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**PLANT PARASITIC ALGAE (TRENTEPOHLIALES, CHLOROPHYTA)
IN AMERICAN SAMOA**

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ABSTRACT

A survey conducted between June 2000 and May 2002 on the island of Tutuila, American Samoa, recorded filamentous green algae of the order Trentepohliales (Chlorophyta) and their plant hosts. Putative pathogenicity of the parasitic genus *Cephaleuros* and its lichenized state, *Strigula*, was also investigated. Three genera and nine species were identified: *Cephaleuros* (5 spp.), *Phycopeltis* (2 spp.), and *Stomatochroon* (2 spp.). A widely distributed species of *Trentepohlia* was not classified. These algae occurred on 146 plant species and cultivars in 101 genera and 48 families; 90% of the hosts were dicotyledonous plants. *Cephaleuros* spp. have aroused worldwide curiosity, confusion, and concern for over a century. Their hyphae-like filaments, sporangiophores, and associated plant damage have led unsuspecting plant pathologists to misidentify them as fungi while some phycologists question their parasitic ability. Of the five species of *Cephaleuros* identified, *C. virescens* was the most prevalent, followed by *C. parasiticus*. Leaf tissue beneath thalli of *Cephaleuros* spp. on 124 different hosts was dissected with a scalpel and depth of necrosis evaluated using a 4-point scale. No injury was observed beneath thalli on 6% of the hosts, but full-thickness necrosis occurred on leaves of 43% of hosts. Tissue damage beneath non-lichenized *Cephaleuros* thalli was equal to or greater than damage beneath lichenized thalli (*Strigula elegans*). In spite of moderate to severe leaf necrosis caused by *Cephaleuros* spp., damage was usually confined to older leaves near the base of plants. Unhealthy, crowded, poorly maintained plants tended to have the highest percentage of leaf surface area affected by Trentepohliales. At present, parasitic algae are not a problem in American Samoa as few crops are affected and premature leaf abscission or stem dieback rarely occur.

Key words: *Cephaleuros*, Chlorophyta, lichen, *Phycopeltis*, plant parasitic algae, *Stomatochroon*, *Strigula*, *Trentepohlia*, Trentepohliales.

INTRODUCTION

Previous reports of plant-parasitic algae in American Samoa were limited to an unidentified species of *Cephaleuros* Kunze in Fries, 1827, on mango (*Mangifera indica* L.), guava (*Psidium guajava* L.), and avocado (*Persea americana* Mill.) (McKenzie 1996). *Cephaleuros* is a member of the Trentepohliales, a unique order of filamentous green algae (Chlorophyta) that are aerial rather than aquatic, brightly colored by orange carotenoid pigments, and uncommon in appearances and lifestyles. A study of this order was initiated in 2000 based on a grower's anxiety over orange, downy growths covering mango and guava leaves. It was also a response to previous authors who hoped to stimulate continued work on these interesting organisms (Joubert and Rijkenberg 1971), and to document existing species of *Cephaleuros* in the tropics before their hosts and habitats were destroyed by population growth (Chapman and Good 1983). The goal of this project was to increase our knowledge of algae in the Trentepohliales still existing in American Samoa.

At present, the Trentepohliales comprises six genera (Thompson and Wujek 1997). *Cephaleuros* grows beneath the host's cuticle and is considered an obligate epiphyte and occasional parasite by some (Thompson and Wujek 1997) and a plant pathogen by others (Cunningham 1879, Marlatt and Alfieri 1981, Holcomb 1986, Holcomb et al. 1998). *Stomatochroon* Palm, 1934, lives in the substomatal chambers of its host and is described as an "obligate endophyte (parasite)" by Chapman and Good (1983) and a commensal organism by Timpano and Pearlmutter (1983). *Phycopeltis* Millardet, 1870, and *Physolinum* Printz, 1921, are supracuticular epiphytes but may be found on other surfaces under very humid or moist conditions (Thompson and Wujek 1992, Davis and Rands 1993, Rindi and Guiry 2002). The free-living algae *Trentepohlia* Martius, 1817, and *Printzina* Thompson and Wujek, 1992, occur widely on living and nonliving substrates (Chapman 1984, Rindi and Guiry 2002, Thompson and Wujek 1992).

Few plant pathologists have the opportunity to identify plant pathogenic Trentepohliales as causal

agents of disease for several reasons. First, these algae are mainly found in tropical and subtropical climates (Chapman and Good 1983, Thompson and Wujek 1992). Second, though they have a broad host range, their damage is often minimal and the presence of a few small thalli on leaves or stems may go unnoticed (Joubert and Rijkenberg 1971, Holcomb 1986). Finally, algae in this order are sometimes mistaken for fungi due to their filamentous nature and formation of setae, sporangiophores, and zoospores (Cunningham 1879, Singh 1962, Wellman 1965, Chapman 1984, Holcomb and Henk 1984, Reynolds and Dunn 1984). Misidentification is enhanced when fungi invade these algae, forming lichens such as *Strigula* and *Raciborskiella* (Santesson 1952, Joubert and Rijkenberg 1971, Chapman and Good 1983, Thompson and Wujek 1997).

Cephaleuros is the genus commonly linked to plant damage (Joubert and Rijkenberg 1971, Marlatt and Alfieri 1981). Four of the thirteen most damaging species grow intercellularly: *C. biolophus* Thompson and Wujek, *C. minimus* Karsten, *C. parasiticus* Karsten, and *C. pilosa* Thompson and Wujek (Thompson and Wujek 1997). The other nine species, including *C. virescens*, grow beneath the plant's cuticle but above the epidermis and may cause little or no damage to the host. *Stomatochroon* can cause incidental water-soaking of tissues but is not usually considered a plant parasite.

Cephaleuros virescens is the most frequently reported algal pathogen of higher plants worldwide and has the broadest host range (Joubert and Rijkenberg 1971, Marlatt and Alfieri 1981, Chapman and Good 1983, Holcomb 1986, Thompson and Wujek 1997). It usually occurs on the upper leaf surfaces of perennial dicotyledonous plants but its thalli are occasionally found on lower leaf surfaces and on monocots (Joubert and Rijkenberg 1971, Chapman and Good 1983). The roughly circular thalli appear velvety due to setae (sterile hairs) and sporangiophores erupting through the host cuticle. The hematochrome pigments astaxanthin and β -carotene (Thompson and Wujek 1997, Lopez-Bautista et al. 2002) color the

Trentepohliales yellow-green to dark reddish-orange, reportedly due to changes in light, temperature, and available nutrients (Joubert et al. 1975, Lorenz 1999).

The non-intercellular, subcuticular species of *Cephaleuros* may not induce an obvious response on some hosts (Chapman 1984, Thompson and Wujek 1997). On other hosts, however, cell death occurs beneath the algal thallus (Thomas 1913, Joubert and Rijkenberg 1971, Chapman and Good 1983, Holcomb 1986). There may be tissue hyperplasia, with or without the formation of suberin, either below or at the margins of lesions (Joubert and Rijkenberg 1971, Thompson and Wujek 1997). Stem infections have been implicated in twig death and branch dieback (Ruehle 1936, Knorr 1964, Chapman and Good 1983, Holcomb 1986, Holcomb et al. 1998) and algal spots on guava, avocado, and citrus fruits may reduce their marketability (Winston 1938, Ruehle 1941, Joubert and Rijkenberg 1971, Chapman and Good 1983). Reports have described *Cephaleuros* spp. as causal agents of disease for over a century (Cunningham 1879, Ruehle 1936, Winston 1938, Crandall and Davis 1944). Steps to confirm its role as a plant pathogen (Koch's postulates), however, have not been completed. This is probably due to the difficulty in producing zoospores for reinoculation on artificial media (Chapman and Good 1983, Holcomb et al. 1998).

The objectives of this study were to identify existing species of Trentepohliales in American Samoa and record their host range. The emphasis of this report, however, is on *Cephaleuros* spp. and their reputed role as plant pathogens.

MATERIALS AND METHODS

Specimens were collected between June 2000 and May 2002 from a wide range of plant species on Tutuila, main island of the U.S. Territory of American Samoa. Tutuila is located at approximately 14° 18' S latitude and 170° 41' W longitude, has a mean annual temperature of 26.4°C, and annual rainfall from 2500 mm at lower elevations to over 6000 mm on Matafao Peak (660 m). Genera of the

Trentepohliales can sometimes be identified in the field with a hand lens, but all specimens were taken to the laboratory for species determination by stereo- and light microscopy. Several factors make species identification difficult. The historical use of different morphological characters to distinguish between species has led to incorrect descriptions (Thompson and Wujek 1997) and a need to revise the order (Joubert and Rijkenberg 1971, see Lopez-Bautista 2002). Further, variability within and between species is possible due to season and exposure (Thompson and Wujek 1997). Species of *Cephaleuros*, *Phycopeltis*, and *Stomatochroon* were classified in this study based on recently published keys and descriptions by Thompson and Wujek (1997). These characteristics included morphology and location of thalli and sporangiophores, measurements of central filament cells and their width-to-length ratio, and measurements of gametangia and sporangia. Specimens are deposited in the Land Grant Herbarium, American Samoa Community College, Malaeimi. Hosts with only a few algal thalli were accessioned as semi-permanent microscope slides and photomicrographs.

Two methods were used to estimate disease severity caused by *Cephaleuros* spp. First, the most seriously affected host leaves were assessed by estimating the percent of their upper leaf surfaces covered with algae: light (<5%), moderate (6-25%), or heavy (>25%). Disease severity was also measured for mature thalli from a nonrandom sample of hosts using a four-point necrosis index: (0) No necrosis; (1) superficial necrosis of the cell layer beneath the algal thallus, with or without tissue hyperplasia; (2) necrosis of >1 cell layer but not full leaf thickness, with or without tissue hyperplasia, erosion, or suberin formation; and (3) necrosis from upper to lower leaf surface, including “shot-hole” symptoms. Damage was assessed under a stereoscope by dissecting fresh and dried lesions with a scalpel.

Lichens with mature fruiting bodies and a species of *Cephaleuros* as the algal partner were recorded and sent to a lichenologist (C. Smith, University of Hawaii) for identification. Tissue damage beneath

lichen thalli was assessed with the necrosis index and compared with damage by non-lichenized thalli on the same host.

RESULTS

Cephaleuros, *Stomatochroon*, *Phycopeltis*, and *Trentepohlia* were collected on the island of Tutuila during this study. The two remaining genera of the Trentepohliales, *Printzina* and *Physolinum*, were not found. Algal species identified and the number of plant hosts affected by each (in parentheses) were: *Cephaleuros expansa* Thompson and Wujek (7); *C. karstenii* Schmidle (7); *C. minimus* Karsten (4); *C. parasiticus* Karsten (19); *C. virescens* Kunze in Fries (115); *Phycopeltis epiphyton* Millardet (43); *P. irregularis* (Schmidle) Wille (1); *Stomatochroon coalitum* Thompson and Wujek (1); and *S. consociatum* Thompson and Wujek (4). Specimens collected and not identified to species level included *Cephaleuros* (16), *Phycopeltis* (4), and *Trentepohlia* (5). Four hosts of *C. virescens* remain unidentified.

There were similarities and differences between the five *Cephaleuros* spp. that aided in their classification. Thalli of *C. expansa*, *C. karstenii*, and *C. virescens* grew beneath the host cuticle and were more or less circular. The thallus of *C. expansa*, however, was composed of radiating filaments that occasionally crossed each other, or became laterally fused, forming narrow, false ramuli (Figure 1A). Thalli of *C. karstenii* and *C. virescens* were either open- or closed-ramulate (Figure 1B, 1C). Ramuli of *C. karstenii* were 4-6 filaments wide and fan-shaped, while ramuli of *C. virescens* were 1-2 filaments wide and usually parallel. The width/length ratio of central filament cells was 1:4 for *C. karstenii* and 1:2 for *C. virescens*.

Cephaleuros parasiticus and *C. minimus* formed scant, filamentous thalli beneath the cuticle on upper leaf surfaces, grew intercellularly, and produced sporangiophores through lower leaf surfaces. Sporangioophores of *C. parasiticus* were typical for the genus, composed of a terminal head cell with radiating sporangiate-laterals (crooked suffultory

cells and attached zoosporangia) (Figure 2A). Conversely, sporangiophores of *C. minimus* were unique, with head cells and sporangiate-laterals along one side and ending in two to three tapered, sterile, apical cells (Figure 2B).

Trentepohliales were collected from 146 plant species and cultivars in 101 genera and 48 families (Table 1). Ninety percent of the hosts (129) were dicotyledonous species. Most algae grew on leaves but were occasionally found on stems and fruit. Sapotaceae was the most commonly affected family with 14 host species and cultivars.

Percent of leaf surface area covered by *Cephaleuros* spp. varied by algal and plant host species: 66% (109/165) of infections were light, 25% (42/165) were moderate, and 9% (14/165) were heavy (Table 2). Because of mixed infections, e.g. *C. virescens* and *C. parasiticus* on the same plant, the number assessed is greater than the total number of plant species collected. Twenty-nine percent of the infections associated with *C. virescens* (33/112) were moderate and nine percent (10/112) were heavy. Only nine of the 145 hosts examined had moderate to heavy leaf area covered by the other Trentepohliales, *Phycopeltis*, *Stomatochroon*, and *Trentepohlia*.

Of 126 algal infections assessed with the necrosis index, no visible tissue death or discoloration was caused by *Cephaleuros* spp. on 6% (8/126) of the hosts, 39% (48/126) scored 1, 12% (15/126) scored 2, and 43% (54/126) scored 3 (Table 3). The number of algal infections assessed with the necrosis index was less than either the number of hosts collected or estimates for percent leaf surface area covered, as the necrosis index was initiated near the end of the study and some host specimens were not available for sectioning.

Lichenized thalli of *Cephaleuros* spp. with mature perithecia were found on 33 of 124 hosts and identified as *Strigula elegans* (C. Smith, pers. comm.). Tissue damage caused by *S. elegans* was less severe than (16/33) or the same as (17/33) damage caused by the alga alone. Recording

lichenized forms of the nonparasitic species *Phycopeltis* and *Trentepohlia* was outside the objectives of this study.

DISCUSSION

Algae of the order Trentepohliales, especially *C. virescens* and *P. epiphyton*, have a broad plant host range in American Samoa (Table 1). Most of the hosts are perennial dicots, agreeing with reports from other tropical and subtropical locations (Holcomb 1986, Marlatt and Alfieri 1981, Thompson and Wujek 1997). However, the number of algal species identified in American Samoa, especially the five *Cephaleuros* spp., was higher than reported in many areas (Thompson and Wujek 1997). For example, Holcomb (1986) reported 218 plant hosts in Louisiana but only one algal species, *C. virescens*. Marlatt and Alfieri (1981) did not identify the species of *Cephaleuros* found on 157 hosts in Florida.

The only plant damage associated with *Stomatochroon* spp. during this study was watersoaking caused by a heavy infection of *S. consociatum* on the underside of leaves of the firecracker plant (*Cuphea* sp.). Watersoaking and browning of tissue may occur when sporangiophores of the alga block stomates and inhibit gas exchange (Chapman and Good 1983, Timpano and Pearlmutter 1983). This incidental damage might not qualify *Stomatochroon* as a plant pathogen, but it appears to be more than a space opportunist. The autotrophic *S. consociatum*, for example, was grown on an inorganic salts medium by Timpano and Pearlmutter (1983), but all stages of its life cycle could not be induced. These researchers suggest the alga receives necessary chemicals from its host, but neither benefits nor harms the plant (commensalism).

McKenzie (1996) was probably correct in suggesting that species of Trentepohliales collected in American Samoa from mango, guava, and avocado, were *Cephaleuros virescens*. This was the most commonly identified species in the present study and the most abundant alga of the Trentepohliales found on these three trees species. *Cephaleuros parasiticus*, *Phycopeltis epiphyton* and

Stomatochroon consociatum were also isolated from these hosts (Table 1).

Thalli of *C. virescens* usually grow on upper leaf surfaces, but were also common on the undersides of heavily infected leaves. This distribution was especially apparent when leaves were either twisted to expose their lower surfaces, had infections along their margins, or were split, with thalli surrounding the break on the upper leaf surface. These conditions would favor infection of the lower leaf surface by zoospores swimming in a film of water connecting the two leaf surfaces (Chapman and Good 1983). In a cumulative study in Louisiana from 1972 to the mid-1980s, Holcomb (1986) reported *C. virescens* only on upper leaf surfaces of all hosts except *Camellia japonica*, which had thalli on both surfaces.

Stem infections associated with *C. virescens* were rare in the present study, appearing only on kava (*Piper methysticum*) and the zigzag plant (*Pedilanthus tithymaloides*). In the Louisiana study (Holcomb 1986), however, 17 stem infections were reported, and recently workers described cane infections on cultivated blackberry in Arkansas and Louisiana (Holcomb et al. 1998).

Thompson and Wujek (1997) considered *C. virescens* a “relatively innocuous” species, causing obvious necrosis on only a few plant hosts. They disagreed in general with published reports identifying *C. virescens* as a primary agent of disease. Thompson and Wujek attributed the errors in these reports to either: (1) misidentification of the alga, (2) the alga growing opportunistically in lesions made by other organisms or environmental conditions, (3) or to the fungal component of the lichenized alga being the actual cause of the damage. Results of the American Samoa study differ from those of Thompson and Wujek. Thalli of *C. virescens* usually occurred in the absence of signs or symptoms of other biotic agents or visible damage caused by the environment. As algae matured the diameter of tissue necrosis mirrored thallus growth. This relationship between the presence of an algal thallus and host necrosis in the absence of other lesion forming

organisms suggests *C. virescens* is a primary pathogen, able to cause disease. Until plants can be inoculated with zoospores of *C. virescens* and the same symptoms produced (Koch’s postulates), however, its pathogenicity remains tentative (Agrios 1997).

Damage caused by *C. virescens* on 33 plant hosts in American Samoa was greater than or equal to damage caused to the same hosts by its lichenized form, *Strigula elegans*. This observation argues against Thompson and Wujek’s contention (1997) that the fungal partner of the lichen is the cause of disease, but agrees with Chapman and Good’s finding (1983) that necrosis beneath a lichenized *Cephaleuros* thallus is produced by the alga before lichenization. Ultrastructural studies have shown the fungus parasitizes its algal host and not the plant (Chapman 1976). If a plant pathogenic fungus were to associate with *C. virescens* damage could occur (Chapman and Good 1983), but that was not the case with *S. elegans* in this study.

Host tissue necrosis was present beneath *Cephaleuros* thalli on over 90 % of the 126 hosts indexed and was moderate to severe on 55 % (Table 3). Comparatively, Holcomb (1986) described moderately severe to severe host responses, and leaf spotting, on only 8 % of 218 hosts. The terms moderately severe and severe were not defined in the Louisiana report, however, and may not be comparable to the disease severity scales used in the present study.

Tropical fruit trees in the Sapotaceae were more heavily affected by Trentepohliales than other plant families (Table 1). They had the broadest host range, a moderate to heavy percent leaf area covered by the algae, and full-thickness necrosis on many leaves. Most specimens, however, were collected from a crowded, poorly maintained fruit orchard where heavy shading, lack of nutrients, and high inoculum levels may have increased host susceptibility. Control measures under these conditions would include: plant spacing and thinning to improve aeration and light, optimum fertilization, orchard sanitation, and selecting cultivars for the local environment.

Algae in the order Trentepohliales remain a mystery to most American Samoans, as plant parasitic *Cephaleuros* species do not affect important subsistence crops, such as banana and taro. Occasional blemishes caused by algae on other types of produce and on landscape plants are tolerated. Since control measures are not usually applied and most Trentepohliales have a broad host range, their existence in American Samoa is relatively secure in spite of habitat destruction due to population pressure and natural disaster.

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Table 1. A list of plant hosts¹ of *Cephaleuros*, *Phycopeltis*, and *Stomatochroon* on Tutuila, American Samoa. The name of each host is followed by its authority, algal species², and severity of disease³ caused by *Cephaleuros* spp.

ACANTHACEAE

Aphelandra sinclairiana Nees; Cvir
Odontonema tubiforme (Bertoloni) Kuntze; Cvir
Pseuderanthemum carruthersii var. *reticulatum* (Seem.) Guillaumin; Cvir

AGAVACEAE

Cordyline terminalis (L.) Chevallier; Csp
Pleomele sp. (Roxburgh) N.E. Brown; Pepi

AMARYLLIDACEAE

Crinum asiaticum L.; Cexp

ANACARDIACEAE

Anacardium occidentale L.; Cvir⁺
Mangifera indica L.; Cvir, Cpar*, Scon

ANNONACEAE

Annona muricata L.; Cvir*
A. muricata ‘Cuban Fiberless’ L.; Cvir*
A. muricata ‘Dulce Cuban’ L.; Cvir
A. squamosa ‘Seedless’ L.; Cvir
A. squamosa x *A. cherimoya* ‘Pink Mammoth’ L.; Cvir*, Cpar*
Rollinia deliciosa Saff.; Cvir⁺, Pepi, Scoa

APOCYNACEAE

Allamanda sp. L.; Cexp
A. cathartica L.; Cvir
Carissa grandiflora (E. Meyer) A.L.P.P. de Candolle; Cvir

ARACEAE

Anthurium sp. Linden ex Andre; Cvir, Pepi
Epipremnum pinnatum (L.) Engler; Cexp, Cvir*

ARALIACEAE

Polyscias fruticosa (L.) Harms; Cvir*
P. scutellaria (N.L. Burman) Fosberg; Cvir

ARECACEAE

Chrysalidocarpus lutescens H. Wendl.; Pepi
Metroxylon vitiense (H. Wendl.) Hook.f.; Cvir; Psp
Pritchardia pacifica Seem. & H. Wendl.; Cvir; Pepi
Veitchia merrillii (Becc.) H.E. Moore; Cpar*, Pepi

ASCLEPIDACEAE

Hoya australis R. Brown; Cvir, Pepi

BEGONIACEAE

Begonia sp. Linn.; Ckar

BIGNONIACEAE

Tabebuia heterophylla (DC.) Britton; Cvir

BIXACEAE

Bixa orellana L.; Cpar*, Cvir

BOMBACACEAE

Cieba pentandra (L.) Gaertn.; Cvir
Durio zibethinus Moon; Cvir*, Pepi⁺
Pachira aquatica Aubl.; Cvir

BURSERACEAE

Canarium ovatum Engl.; Cvir

CLUSIACEAE

Calophyllum inophyllum L.; Cvir⁺
C. neo-ebudicum Guillaumin; Pepi

COMBRETACEAE

Terminalia samoensis Rechinger; Cvir*

CONVOLVULACEAE

Operculina turpethum (L.) Silva Manso; Csp

CUPRESSACEAE

Cupressus sp. L.; Ckar

EBENACEAE

Diospyros samoensis A. Gray; Pepi

EUPHORBIACEAE

Aleurites moluccana (L.) Willd.; Cvir*
Codiaeum variegatum (L.) A.H.L. Jussieu; Cvir*, Pepi
C. v. pictum ‘Acubifolium’ (L.) A.H.L. Jussieu; Cvir

C. v. pictum 'Majesticum' (L.) A.H.L. Jussieu; Cvir*, Pepi
C. v. pictum 'Stewartii' (L.) A.H.L. Jussieu; Csp
Euphorbia neriifolia L.; Cvir
Flueggea flexuosa Muell. Arg.; Cvir, Pepi
Jatropha integerrima Jacquin; Cvir, Pepi
Pedilanthus tithymaloides L.; Cvir*, Pepi

FABACEAE

Acacia sp. Linn.; Cvir, Csp, Pepi, Scon
A. mangium Willd.; Csp
Calliandra surinamensis Benth.; Cvir
Cassia javanica L.; Cvir
Intsia bijuga (Colebr.) Kuntze; Ckar, Cvir+, Pepi
Pterocarpus indicus Willd.; Csp
Sophora tomentosa L.; Cvir

HELICONIACEAE

Heliconia x 'Golden Torch' L.; Cpar

LAURACEAE

Persea americana Miller; Cvir

LEEACEAE

Leea guineensis G. Don; Cexp*, Cpar*, Cvir*, Csp*

LOGANIACEAE

Fagraea berteroana A. Gray ex Benth.; Cvir

LYTHRACEAE

Cuphea melvilla Lindl.; Cpar*, Csp+, Scon
Lagerstroemia speciosa (L.) Pers.; Cmin*, Cpar*, Cvir*+, Csp, Scon

MAGNOLIACEAE

Michelia champaca Linn.; Ckar, Pepi

MALVACEAE

Hibiscus rosa-sinensis L.; Cmin, Cvir, Csp, Pepi
H. tiliaceus L.; Cvir
H. tiliaceus cv. L.; Cvir

MARANTACEAE

Maranta arundinacea 'Variegata' L.; Cpar*, Cvir, Pepi

MELIACEAE

Lansium domesticum Correa; Cvir
Melia azedarach Blanco; Cvir, Psp
Swietenia macrophylla King; Ckar, Pepi

MORACEAE

Artocarpus altilis (J.D. Hooker) Schlechter; Cvir
Ficus benghalensis L.; Cvir
F. benjamina L.; Cvir*
F. elastica Roxb. Ex Hornem.; Cvir
F. prolixa Forst.f.; Cvir, Pepi
F. tinctoria Forst.f.; Cvir

MYRTACEAE

Eugenia uniflora L.; Cvir*
Psidium guajava L.; Cvir*, Pepi
P. guajava 'Waikea' L.; Cpar*, Cvir+
Syzygium corynocarpum (A. Gray) C. Muell.; Cpar
S. inophylloides C. Muell.; Cpar
S. jambos (L.) Alston; Cvir*, Pepi

NYCTAGINACEAE

Bougainvillea spectabilis Willd.; Cvir

OLEACEAE

Jasminum multiflorum (N.L. Burman) Andrews; Cvir, Pepi
J. sambac (L.) Aiton; Cvir
Ligustrum sinense Lour.; Cvir, Pepi

ORCHIDACEAE

Arachnis x *maingayi* (J.D. Hooker) Schlechter; Cexp*+, Csp*, Pepi+
Arundina graminifolia (D. Don) Hochreutiner; Cexp*, Cpar, Pepi
Dendrobium lepidochilum; Cmin, Pepi
Spathoglottis plicata Blume; Csp
Unidentified epiphytic orchid; Pepi

OXIDALIDACEAE

Averrhoa carambola 'Jurong' Linn.; Cvir, Psp
A. carambola 'Kajang' Linn.; Cvir
A. carambola 'Kembangan' Linn.; Cvir

PANDANACEAE

Pandanus whitmeeanus Mart.; Cvir, Pepi

PIPERACEAE

Piper graeffei Warb.; Csp*, Pepi
P. methysticum Forst.f.; Cvir

POLYGONACEAE

Homalocladium platycladium (F. Von Mueller)
L.H. Bailey; Cvir

RUBIACEAE

Gardenia jasminoides 'Veitchii' Ellis; Cvir, Csp
G. taitensis A.L.P.P. de Candolle; Csp
Ixora casei Hance; Cvir
I. finlaysoniana Wallich ex G. Don; Cexp, Cvir
Morinda citrifolia L.; Cmin*
Mussaenda erythrophylla 'Rosea' Schumacher;
Csp, Pepi
M. frondosa Blanco; Cvir
M. philippica L.C. Richard; Cvir
Tarenna sambucina (Forst.f.) Durand; Cvir

RUTACEAE

Citrus aurantifolia (L.) Swingle; Cvir
C. aurantifolia 'Thornless Mexican' L.; Csp
Murraya paniculata L.W. Jack; Cvir

SAPINDACEAE

Euphoria longan 'Bai Dum' (Lour.) Steud.; Cvir*
E. longan 'Chompoo' (Lour.) Steud.; Cvir
Litchi chinensis Sonn.; Cvir*
Pometia pinnata Forst.; Cvir, Pepi

SAPOTACEAE

Chrysophyllum cainito 'Grimal' L.; Cvir⁺, Pepi
C. cainito 'Hatian' L.; Cvir, Pepi
C. cainito 'Philippine Gold' L.; Cvir
C. cainito 'Seedless' L.; Ckar*
Lucuma mammosum (Jacq.) Merr.; Csp, Pepi⁺
L. nervosa 'Bruce' A. DC.; Csp*
Manilkara zapota 'Alano' (L.) D. Royen; Cvir*
M. zapota 'Betawi' (L.) D. Royen; Cvir*
M. zapota 'Ponderosa' (L.) D. Royen; Cpar*,
Cvir*
Planchonella samoensis H.J. Lam ex Christoph.;
Psp
Pouteria sapota (Jacq.) H. Moore & Stearn;
Cpar*, Cvir⁺, Pepi

Sandoricum koetjape 'Bangkok' Merrill.; Cpar*,
Cvir
S. koetjape 'Chompoo' Merrill.; Cvir, Pepi
Synsepalum dulcificum (Schumach. & Thonn.)
W.F. Daniell; Cpar*, Cvir*

SOLANACEAE

Brunfelsia americana L.; Cvir*
B. pauciflora (Chamisso & Schlechtendal)
Bentham; Cvir
Cestrum diurnum L.; Cvir, Pepi, Scon

STERCULIACEAE

Theobroma cacao L.; Cvir, Pepi, Pirr

VERBENACEAE

Clerodendrum wallichii Merrill; Cvir, Pepi
C. x speciosum Van Geert ex Morren.; Cvir
Congea griffithiana Munir; Cvir
Faradaya amicorum Seem.; Cvir
Premna serratifolia L.; Cvir*

ZINGIBERACEAE

Alpinia purpurata K. Schum.; Ckar

¹ Table does not include unidentified hosts, except two orchid spp., nor hosts of *Trentepohlia*.

² Csp = *Cephaleuros* sp., Cexp = *C. expansa*, Ckar = *C. karstenii*, Cmin = *C. minimus*, Cpar = *C. parasiticus*, Cvir = *C. virescens*, Psp = *Phycopeltis* sp., Pepi = *P. epiphyton*, Pirr = *P. irregularis*, Scoa = *Stomatochroon coalitum*, Scon = *S. consociatum*.

³ Disease severity caused by *Cephaleuros* spp.: (+) = >25% of leaf area covered by the alga; (*) = full-thickness leaf necrosis.

Table 2. Percent upper surface of plant host leaves covered by *Cephaleuros* spp., island of Tutuila, American Samoa.

ALGA	No. hosts affected at each level of leaf area covered ¹		
	<5%	6-25%	>25%
<i>Cephaleuros expansa</i>	6	— ²	1
<i>C. karstenii</i>	7	—	—
<i>C. minimus</i>	3	1	—
<i>C. parasiticus</i>	12	4	3
<i>C. virescens</i>	69	33	10
<i>C. sp.</i>	12	4	—
Total	109	42	14

¹ Some host leaf surfaces were infected by more than one species of *Cephaleuros*.

² No hosts recorded for the algal species at this level.

Table 3. Host leaf damage caused by *Cephaleuros* spp. on Tutuila, American Samoa, as measured by a necrosis index¹.

ALGA	No. hosts affected at each level of necrosis ²			
	0	1	2	3
<i>Cephaleuros expansa</i>	— ³	3	—	4
<i>C. karstenii</i>	—	4	—	1
<i>C. minimus</i>	—	2	—	2
<i>C. parasiticus</i>	—	—	—	14
<i>C. virescens</i>	8	39	15	30
<i>C. sp.</i>	—	—	—	4
Total	8	48	15	55

¹ Necrosis index: 0 = no necrosis; 1 = superficial necrosis of the cell layer beneath the thallus, with or without tissue hyperplasia; 2 = necrosis of >1 cell layer but not full leaf thickness, with or without tissue hyperplasia, erosion, or suberization; 3 = full-thickness necrosis from upper to lower leaf surface, or “shot hole” symptoms.

² Some hosts were infected by more than one species of *Cephaleuros*.

³ No hosts recorded for the algal species at this level.

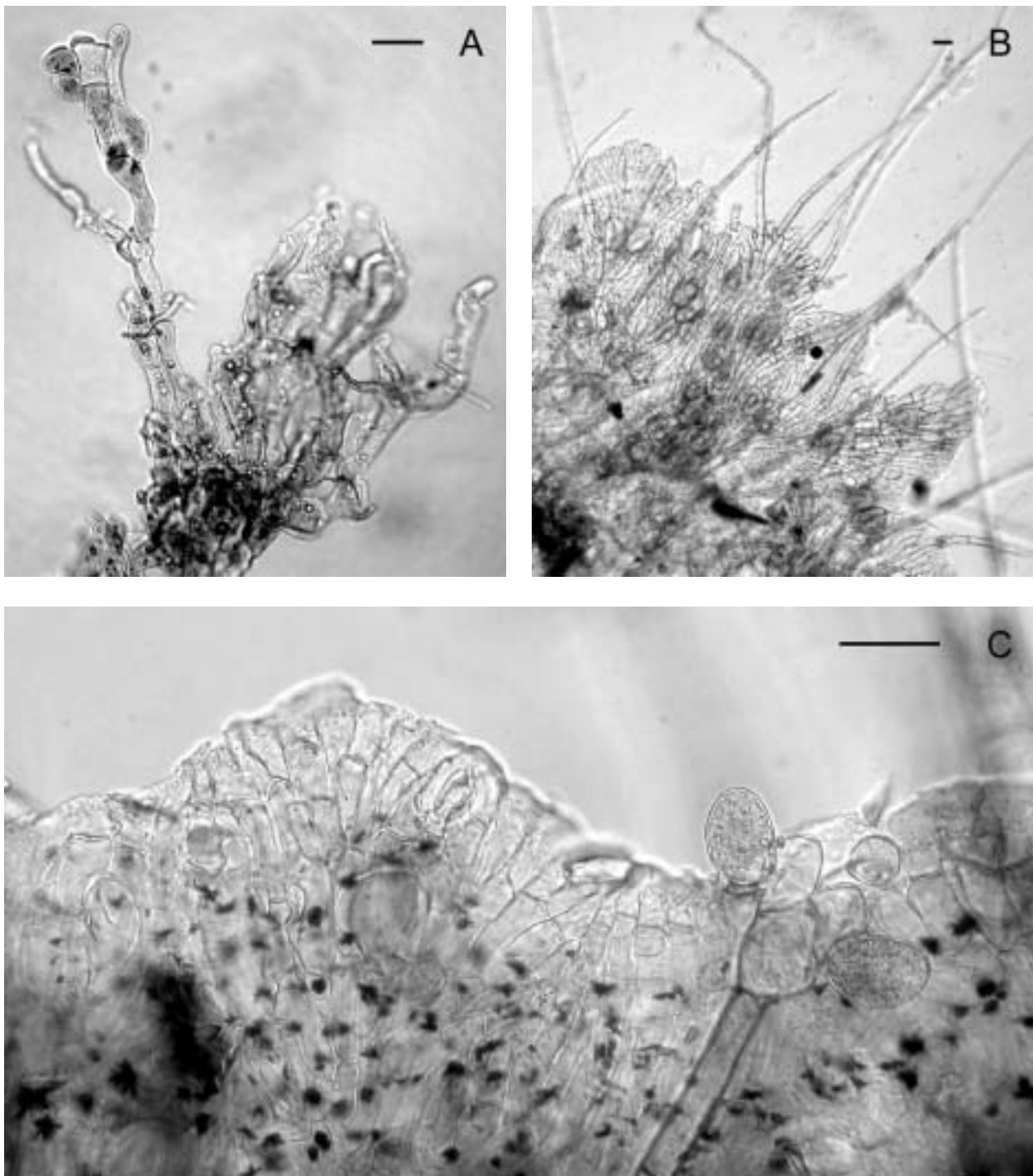


Figure 1. Sub-cuticular species of *Cephaleuros* removed from the upper leaf surface of hosts. (A) Filaments of *C. expansa* fusing to form a false ramulus (branch). (B) Irregularly lobed thallus (body) of *C. karstenii* with multi-cellular, sterile hairs. (C) Entire, closed-ramulate thallus of *C. virescens* (Note: sporangiophore (right) with head cell and two sporangiate-laterals). Scale bars = 25 μ m.

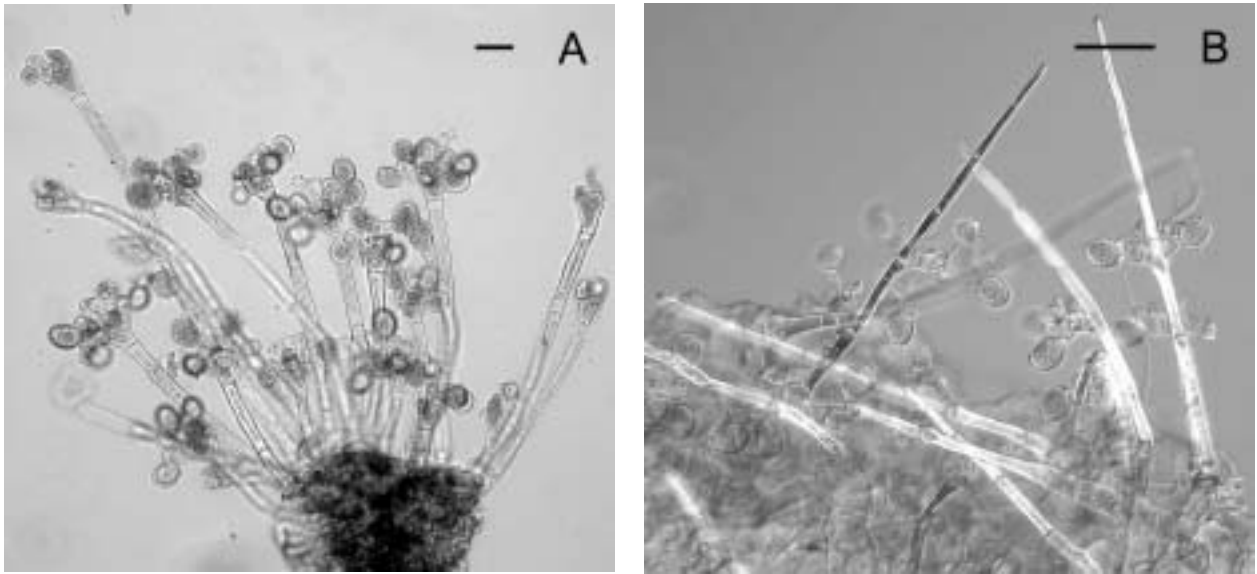


Figure 2. Sporangiohores of two intercellular species of *Cephaleuros*, with attached host tissue, excised from lower leaf surfaces. (A) Sporangiohores of *C. parasiticus* with terminal whorls of sporangiate-laterals. (B) Sporangiohores of *C. minimus* with sporangiate-laterals in twos and threes along one side, and ending in sterile tapered, cells. Scale bars = 25 μ m.