0.4	0.1^{-}		0.6
Cladonia theiophila Asah.		0.3°					0.2^{-}			
Stereocaulon vesuvianum var. *nodosum* (Wallb.) Lamb								0.4		0.7
Transect descriptors										
Number of quadrats	10	9	8	18	15	10	14	12	19	7
Total species	9	5	2	5	5	6	7	6	1	7
Crustose/macrolichen species	α	4	α	4	4	5	2.5	3	α	2.5
Observed crustose occurrences closer than nearest macrolichen	34	4	6	26	15	21	0	1	9	0

[1] Superscripts: None = Most specimens in a stand apotheciate with spores; $^{\circ}$ = Apothecia present, but no spores seen; $^{-}$ = Sterile, no apothecia



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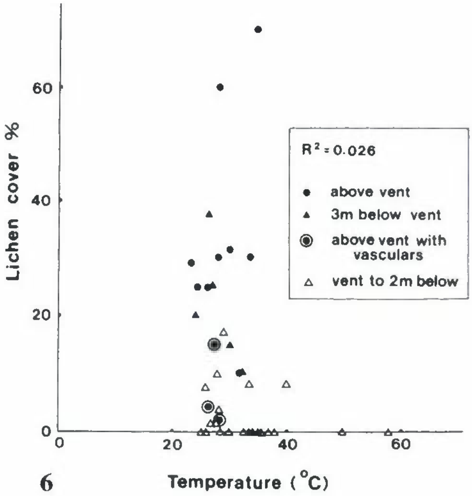

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Figure 5. A plot of lichen cover against distance along transects across four small vents at Ponponyama, Hokkaido, Japan. The direction of gas movement is toward the right.

Figure 6. A plot of temperature against lichen cover in quadrats near fumaroles in the Io-san area of Hokkaido, Japan.

Identification was sometimes difficult because in the most exposed quadrats individual thalli were small, some were sterile, and crustose specimens were prone to fragmentation during removal from rocks; 13 could not be identified and 10 were assignable only to genus. In all, 26 species of lichens were found along Hokkaido transects (Table 2), and 23 were encountered in Kyushu (Table 3). Only one crustose species, *Fuscidea submollis,* and one fruticose lichen, *Cladonia theiophila,* occurred in both islands. The species most commonly found in Hokkaido transects were *Rhizocarpon badioatrum, Cladonia theiophila* and an unidentified crustose lichen. In Kyushu, a species of *Acarospora* that may be new for Japan occurred in all transects but one and *Cladonia pseudomacilenta* was the next most constant. *Stereocaulon vesuvianum* var. *nodosum* occurred on two transects, but no cephalodia were found on the specimens. Nine was the maximum number of lichens recorded in one site, and one was the least, the total number depending partly on the length of the transect and presumably also on conditions in the site.

Mosses appeared in closer proximity to the source of gases than lichens in one of the sites, Wakato I. On another transect, Meakan N, mosses and lichens occurred together in the quadrat that was nearest vents. Lichens and vascular plants first appeared together at the same position on five transects: Wakato II, Mt. Kuju, Unzen II, Shinmoedake and Ohachidake. On the remaining 13 transects, or well over half, lichens occurred closer to the point of emission than any other macroscopic lifeform.

Lichen growth forms

Macrolichens and microlichens often occurred together in study areas, the former on soil and litter as well as rocks and the latter on rock and boulder substrates. In total, six macrolichens were found in Hokkaido and three in Kyushu, while 20 crustose taxa were recorded from each. The largest number of macrolichens in one site was three, though one or none was more common. At Wakoto I there were only macrolichens and no crustose records, but on five other transects in Hokkaido that included rock as available substrate only crustose species were encountered. There were commonly two to five times more crustose occurrences than macrolichens within any one transect (Tables 2 and 3). Furthermore, there were usually a considerable number of crustose records closer to vents than the nearest macrolichen (Tables 2 and 3). On most transects, the estimated lichen cover was lower in more heavily fumigated zones near fumaroles, although at Kamuiwakka this trend was less evident (Table 4).

Table 4 Lichen cover (%) along a transect laid from vent at 740 m elevation at Kamuiwakka, Hokkaido, Japan[1]

Lichen	Distance from vent (m)							
	25	30	35	40	45	50	55	60
Rhizocarpon badioatrum	1*	5	3		1	3	5	
Cladonia theiophila	4	5		2	6	4*		
Lecanora polytropa	2	t	5*		1	2	2	
Fuscidea submollis	t*	t					2	
Lecidea plana		t*			t			
Buellia indissimilis					t*			
Acarospora asahinae				1*			1	1
Parmelia stygia			1					
Umbilicara torrefacta			1					

1* = The apotheciate specimen of a given species that was closest to the source of gases; those more distant were also apotheciate.

Reproductive aspects

Thirteen species of crustose lichens with both apothecia and spores were found in study sites in Hokkaido (Table 2) and 10 in Kyushu (Table 3). Apothecia were often noted, even in specimens near vents, but for 17 of the crustose taxa, spores were never found. Macrolichens generally had fruiting bodies without ascospores or no apothecia at all, although *Stereocaulon vesuvianum* var. *nodosum* possessed sporulating ascocarps at both sites where it occurred. Apothecia were sometimes lacking in specimens closest to the source of gases, but present in the same species somewhat further away (e.g., Table 4).

4. Discussion

Plant communities near both large and small vents were obviously different from surrounding areas in spite of similar topography, altitude and directional exposure. Vegetation affected by solfataras was sparce and the stature of woody plants greatly reduced. Although there were a few species of higher plants that became more prominent near vents, most were totally eliminated, and in alpine locations the tree line was visibly lowered. Such effects must be primarily due to gases that are distributed by diffusion and air currents, rather than to high soil temperatures that reflect the position of conduits underground and often are quite localized. Gas plumes can be enormous, particularly those from volcanoes, and can be seen enshrouding areas that are far down the prevailing winds. Of course when winds shift, fumes temporarily envelop other areas. The surrounding vegetation is frequently subjected to gases, but at any appreciable distance from fumaroles there would seldom or never be geothermally heated soils.

Mt. Meakan is a location at which gases are monitored periodically and constituents in the plumes, which are often 200 m high, include both H_2S and SO_2, as well as CO_2 and steam (Anonymous, 1988). In Hokkaido low winds come primarily from the S during half of the year and stronger ones blow from the NNW in the other months (Espenshade et al., 1990). Annual winds are thus predominantly SSE, and vegetational effects of fumes are correspondingly most pronounced on the south side of Mt. Meakan, as well as on facing slopes of adjacent Akanfuji (Fig. 1). Similar zonation is evident near other active volcanoes.

Opportunities for lichens depend in part on the status of vascular vegetation. Superoptimal temperatures in the rooting zone greatly simplify the structure of vascular communities and, as a result, the representation of fumarole tolerant lichens is enhanced (Glime and Iwatsuki, 1990). Microclimate and substrate availability are both changed drastically when vascular plants are eliminated; epiphytic lichens disappear and terricolous and saxicolous species become more apparent.

The relatively restricted areas of extremely high soil temperature that are associated with large geothermal features do not support growth of lichens.

The observation that lichens were absent on hot soil near small vents, such as those at Ponponyama and Numayu, also supported the idea that survival is precluded by high temperature (Glime and Iwatsuki, 1990). However, distribution of lichen cover in relation to distance from fumaroles showed that exposure to gases was important as well. Cover near vents was characteristically low, thalli were small and in many close quadrats lichens were totally absent. Erosion of lichen mats on the side most exposed to gases, as well as the occurrence of saxicolous thalli mainly on the protected side of boulders, are other observations consistent with the idea that fumarolic emissions are debilitating to lichens.

Near active fumaroles where exposure to toxic gases was most intense, lichens were frequently the only macroscopic form of life. The physiological integration of a lichen photobiont and mycobiont permits survival under various kinds of environmental extremes (Kappen, 1973), such as heat and cold (e.g., A.L. Smith, 1921), drought and nutrient limitations (e.g., D.C. Smith, 1973). Perhaps it facilitates persistence in stressful fumarolic environments, just as it does in deserts (e.g., Marton and Galun, 1981; Büdel, 1990) and severely limiting polar systems (e.g., Kappen, 1985; Inoue, 1989; Maycock and Fahselt, 1992).

Growth forms

At Wakoto II and Kamuiwakka in Hokkaido and in the craters of two neighboring Kyushu volcanoes, Ohachidake and Shinmoedake, *Cladonia* or *Stereocaulon* species were found as close to vents, or nearly as close, as crustose lichens. However, microlichens usually occurred nearer a source of gases than macrolichens or vascular plants. Various aspects of vent chemistry or substrate could be responsible, but more detailed data on a full range of environmental conditions would be needed to explain site-to-site differences in the success of these growth forms. Nevertheless, it appears that substrate dependency may play a role in determining species composition in lichen communities. The presence of organics on the soil surface may have promoted establishment of terricolous lichens at Wakoto II, while the lack of litter and humus may have mitigated against fruticose macrolichens in other sites. Stability could also be required for establishment on soils and lack of this may in some cases have been limiting. Crustose species that are vent-tolerant occur mainly on rocks and boulders, and the ability of many of these lichens to grow in geothermal environments was probably under-estimated in previous studies because the necessary substrates were not available.

It is not clear that one lichen growth form is better adapted to grow in fumarolic environments than another, and it may not be possible to generalize.

However, microlichens, especially endolithic forms, offer less exposed surface area. Certainly crustose species, like fruticose and foliose lichens, can survive near solfataras.

Reproduction

The macrolichens, *Cladonia carassensis, P. fertilis* and *U. torrefacta* do not produce isidia or soredia, and near vents they also developed no apothecia. However, for these species, fragmentation is a possibility. On the other hand, many crustose lichens occurring in stressful fumarolic communities are not inclined to fragment and have no vegetative propagules either. In this regard they are similar to crustose lichens in severe growth-limiting polar regions (Fahselt et al., 1989; Sancho and Valladares, 1993). Because vegetative reproduction was not an option for most fumarolic microlichen species, propagation must be via ascospores and spores must be able to germinate in spite of heavy fumigation.

The viability of spores produced in vent fields was not tested, and it may well have been impaired. Apothecia were certainly produced less frequently near solfataras. Nevertheless, spores could be introduced from more distant populations, a strong possibility because fumarole-tolerant lichens appear to be missing or rare in the more typical vegetational communities adjacent to vent fields. Because sexual lichens establish in geothermally active areas, suitable photobionts must be present in substrates. Microscopic photosynthesizers considered to have originated from airborne sources (Fredriksson, 1982) were documented on the volcanic island of Surtsey, Iceland, shortly after it was first formed. Wind was also the suspected means by which propagules were transported to volcanic areas in the Antarctic (Cameron and Benoit, 1970; Smith, 1984). Colonization in geothermal areas elsewhere is probably accomplished in a similar way. *Cladonia parasitica, C. theiophila* and *Stereocaulon vesuvianum* var. *nodosum* reproduce by soredia, suggesting that these propagules are also functional in vent fields.

Explanations for the observed differences observed between fumarolic lichen species in Hokkaido and Kyushu were not established. Emissions had a sulphurous character in most or all of the study sites, but complete details of gas composition were not investigated. It is possible that aspects of vent chemistry may have differed between these two regions of Japan. Lichen floras probably differ also for climatic reasons, since sampled areas of the two islands are at least 1500 km apart and the Kyushu sites lie approximately 1100 km further south.

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