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Dictyostelid Cellular Slime Molds from Hawai'i[1]

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ABSTRACT: Soil and litter samples, collected from Hawai'i on the islands of Hawai'i, O'ahu, and Kaua'i, were examined for occurrence and distribution of dictyostelid cellular slime molds. In total, 194 samples, from 20 different sites and representing several plant communities, were collected during June 1995 and processed in the laboratory soon thereafter. A total of 10 species and one variety was recovered, seven of which have not been reported previously from Hawai'i. The greatest species richness (seven) and highest densities (up to 63 clones per gram of fresh soil/litter) were found on the island of Hawai'i, with lower values obtained for sites on O'ahu and Kaua'i. It was rare for dictyostelids to be recovered from more than 30% of the samples collected at any given site. A number of sites were characterized by recovery of a single species, and at least one site on each island sampled was devoid of recoverable dictyostelids. Overall, dictyostelid densities were quite low compared with those at other locations in subtropical and temperate regions of the Northern Hemisphere, and the values for species richness are lower than those reported for most neotropical mainland locations. These observations suggest a rather modest dictyostelid community in Hawai'i, at least during the relatively dry period when sampling was carried out. Lack of a windborne dispersal mechanism may be responsible for the limited distribution of dictyostelids in Hawai'i and possibly other island groups that are remote from continental land masses.

DICTYOSTELID CELLULAR SLIME MOLDS are rather ubiquitous components of the soil-litter interface, particularly in tropical, subtropical, and temperate regions (Raper 1984). There are approximately 60 recognized species composing three genera (Hagiwara 1989). Most of the life cycle of a dictyostelid is spent in a unicellular, amoeboid state, with cells feeding upon bacteria, protists, and microfungi. When such food supplies are abundant, slime mold myxamoebae proliferate by mitotic cell division. As the local bacterial food supply becomes relatively depleted, hundreds to thousands of myxamoebae, responding to chemotactic signals, aggregate and collectively differentiate as a stalked fruiting body or sorocarp. The sorocarp consists of vacuolated cells, with cellulosic cell walls, which form a branched or unbranched stipe, with a cluster of spores at each stipe terminus.

Although there are a number of described species that seem to be rather cosmopolitan in distribution, several species of dictyostelids seem to be associated with narrower geographic or edaphic situations. In general, species richness is greatest in the American Tropics, with 35 species recovered from just a small area, near Tikal, in Guatemala (Vadell et al. 1995). Species richness declines with increasing latitude or elevation (Cavender 1973). There are indications that species richness and composition may be correlated with aspects of ecological disturbance and patterns of community succession arising thereafter (Cavender et al. 1993).

There have been few dictyostelids reported in the literature from Hawai'i. In his 1975 monograph on the Mycetozoa, Olive made only passing reference to the occurrence of

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dictyostelids in Hawai'i. Nelson et al. (1967) described one species, *Dictyostelium irregularis,* from an O'ahu collection, but it has not since been reported from Hawai'i or elsewhere. Several persons, during their tenure at the University of Hawai'i at Mānoa, recall the occasional isolation of dictyostelids (G. E. Baker, pers. comm.; H. R. Hohl, pers. comm.; R. D. Goos, pers. comm.), and there are specific citations for a few collections on file in the records of the Department of Botany at the University of Hawai'i at Mānoa. However, these reports have not been recorded in the literature.

Although relatively small in total area and rather distantly isolated from continental land masses, the islands of the Hawaiian archipelago support a diverse assemblage of plant communities resulting from a combination of tropical location, serial volcanic origin, and highly variable topography compared with land area (Armstrong 1973). In addition to remnants of endemic flora and fauna, this island group has experienced the introduction of many alien plants and animals, first by Polynesian Hawaiians and more recently as the result of European rediscovery (Gagné and Cuddihy 1990). Thus, one might expect that such an area would harbor a diverse assemblage of dictyostelids associated with the topological and vegetational diversity and extensive human introduction of biota from elsewhere. However, the geographically isolated nature of the geologically young Hawaiian island group might, conversely, limit dictyostelid exploitation.

We report here the results of a preliminary survey to catalog the occurrence and distribution of dictyostelids from a variety of vegetation associations on three of the larger islands of Hawai'i.

MATERIALS AND METHODS

Samples of soil and litter were collected from several locations that represented a selection of vegetation community types present on three of the larger Hawaiian islands, specifically the island of Hawai'i, which is the largest in area and youngest in geologic history; O'ahu, which is the third largest (after Maui) and most densely populated by humans; and Kaua'i, which is the fourth largest in land area and is geologically the oldest among the larger islands (Table 1).

TABLE 1

PLANT COMMUNITY ASSOCIATIONS IN HAWAI'I (AFTER GAGNÉ AND CUDDIHY [1990]) FROM WHICH SAMPLES FOR ISOLATIONS OF DICTYOSTELIDS WERE COLLECTED

Coastal Mesic Forest, Hala (*Pandanus*): Kalalau Trail, Kaua'i (Q)[a]
Coastal Wet Shrubland, Hau (*Hibiscus*): Kolekole Beach, Hawai'i (C)
Lowland Mesic Shrubland, Guava (*Psidium*), Christmas Berry (*Schinus*), *Eucalyptus:* Kaua'i (P)
Lowland Mesic Forest/Shrubland, Kukui (*Aleurites*), common ironwood (*Casuarina*): Waipi'o Valley, Hawai'i; Sacred Falls, O'ahu, (F; K)
Lowland Mesic Forest, Koa/'Ōhi'a (*Acacia/Metrosideros*): Manukā State Park, Hawai'i (G)
Lowland Mesic Forest, Christmas Berry (*Schinus*): Pu'uomahuka, O'ahu (J)
Lowland Mesic Forest, alien vegetation: Keaīwa Heiau, O'ahu; Wa'ahila State Park, O'ahu (N; M)
Lowland Wet Forest, 'Ōhi'a/Uluhe (*Metrosideros/Dicranopteris*) fern: Maunawili Trail, O'ahu (O)
Lowland Wet Forest, alien wet forest: Mānoa Falls Trail, O'ahu (I)
Montane Mesic Forest, 'Ōhi'a (*Metrosideros*): Kalōpā State Park, Hawai'i (D)
Montane Mesic Forest, Koa/'Ōhi'a (*Acacia/Metrosideros/Sapindus*): Kīpuka Puaulu, Hawai'i; Hawai'i Volcanoes National Park, Hawai'i (A; H)
Montane Mesic Forest, diverse: Kōke'e State Park (Nu'alolo Trail, and Pihea Trail), Kaua'i (R, S)
Montane Mesic Forest, alien vegetation: 'Akaka Falls State Park, Hawai'i (B)
Montane Wet Mixed Community: Alaka'i Swamp Trail, Kaua'i (T)
Montane Wet Forest, 'Ōhi'a/Hāpu'u (*Metrosideros/Cibotium*) tree fern forest: Kīlauea Iki Trail, Hawai'i Volcanoes National Park, Hawai'i (E)
Agricultural mulch pile: Campus of the University of Hawai'i at Mānoa, O'ahu (L)

[a] Letters refer to types of plant communities in Tables 2–4.

The soil/litter samples were processed in the laboratory within 24 hr of collection using methods similar to those of Cavender and Raper (1965). Sterile, distilled water was mixed with 5.0-g samples of fresh soil/litter to create 1:25 soil:water dilutions. A 0.5-ml aliquot (0.02 g soil) of every diluted sample was added to the surface of each of two culture dishes (95-mm diameter) containing a phosphate-buffered, hay infusion agar (filtered, sterile infusion of well-leached hay, 1.5 g/liter KH_2PO_4, 0.62 g/liter $Na_2HPO_4 \cdot 7H_2O$, 15.0 g/liter granulated agar) together with 3–4 drops of a suspension of *Escherichia coli* to serve as a food source. These culture dishes were maintained at 20–23°C, were examined daily with a dissecting microscope for 14 days, and the number and species of dictyostelid fruiting body clonal clusters that appeared were recorded. When necessary, isolates were subcultured for further examination. Spores of representative dictyostelids have been conserved and are available from J.C.L.

RESULTS AND DISCUSSION

In total, 11 different dictyostelids were isolated in this preliminary survey (Tables 2–4). This total includes nine formally described species and one variety, and one species that currently is undescribed. The latter species was isolated from O'ahu (designated as NAH 8) and Kaua'i (designated as KU 14). Several of the species isolated are widespread and common, such as *Dictyostelium brefeldianum* Hagiwara (= *D. mucoroides* Brefeld sensu Norberg [in Hagiwara 1984]) and *Polysphondylium pallidum* Olive. It should be noted that there are currently two recognized concepts of *D. mucoroides*. According to Hagiwara (1984), the original concept of *D. mucoroides*, which was published in 1865, was difficult to understand because the isolates identified as this species exhibited a wide range of morphological variation. It was not until 1959 that Bonner suggested that *D. mucoroides* actually represented a complex of species, from which Norberg, in 1971, was able to recognize six species and one variety (in Hagiwara 1984). Among the species that Norberg recognized in this complex were *D. mucoroides* and *D. sphaerocephalum* (Oud.) Sacch & March. However, Hagiwara (1984) believed that Brefeld's concept of *D. mucoroides* was misinterpreted by Norberg and that the original description was based upon another species, which he formally described as *D. brefeldianum*, and that *D. sphaerocephalum*, a species originally described in 1885, was synonymous with Brefeld's original concept of *D. mucoroides*. Because *D. mucoroides* was the earliest name to be validly published, Hagiwara (1984) selected it as the correct name for this species. However,

TABLE 2

DICTYOSTELIDS RECOVERED FROM THE ISLAND OF HAWAI'I

SPECIES	PLANT COMMUNITIES[a]							
	A	B	C	D	E	F	G	H
Dictyostelium aureo-stipes	X	—	—	X	—	—	—	—
D. gigantium	X	—	—	—	—	—	—	—
D. macrocephalum	—	—	—	—	—	X	—	—
D. brefeldianum (= *D. mucoroides* sensu Norberg)	—	X	—	X	X	—	—	—
D. polycephalum	X	—	X	—	—	—	—	—
D. purpureum	—	X	—	—	—	—	—	—
Polysphondylium pallidum	—	X	—	X	—	X	X	—
Total clones per g	48	63	4	43	8	48	3	0

[a]For descriptions of plant communities see Table 1.

TABLE 3

DICTYOSTELIDS RECOVERED FROM THE ISLAND OF O'AHU

SPECIES OR VARIETY	PLANT COMMUNITIES[a] I	J	K	L	M	N	O
D. brefeldianum (= *D. mucoroides* sensu Norberg)	—	—	X	X	—	X	—
D. mucoroides var. *stoloniferum*	—	—	X	—	—	—	—
D. polycephalum	—	X	—	—	—	—	—
Undescribed *Dictyostelium* (NAH 8)	—	—	—	—	—	—	X
P. pallidum	—	—	—	—	X	X	X
P. violaceum	—	—	—	—	—	—	X
Total clones per g	0	15	9	19	20	10	8

[a] For description of plant communities see Table 1.

TABLE 4

DICTYOSTELIDS RECOVERED FROM THE ISLAND OF KAUA'I

SPECIES	PLANT COMMUNITIES[a] P	Q	R	S	T
D. brefeldianum (= *D. mucoroides* sensu Norberg)	—	—	—	X	—
D. purpureum	X	—	—	—	—
Undescribed *Dictyostelium* (KU 14)	—	X	—	—	—
D. mucoroides sensu Hagiwara (= *D. sphaerocephalum*)	—	—	—	—	X
Polysphondylium pallidum	—	X	X	—	—
Total clones per g	5	7	5	3	73

[a] For description of plant communities see Table 1.

Hagiwara's (1984) concepts have not been universally accepted (e.g., Cavender and Lakhanpal 1986). Thus, we have included both positions in our assignment of identity.

Some species isolated in this study of Hawaiian dictyostelids (e.g., *D. giganteum* Singh, *D. macrocephalum* Hagiwara, Yeh & Chien, and *P. violaceum* Brefeld) were recovered from only a single site. One of the more commonly isolated species in this study, and also one of the few that has been previously reported from Hawai'i, is *D. polycephalum* Raper. This species, with its distinctive pseudoplasmodia and coremiform sorocarps, has a worldwide distribution, but it is relatively uncommon compared with many other species. However, it is fairly common in subtropical and tropical seasonal forest (Cavender and Raper 1968). Recently, *D. polycephalum* has been recovered from the Pacific islands of Guam and Moorea and one of the small outlying islands of the Bahamas (unpubl. data), and Hagiwara (1989) reported this species from Japan, Malaysia, and the Philippines, which suggests a possible correlation to island habitats. No isolates considered to be *D. irregularis* as described from Hawai'i by Nelson et al. (1967) were recovered.

Within the island vegetation types sampled, the greatest species richness and the greatest densities of recovered dictyostelids appear to be from Montane Mesic-Wet and Lowland Mesic communities, particularly those present on the island of Hawai'i.

The overall degree of species richness in Hawai'i is actually relatively high for isolated island situations. However, species richness and densities of dictyostelids on islands closer to the mainland, in tropical and subtropical zones, appear to be more comparable with those of the mainland. Fourteen species were identified by Cavender (1970) from Trinidad and Tobago and from Lambuan, on the island of Panay, in the Philippines; nine species were identified by Cavender (1976). Nevertheless, not all studies support this conclusion. Dogma and Blancaver (1965) recovered only four species from Luzon and Mindanao, and Cavender (1976) recovered six species from Luzon, both in the Philippines. It is, however, uncertain as to how meaningful the number of species are that were recovered by Dogma and Blancaver (1965) because they did not indicate the number of samples that were taken in their study. In the case of secluded islands, fewer species are generally recovered. Only five species of dictyostelids were isolated from New Zealand (unpubl. data), and only three species each were recovered from Guam and Moorea (unpubl. data).

It is interesting that Cavender (1976) reported finding that the same six species of dictyostelids ranked in highest importance in both tropical American and Asian forests. Five of these six species (*D. mucoroides, D. purpureum, D. polycephalum, P. pallidum,* and *P. violaceum*) were recovered from Hawaiian soils sampled in the study reported here. The level of dictyostelid density in the Hawaiian soil and litter sampled is somewhat sparse when compared with that found in many mainland tropical, subtropical, and temperate locations in the Americas. The most obvious explanation for this low density and modest species richness might be associated with the relatively isolated position of the Hawaiian archipelago together with the fact that dictyostelid spores and other propagules are not especially adapted for windborne dispersal (Cavender 1973). The extreme isolation of Hawai'i from the mainland also makes it difficult for propagules of dictyostelids to be dispersed there by known vectors such as songbirds (Suthers 1985) or by other vertebrates (Stephenson and Landolt 1992).

It is certainly possible that further investigation might add to the list of dictyostelid species of Hawai'i, particularly if sampling included a wider range of vegetation types (e.g., subalpine and alpine zones and relict "native" vegetation communities) and collecting on other islands (e.g., Maui and Moloka'i). All isolations in this study were done in June, so sampling at other times of the year may yield additional species at perhaps higher densities.

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