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Ecology and morphological characterization of gametophyte and 'Chantransia' stages of *Sirodotia huillensis* (Batrachospermales, Rhodophyta) from a stream in central Mexico

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SUMMARY

The morphology and phenology of *Sirodotia huillensis* was evaluated seasonally in a central Mexican first-order calcareous stream. Water temperature was constant (24–25°C) and pH circumneutral to alkaline (6.7–7.9), and calcium and sulfates were the dominant ions. The gametophyte stages were characterized by the presence of a distinctive mucilaginous layer, a marked difference in phycocyanin to phycoerythrin ratio between female and male plants, and the presence of a carpogonia with a large trichogyne (>60 μm). Occasionally three capogonia were observed on a single basal cell. The 'Chantransia' stages were morphologically similar to those described for the other members of Batrachospermales. A remarkable observation was the formation of dome-shaped structures, consisting of prostrate filaments that are related with the development of new gametophytes. Chromosome numbers were $n = 4$ for fascicle cells, cortical filament cells and dome-shaped cells, and $2n = 8$ for gonimoblast filament cells and 'Chantransia' stage filaments. Gametophytes and 'Chantransia' stages occurred in fast current velocities (60–170 cm/s) and shaded (33.1–121 μmol photons/m^2/s) stream segments. The population fluctuated throughout the study period in terms of percentage cover and frequency: the 'Chantransia' stages were most abundant in the rainy season, whereas gametophytic plants had the highest frequency values during the dry season. These results were most likely a result of fluctuations in rainfall and related changes in current velocity. Some characteristics of this population can be viewed as probable adaptations to high current velocities: the mucilaginous layer around plants that reduces drag; potential increase in fertilization by the elongate and plentiful trichogynes and abundant dome-shaped structures producing several gametophytes.

Key words: Batrachospermales, 'Chantransia' stages, ecology, gametophyte, morphology, Rhodophyta, *Sirodotia huillensis*, stream.

INTRODUCTION

The genus *Sirodotia* was established by Kylin (1912) based on specimens of *Sirodotia suecica* from Osby, Skane in Sweden. *Batrachospermum huillense* Welwitsch ex W. et G. S. West (1897) from Lopollo, Huilla, Angola in Africa was assigned to the genus *Sirodotia* as *Sirodotia huillensis* by Skuja (1931). It has the typical vegetative morphology of members of the family Batrachospermaceae (Necchi *et al*. 1993; Kumano 2002), but it is distinguished by its asymmetrical carpogonia with elongate conical or club-shaped tricogynes and indeterminate carposporophyte filaments extending over the axial cortical filaments. Species delimitation is based on the size, arrangement and shape of spermatangia, carpogonia and gonimoblast filaments (Necchi *et al*. 1993; Kumano 2002). Molecular tools have been used to determine phylogenetic relationships using sequence analyses for ruBisCo large and small subunits (*rbc*L, *rbc*S) genes (Vis & Sheath 1999). Eight species have been recognized within the genus worldwide (Kumano 1982; Necchi *et al*. 1993; Vis & Sheath 1999): *Sirodotia yutakae* Kumano, *Sirodotia segawae* Kumano, *Sirodotia sinica* Jao, *Sirodotia geobelii* Entwisle et Foard, *Sirodotia delicatula* Skuja, *Sirodotia suecica* Kylin, *S. huillensis* Welwitsch ex West et

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G. S. West and *Sirodotia gardneri* Skuja ex Flint. Only two species have been reported for North America: *S. huillensis* and *S. suecica*. Vis and Sheath (1999) conclude that *S. suecica* and *Sirodotia tenuissima* are conspecific and morphological characters used to distinguish between these species are not phylogenetically informative, because the sequence data for ruBisCo (*rbc*L, *rbc*L-S spacer, *rbc*S) genes revealed little variation among specimens of the two species. One population identified as *S. huillensis* has been reported from Mexico (Carmona *et al*. 2004) and corresponds morphologically and ecologically with the description of the species.

Reproduction, development and life history are poorly known in *Sirodotia* and few studies have been published. Vegetative and reproductive characteristics of *Sirodotia* species are reported by Necchi (1991), Necchi *et al*. (1993) and Kumano (2002). Balakrishnan and Chaugule (1975, 1980) found elimination cells in the life history of Batrachospermaceae, whereas Necchi and Carmona (2002) describe somatic meiosis and development of juvenile gametophytes. Necchi and Sheath (1992) report chromosome numbers for *S. delicatula* (as *Batrachospermum delicatulum*) as $n = 3$, $2n = 6$. Ecological studies of the Batrachospermales focus primarily on *Batrachospermum* species (Sheath & Hambrook 1990; Hambrook & Sheath 1991; Necchi 1997; Necchi & Branco 1999). *S. huillensis* appears to be more abundant in desert and tropical regions, in warm, neutral to alkaline and high ion content waters (Necchi *et al*. 1993; Carmona *et al*. 2004). However, nutrient and microhabitat requirements for this species are virtually unknown.

The present investigation was conducted to describe morphological and cytological details, as well as the environmental conditions favoring the occurrence of gametophytes and the 'Chantransia' stages based on laboratory culture and field monitoring for one population of *S. huillensis* in central Mexico.

MATERIALS AND METHODS

The material used in the present study was collected from the Santa Anita River, a fast-running stream through a calcareous region at an altitude of 160 m (Montejano *et al*. 2000) in a tropical region from central Mexico (21°58′N, 99°11′W). Fieldwork was conducted from November 2003 to May 2004, including the most important parts of the seasonal cycle, the rainy and the dry season. One sampling was carried out at the end of the rainy season (November) and two during the dry season (January and May). The following environmental variables were measured: temperature, pH and specific conductance with a Conductronic PC-18 conductivity meter. Water samples were collected to determine nutrients according to APHA *et al.* (1980) and ASTM (1989). The variation coefficient (VC) was used to determine whether environmental parameters were consistent (those that do not change along time and space in a water body, usually VC, VC < 5–10%) or variable (those that do change along time and space, usually because they are affected by dilution/evaporation process and biological activity, *sensu* Margalef 1983). A descriptor was calculated by the equation: $VC = s/a \cdot 100$, where s = standard deviation and a = average.

Observations were made on the natural substrata (boulders) directly on the river bed. Temporal variation was monitored using the quadrat technique (Necchi *et al*. 1995; Necchi 1997; Necchi & Branco 1999), which evaluates the influence of variables at microhabitat level (current velocity, depth and underwater irradiance) on the vegetative and reproductive characteristics of the populations (proportion of both female and male plants and of the 'Chantransia' stages). Ten sampling units were distributed in ten equally spaced intervals along the stream segment (58 m^2). Microhabitat variables were measured *in situ* at the center of each sampling unit: current velocity and irradiance were measured as close to the alga as possible using, respectively, a Swoffer 2100 current velocity meter and a Li-Cor LI-1000 quantum meter with a flat subaquatic sensor of photosynthetically active radiation. The number of plants was recorded within each sampling unit by visual estimate (Necchi 1997), with a 175 cm^2 viewfinder. Frequency of occurrence was calculated from the number of sampling units with algal thalli compared with the total units sampled (10). Twenty thalli were randomly selected (2–3 in each sampling unit).

Plants were preserved in 3% formaldehyde and Carnoy's solution for subsequent analysis in the laboratory. For chromosome observations, plants were stained by Wittmann's hematoxylin (Necchi & Sheath 1992; Sheath & Cole 1993). Chromosome counts were made on the basis of a minimum of 10 observations for each cell type. In addition, extra cellular polysaccharides were stained with 0.3% Alcian-Blue, in 3% acetic acid at pH 2.5 (Sheath & Cole 1990). For microscopic analyses and photographic documentation of cytological characters, we used an Olympus BX51 microscope, with an SC35 microphotography system. Morphometric characters were measured in 20 replicates; the number of replicates was determined using the equation: $n = (s/E\xi)^2$, where s = standard deviation, E = standard error (0.05 and ξ= average (Southwood 1978).

Cultures were initially obtained from germination of carposporangia. Isolation into culture followed the procedures described previously (Necchi & Zucchi 1997). The isolates were kept in 20:1 water–soil culture medium inside MLR-350 HT Sanyo incubators with illumination from above supplied by cool-white fluores-

cent lamps (Phillips 15 W) under the following conditions: temperature 20°C; irradiance 21.5–41.9 μmol photons/m^2/s; photoperiod of 12:12 h LD. Pigments were obtained from male and female plants in natural conditions. Phycobiliproteins (phycocyanin and phycoerythrin) were extracted in 0.1 mol/L phosphate buffer (pH 6.8) and quantified according to the spectrophotometric technique of Beer and Eshel (1985), with a Genesys series 10 spectrophotometer (1 nm resolution). Chorophyll *a* was extracted by resuspending the pellet resulting from phycobiliprotein extraction in 90% alkaline acetone, and determined following the spectophotometric technique (Wetzel & Likens 1991).

RESULTS

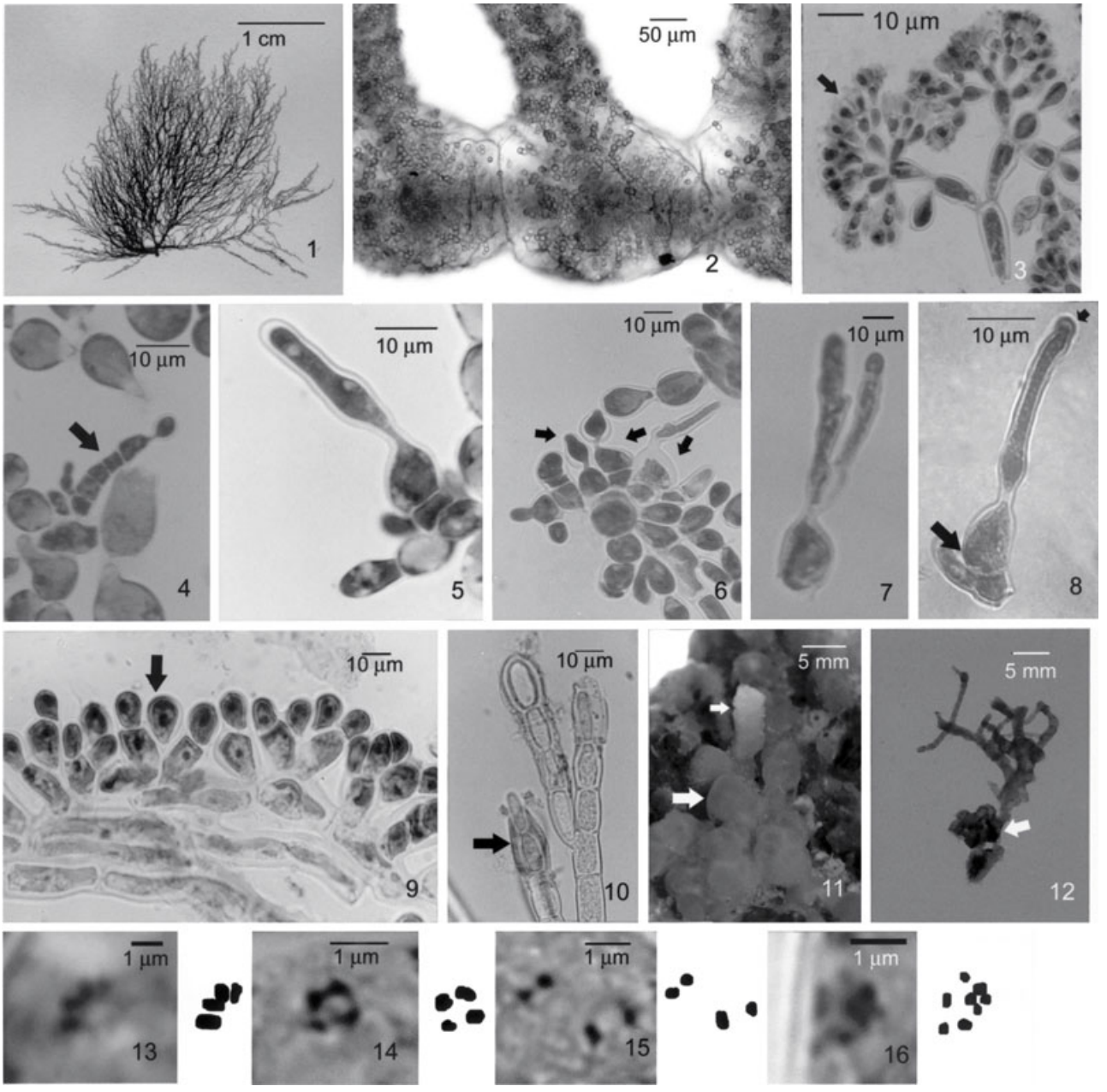
Morphological analysis

Based on population characteristics, the specimens were ascribed to *S. huillensis.* Plants were dioecious, with male and female plants occurring intermingled with each other in patches (Fig. 1). Female plants were dark-green (Phycocyanin [PC] : Phycoerythrin [PE] ratio = 0.62 ± 0.4; Phycobiliprotein [PB] : Chlorophyll *a* [Chl*a*] ratio = 8 ± 3.8), whereas male plants were blue-green (PC : PE ratio = 1.34 ± 0.3; PB : Chl*a* ratio = 14.2 ± 3.4) (Table 1). Plants were 1–5 cm in length (ξ = 3 cm) with abundant extracellular polysaccharides in the outer mucilaginous layer and intense staining with Alcian Blue (Fig. 2). Plant branching was abundant and irregular, and whorls were ellipsoidal to obconical, 100–545 μm (ξ = 250 μm) in diameter, separated from each other when young, truncate-pyramidal and confluent as a result of development of secondary fascicles when mature. Primary fascicles were abundantly branched with 4–7 cell-layers. Spermatangia were hyaline, elliptical to spherical, 2.4–8.4 μm (ξ = 5.6 μm) and borne terminally or subterminally in dense fascicles (Fig. 3). Spermatangial cell wall and spermatangial filaments were intensely stained by Alcian Blue. Carpogonia were profusely formed on the younger parts of primary and secondary branches. Carpogonial branches consisted of 1–4 barrel-shaped cells arising from periaxial cells (Fig. 4); involucral filaments were short and sparse. Carpogonia had a distinct hemispherical protuberance on one side of the basal portion (Fig. 5), were 20–60 μm in length (ξ = 47 μm) and 6–9.6 μm in diameter (ξ = 7.4 μm) at the base. Up to three carpogonia were borne on short carpogonial branches attached to a single pericentral cell (Fig. 6). Trichogynes were elongate-conical, cylindrical or club-shaped, more or less indistinctly stalked. Abnormal carpogonia, with branched trichogyne, were observed in carposporophytic plants (Fig. 7). Mature carposporophytes were indefinite in shape, with gonimoblast initial developing from the protuberant side of the carpogonium (Fig. 8), creeping along cortical filaments (Fig. 9). Carposporangia were obovoid or spherical, occurring in dense clusters, 6–12 μm in diameter (ξ = 8 μm). The 'Chantransia' stages were observed under natural and culture conditions. Specimens in culture had the following characteristics: tuft-shape plant, blue-green color, >4 mm length, with erect and densely branched filaments, open branches >40°, cylindrical cells 24–52.8 μm in length (ξ = 40 μm), 7.2–10.8 μm in diameter (ξ = 9 μm), and reproducing by abundant (>50 per plant) ovoboid or elliptical monosporangia, 18–22.8 μm in length (ξ = 21 μm) and 8.4–13.2 μm in diameter (ξ = 10.6 μm). Monosporangia cell walls were stained with Alcian Blue (Fig. 10). Abundant dome-shaped structures were observed under natural conditions (Figs 11,12) with the following characteristics: <2 mm length, with short and irregularly branched filaments; branches <40°, cylindrical cells 7.2–19.2 μm in length (ξ = 12.6 μm) and 6–19.2 μm in diameter (ξ = 9.7 μm). Juvenile gametophytic plants were frequently observed in close relation with dome-shaped structures and apparently developed from them (Figs 11,12). Later stages of the juvenile gametophyte showed the typical uniaxial construction of the Batrachospermaceae. Both structures, dome-shaped and juvenile gametophyte, have the same chromosome number ($n = 4$, Figs 13–15). Chromosome numbers were $n = 4$ for fascicle intercalary cells (Fig. 14), cortical filament cells (Fig. 15) and spermatangia, and $2n = 8$ for gonimoblast filament, carposporangia and 'Chantransia' stages (Fig. 16).

Table 1. Seasonal differences in pigment content in the macroscopic gametophyte of the *Sirodotia huillensis* from Santa Anita Stream, central Mexico

	Dry season 31.i.2004	5.v.2004
PC : PE male plants	1.1–1.2	0.95–1.92
	1.1 ± 0.02	1.5 ± 0.5
PC : PE female plants	–	0.5–1.0
		0.6 ± 0.4
PB : Chl*a* male plants	12.0–18.1	8.9–16.9
	15.2 ± 3.08	13.1 ± 4.0
PB : Chl*a* female plants	–	4.6–12.1
		8.0 ± 16.9
Total pigment male plants	5.3–19.45	5.5–15.8
	12.8 ± 7.1	10.3 ± 5.1
Total pigment female plants	–	12.4–19.7
		16.0 ± 3.6

$n = 3$ for phycobiliprotein (PB), chlorophyll and total pigments. Chl*a*, Chlorophyll *a* (measurements in μg mg/L); PC, phycocyanin; PE, phycoerythrin. Ranges with averages ± standard-deviations below.



Figs 1–16. Morphological features of S*irodotia huillensis*. 1. General habit of a male plant. 2. Gametophyte mucilage. 3. Spermatangial filaments (arrow). 4. Inmature carpogonia on a branch consisting of four cells (arrow). 5. Carpogonia with a distinct hemispherical protuberance on one side of the basal portion. 6. Three carpogonia (arrows) on one-celled carpogonial branches attached to a single pericentral cell. 7. An abnormal carpogonia with branched trichogyne. 8. A fertilized carpogona with attached spermatium (arrow small) and a gonimoblast initial (arrow). 9. Mature carposporophyte with carposporangia in terminal cluster (arrow). 10. Monosporangia and monosporangial walls (arrow) of the 'Chantransia' stages filament. 11. Detail of dome-shaped structure (arrow) and early stage of the juvenile gametophyte growing in close relation with dome-shaped structure (arrow small). 12. General habit of a dome-shaped structure (arrow) and mature gametophyte. 13. Dome-shaped structure cell with chromosome number $n = 4$. 14. Fascicle cell of gametophyte with chromosome number $n = 4$. 15. Cortical filament cell with chromosome number $n = 4$. 16. 'Chantransia' stage cell with chromosome number $2n = c$. 8. Specimens in Figures 2,3–10 were stained with Alcian Blue and in Figures 8,9–13–16 with hematoxylin.

Table 2. Physical and chemical characteristics for Santa Anita Stream when sampled for *Sirodotia huillensis* (K25, conductance standardized at 25°C)

	Rainy season 21.xi.2003	Dry season 31.i.2004	15.v.2004	Variation (%)†
Temperature (°C)	24.6	24.0	25.0	
K_{25} (µS/cm)	1060	1209	1508	
pH	7.0	6.7	7.9	
Current velocity (cm/s)‡	60–170	66–125	70–157	
100 ± 40	90 ± 20	110 ± 30		
Irradiance (µmol photons/m^2/s)‡	33.1–71.7	64.3–121	36.6–95.9	
	51 ± 17.3	80 ± 18.5	67.2 ± 20.5	
Depth (cm)‡	15–33	8–20	4–51	7
	27.2 ± 8.1	12.6 ± 6.4	29 ± 18.7	
Dissolved oxygen (mg/L)	8.2	6.2	5.0	4
Total dissolved solids (mg/L)	880	1010	1015	8
Total alkalinity (mg $CaCO_3$/L)	276	263	251	235
HCO_3^- (mg/L)	337	321	287	86
$CO_3^=$ (mg/L)	276	0	9	6
Cl^- (mg/L)	2	2	0	8
$SO_4^=$ (mg/L)	358	410	390	5
Si-SiO_2 (mg/L)	7	6	7	4
Total hardness (mg $CaCO_3$/L)	686	750	742	27
Ca^{++} hardness (mg $CaCO_3$/L)	571	608	622	4
Mg^{++} hardness (mg $CaCO_3$/L)	80	141	119	10
Ca^{++} (mg/L)	229	244	249	8
Mg^{++} (mg/L)	28	34	29	0
Na^+ (mg/L)	8	9	0	51
K^+ (mg/L)	1	1	1	19
Dissolved reactive phosphorus (µg/L)	9	7	18	43
N-NO_3^- (µg/L)	17	17	24	33
N-NO_2^- (µg/L)	1	2	1	20
N-NH_3^- (µg/L)	21	17	32	31
DIN : DRP ratio	4	5	3	
Ionic concentration (meq/L)	53	29	54	
Ionic dominance (meq/L)	$SO_4^=$ > HCO_3^- > $CO_3^=$ > Cl^- Ca^{++} > Mg^{++} > Na^+ > K^+	$SO4^=$ > HCO_3^- > Cl^- > $CO_3^=$ Ca^{++} > Mg^{++} > Na^+ > K^+	$SO4^=$ > HCO_3^- > $CO_3^=$ > Cl^- Ca^{++} > Mg^{++} > K^+ > Na^+	

n = 10 for frequency of occurrence, current velocity, irradiance and depth. Water samples were collected to determine nutrients according to APHA *et al*. (1980) and ASTM (1989).

†Margalef (1983): conservative (VC < 10% variation) and not conservative (VC > 20%) variables.

‡average ± standard-deviation.

DIN, dissolved inorganic nitrogen; DRP, dissolved reactive phosphorus.

Ecological analysis

During the three collection periods of the year for *S. huillensis*, the stream water was highly mineralized (880–1015 mg/L of total dissolved solids, TDS) with a neutral to slightly alkaline pH (6.7–7.9), high temperatures (24–25°C), dissolved oxygen (5.0–8.2 mg/L), total alkalinity (251–276 mg $CaCO_3$/L), high ion concentration (29–54 meq/L of total ionic concentration, 1060–1508 µS/cm specific conductance, K25) and calcium/sulfate dominance (Table 2). Dissolved inorganic nitrogen (DIN) and dissolved reactive phosphorous (DRP) showed a dissimilar behavoir: DRP was consistently low, whereas DIN was quite variable, with high values of N-NO_3^-. As a consequence, the DIN : DRP ratio (3–5 ratio) always showed a phosphorous limitation (taking into account an equilibrium level or Redfield ratio, equal to 16) (Steinman & Mulholland 1996). The physical (temperature, irradiance and depth) and chemical (TDS, total alkalinity, bicarbonate, sulfate, silicate, total hardness, calcium hardness, calcium, sodium and potassium) characteristics (Table 2) were consistent in the three sampling periods (VC < 10%). The remaining physical and chemical variables (carbonates, chloride, hardness, DRP, nitrites, ammonia and DIN : DRP ratio) had a wider variation (VC, 20–235%); the high VC in chlorides can be considered as a result of its very low concentrations, and as a result of pH changes for carbonates.

Gametophytes and 'Chantransia' stages of *S. huillensis* tended to occur in fast current (60–170 cm/s) and shaded (33.1–121 µmol photons/m^2/s)

Table 3. Seasonal variation in frequency of occurrence of vegetative and reproductive phases for the *Sirodotia huillensis* population from Santa Anita Stream, central Mexico

	Rainy season 21.xi.2003	Dry season 31.i.2004	15.v.2004
Frequency of occurrence (%)			
Male	–	39	68
Female	–	1	21
'Chantransia' stage	100	60	11
Gametophytic: 'Chantransia' stage ratio	–	0.6–2.0	2.3–23.0
		1.2 ± 0.7	9.4 ± 8.0
Male : female plant ratio	–	3.0–5.0	1.0–7.0
		4.0 ± 1.4	3.4 ± 1.8
Gametophytic: carposporophytic plants ratio	–	Without carposporangia	1.6–7.1
			4.1 ± 2.7

stream segments (Table 2). Current velocity varied widely throughout the study period, with the highest values observed in the rainy season and the lowest during the dry season. The population of *S. huillensis* varied throughout the study period in terms of frequency of occurrence (Table 3). 'Chantransia' stages were found with the highest frequency values (100%) in the rainy season and the lowest frequencies were found in the dry season (11%). Frequency of female and male gametophytic plants showed a clear pattern, with the highest values during the dry season (21 and 68%, respectively) and the lowest during the rainy season (1 and 39%, respectively). The highest male : female plant ratios were observed in the rainy season (Table 3). Gametophytes were not observed during the dry season. The gametophytic : carposporophytic plant ratio was low during one sampling date in the dry season and no carposporangia were found in the other sampling date and the rainy season. *S. huillensis* occurred associated with other freshwater Rhodophyceae during the dry season: *Compsopogon coeruleus* (C. Agardh) Montagne, *Thorea hispida* (Thore) Desvaux and *Hildenbrandia angolensis* Welwitsch ex W. West et G. S. West.

DISCUSSION

The gametophytes of the *S. huillensis* population from central Mexico present several peculiar characteristics. They contain a conspicuous mucilaginous layer in axis nodes and a marked sexual dimorphism. Female and male thalli differ in color. Female plants have a greater concentration of phycocyanin, with a dark green color, whereas male gametophytes have a greater phycoerythrin concentration, and therefore have a dark blue–green color. The female gamethophytes bear particularly long carpogonia (up to 60 μm in length), longer than those reported for other *Sirodotia* species (≤46 μm, Kumano 2002), but are within the range reported by Necchi (1991) for *S. delicatula* (25–60 μm, as *B. delicatulum*) for Brazil. The presence of pericentral cells with up to three carpogonial branches is similar to *S. sinica* with two carpogonium in one basal cell (Kumano 2002). The spermatangia arrangement in dense clusters agree with Necchi *et al*. (1993) and seems to be a good morphologic character to distinguish *S. huillensis*. The morphometric and morphological characteristics of the 'Chantransia' stages of *S. huillensis* are similar to those reported for natural and culture populations of *Batrachospermum* and *Paralemanea* species (Zucchi & Necchi 2003) or *pygmaea* 'Chantransia' according to Pueschel *et al*. (2000). No evidence of meiosis or gametophyte development was observed in the 'Chantransia' stages of the Mexican population, as is reported by Balakrishnan and Chaugule (1975). Instead, we observed the development of gamethophytes related to the dome-shaped structures. This fact is similar to what Necchi and Carmona (2002) found in *Batrachospermum* sp. and *S. delicatula* with a system of rhizoidal filaments or basal prostrate mass with aggregated filaments from which new gametophytes are produced. This feature can considerably increase the formation of new gametophytes from the same plant of the 'Chantransia' stages and enhance the vegetative reproduction of gametophytic plants under favorable conditions. The diploid chromosome number in gonimoblast cells and haploid number in the dome-shaped structures confirm the occurrence of the carposporangia and meiosis, respectively, in agreement with the morphological characteristics. Chromosome numbers are similar to those reported for several species of *Batrachospermum* in North and South America ($n = 3$–6, rarely 9, Necchi & Sheath 1992; Sheath & Cole 1993; Necchi & Carmona 2002), but considerably lower than those reported from Europe ($n = 14$, Del Grosso 1981). The reasons for differences in chromosome number in Batrachospermaceae remain unknown, although some cases could be related with polyploidy (Sheath & Cole 1993).

Gametophytic plants of the *S. huillensis* population are restricted to very specific microhabitat conditions, such as low irradiance, boulder as the substratum and particularly high current velocity. Several characteristics seem to be adaptations to high current velocity: (i) the presence of wide mucilage surrounding the thallus, which could be interpreted as a biomechanical adaptation in reducing the drag; (ii) the development of long and profuse trichogyne and high male to female ratios increase fertilization success; and (iii) abundant dome-shaped structures associated with the 'Chantransia' stages, which offer lower mechanical resistance to water flow and produce several gametophytes. The frequency of female/male gametophytes varies considerably from the dry to rainy season and could be additionally related with the variation in nutrients. The 'Chantransia' stages occurred under different physical and chemical conditions, a trend that suggests tolerance to relatively wide seasonal fluctuations. This fluctuation in ion concentration and current velocity typically occur in rivers from tropical and subtropical regions with marked dry and rainy seasons and relatively narrow variation in temperature (Necchi *et al*. 1999; Sherwood & Sheath 1999; Carmona *et al*. 2004). *S. huillensis,* as with other species of rodophytes studied, has a pantropical distribution and develops in running waters with high specific conductance and high temperatures (Vis *et al*. 1992; Carmona & Necchi 2001; Carmona *et al*. 2002). However, *S. huillensis* is not common in the study area and populations are always restricted to microhabitats with high current velocities and turbulence (>60 cm/s). This fact suggests special morphological and physiological adaptations to stress by water motion that permits successfully competition with other species.

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