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Phenology of *Compsopogon coeruleus* (BALBIS) MONTAGNE (Compsopogonaceae, Rhodophyta) and evaluation of taxonomic characters of the genus

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Phenology of *C. coeruleus* was studied monthly in a third order stream in São Paulo State, southeastern Brazil, from December 1987 to December 1988. All currently employed characters of *Compsopogon* were evaluated and related to stream variables (temperature and current velocity) and local rainfall. Plant height and diameter and size of monosporangia and cortical cells varied significantly throughout the year and between summer (January to March) and winter (July to September). Plant height and diameter were negatively correlated with current velocity and temperature, whereas size of monosporangia and cortical cells were positively correlated with one another. Number of erect branches on the basal system was dependent on the type of basal system and positively correlated with current velocity. Percentage of plants with basal disc and that of plants without basal system was positively and negatively correlated with current velocity, respectively. Rainfall altering seasonal stream current velocity was the key factor controlling phenology of *C. coeruleus*. The variability of taxonomic characters extends to the limits of most species presently recognized within the genus. The difficulties in defining reliable features for species identification and in establishing well defined circumscription for the species of *Compsopogon* were evident.

Key Index Words: Brazil—Compsopogon coeruleus—*phenology*—*Rhodophyta*—*taxonomy*.

The genus *Compsopogon* MONTAGNE is classified in the family Compsopogonaceae, whose members are characterized by possessing a row of axial cells surrounded by a cortex of variable number of layers (BOLD and WYNNE 1985, BOURRELLY 1985) and monospore formation by means of a curved wall (KRISHNAMURTHY 1962). The allied genus *Compsopogonopsis* is also classified in this family and differs from *Compsopogon* in the way of cortex formation (KRISHNAMURTHY 1962). Detailed generic descriptions are found in KRISHNAMURTHY (1962), BOLD and WYNNE (1985) and BOURRELLY (1985). *Compsopogon* was monographed by KRISHNAMURTHY (1962) who recognized six species. Later, five new species were described: *C. argentinensis* (PUJALS 1967), *C. lusitanicus* (REIS 1977), *C. occcidentalis* (TRACANA 1980), *C. corticrassus* (CHIHARA and NAKAMURA 1980) and *C. prolificus* (YADAVA and KUMANO 1985). The more important taxonomic features for species delineation are: type of basal system, size of plant, branches, cells and monosporangia, number of cortical layers and of erect branches on the basal system (KRISHNAMURTHY 1962, BOURRELLY 1985).

According to KRISHNAMURTHY (1962) *C. coeruleus*, the type species of the genus, is the most widespread of the genus and presents the widest range of taxonomic characters. Variability of *Compsopogon* characters has been confirmed by authors who worked with specimens grown in culture. NICHOLS (1964) demonstrated the great variability of some characters used to distinguish species such as basal system, monospore, branching, spore germination and young plantlets, and that they are not of taxonomic value. SHYAM and SARMA (1980) studied specimens of *Com-*

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psopogon combining characteristics of *C. coeruleus, C. corinaldii* and *C. hookeri* in culture. Their study provided evidence that the morphological characters employed for specific delimitation within the genus are highly flexible and unreliable as taxonomic criteria. They stated that on the basis of cultural observations most of the earlier described species in the literature may probably be ecophenes of one and the same alga. NICHOLS (1964) and SHYAM and SARMA (1980) pointed out that if such wide variation occurs within the relatively restricted conditions of the laboratory its occurrence in nature, where the conditions are more diverse, must be considered. Inconsistencies in the infrageneric classification system of *Compsopogon* have been demonstrated (ENTWISLE and KRAFT 1984, NECCHI 1989), especially as to definition of taxonomic criterions for species identification. Some authors (ENTWISLE and KRAFT 1984, NECCHI 1989) have supported the view of SHYAM and SARMA (1980) on ecophenes.

No detailed study on phenology of *Compsopogon* species has been carried out. This investigation was undertaken with the purpose of studying the phenology of *C. coeruleus* and to evaluate the usefulness of the taxonomic characters currently employed for species identification within the genus.

Material and Methods

Phenology of *C. coeruleus* was investigated monthly in a third order stream (STRAHLER 1957) from October 1987 through October 1988. The stream (Córrego da Piedade) is situated in São José do Rio Preto, São Paulo State, southeastern Brazil (20°49′S, 49°27′W). Field work was conducted in a stream reach of 10 m, where the species population developed profusely. Plants were predominantly epiphytic on submerged roots of marginal vegetation and fixed on sticks and, to a lesser extent, epilithic on stones in the stream bed.

Two stream variables were determined: water temperature and current velocity. Temperature was taken at the midpoint of the reach with a mercury thermometer. Surface current velocity was determined by measuring the time required for a fishing float to travel along the 10 m reach. Five measures were taken and the mean calculated. In addition, local rainfall values were obtained from Regional Agricultural Division, Agricultural Secretary of São Paulo State.

A representative sample was monthly collected by hand at successive 1 m transects along the reach and immediately transported to the laboratory where 20 plants were casually chosen from the sample and preserved in a 4% formaldehyde : distilled water solution for study. The remaining part of the sample was taken to estimate the dry weight. Along the study period a total of 260 plants were examined. Voucher specimens were lodged at the Herbarium of Botany Institute, São Paulo (SP).

All characters referred to by KRISHNAMURTHY (1962) and BOURRELLY (1985) were analysed: morphological (type of basal system, shape of monosporangia and cortical cells), morphometric (plant height and diameter, size of monosporangia, cortical cells, axial cells and uniseriate branch cells and width of disc holdfast) and meristic (number of cortical layers and of erect branches on the basal system). Two measures of plant diameter were taken: one at the basal (largest) and other at the apical (smallest) portion. Twenty measures of monosporangia

Table 1. Seasonal values of temperature and current velocity in the stream studied and local rainfall from December 1987 to December 1988.

Season	Temperature (°C)	Current velocity (cm s^{-1})	Total rainfall (mm)
Summer	22−26.5 24.3±1.7*	70−83 82.0± 5.3*	720
Fall	19−22 20.5±1.5	73.5−83 72.7± 9.5	135
Winter	18.5−21 19.7±1.2	30.8−45 43.7±12.1	0
Spring	21−25 23.8±1.9	33−75.5 53.7±18.8	280

* Mean ± standard deviation (n=3).

and cortical cells were taken for each plant, ten at the basal and ten at the apical portion of the plant. We considered the longest axis of these structures since they are irregularly shaped. Width and length of axial cells were measured in the same way as for plant diameter, while for uniseriate filament cells one measure was made near the corticated portion and other near the apex. For observations of axial cells or cortical layers, free hand cross or longitudinal sections were made, when necessary, using razor blades. During the course of the study more than 11,000 measurements or countings were taken.

For obtaining dry weight samples were dried at 85°C to constant weight. Results were expressed as weight (g) per unit area (m^2), based on a gross estimate of the area sampled.

Descriptive statistics (mean and standard deviation) were calculated for the results obtained, as well as analysis of variance (ANOVA—one way) and Pearson's moment product correlation coefficient (SOKAL and ROHLF 1981). Tests were conducted with the computer program APP-STAT (Statistical Package for Apple II Computers) (ANONYMOUS 1985), using an Apple IIe microcomputer.

Results

Phenology

Water temperature ranged from 18.5°C (August) to 26.5°C (December 1988) with a yearly mean of 22.7°C. Seasonally, temperature was maximal during summer (seasonal mean of 24.3°C) and minimal in winter (19.7°C) (Table 1). Current velocity ranged from 30.8 cm s^{-1} (September) to 83 cm s^{-1} (March), with yearly mean of 56.2 cm s^{-1}. Seasonal mean was maximal during summer (82 cm s^{-1}) and minimal in winter (43.7 cm s^{-1}) (Table 1). Current velocity was positively correlated with rainfall ($r=0.65$, $p<0.05$); values of spring were closer to the ones of winter, corresponding to the dry season (late fall to early spring with 205 mm of rainfall), whereas velocities of fall were closer to the ones of summer, coinciding with the rainy season (late spring to early fall with 930 mm of rainfall) (Table 1). In contrast, values of temperature during spring were closer to the ones of summer, while those of fall were closer to the winter temperatures. Local rainfall ranged from 0 in winter (July to September) to 219 mm (February) with a yearly total of 1135 mm (Table 1).

Plant height varied significantly during the study period ($F=54.22$, $p<0.001$) and between the two most clearly distinct seasons (summer—January to March—and winter—July to September) ($F=39.27$, $p<0.001$). Height was minimal in December 1987 (2.7±1.9 cm, monthly mean±standard deviation) and maximal in July (32.5±11 cm) (Fig. 13). Among the stream variables analysed, height was negatively correlated with current velocity ($r=-0.78$, $p<0.01$) and temperature ($r=-0.79$, $p<0.01$).

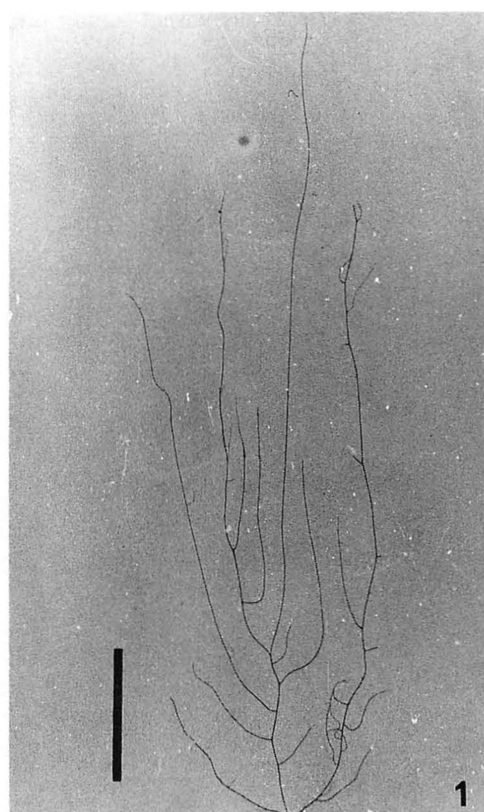


Fig. 1. Habit of a dried small plant of *Compsopogon coeruleus* (June). Scale bar=2 cm.

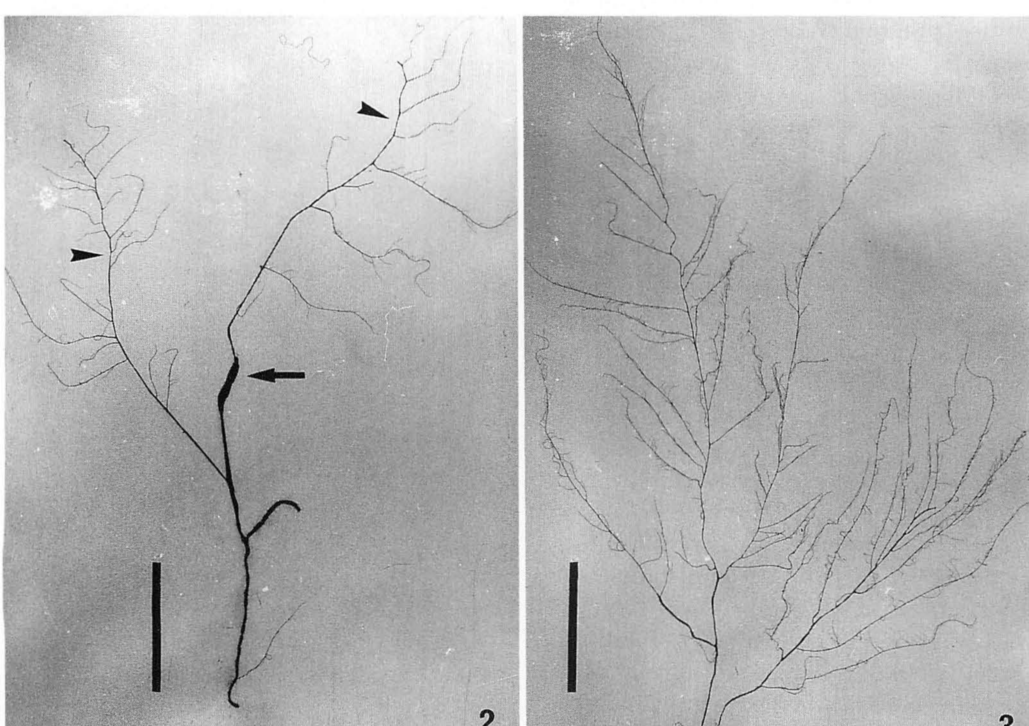
Height was positively correlated with percentage of plants without basal system ($r=0.86$, $p<0.001$) and diameter ($r=0.83$, $p<0.001$) and negatively with percentage of plants with basal disc ($r=-0.86$, $p<0.001$).

Plant diameter varied significantly throughout the year ($F=8.82$, $p<0.001$) and between summer and winter ($F=7.09$, $p<0.001$). Monthly mean diameter was minimal in December 1987 (116 ± 57.8 μm) and maximal in September (882 ± 850 μm) (Fig. 13). As regards stream variables plant diameter correlated negatively with current velocity ($r=-0.83$, $p<0.01$) and temperature ($r=-0.61$, $p<0.05$). Diameter correlated positively with percentage of plants without basal system ($r=0.84$, $p<0.001$) and height ($r=0.83$, $p<0.001$) and negatively with percentage of plants with basal disc ($r=-0.83$, $p<0.001$).

Length of cortical cells varied significantly during the entire study period ($F=14.32$, $p<0.001$) and between summer and winter ($F=5.34$, $p<0.001$). Monthly mean length was minimal in September (21.2 ± 2.5 μm) and maximal in April (27.5 ± 2.9 μm) (Fig. 13). There was no correlation between length of cortical cells and current velocity or temperature. A positive correlation was found between cortical cell and monosporangia length ($r=0.59$, $p<0.05$).

Monosporangia length varied significantly throughout the year ($F=4.81$, $p<0.001$) and between summer and winter ($F=4.84$, $p<0.001$) with a minimum monthly mean in September (14.6 ± 1.2 μm) and maximum in March (16.4 ± 1.7 μm) (Fig. 14). There was no correlation between monosporangia length and stream variables, but a positive correlation was verified with cortical cell length ($r=0.59$, $p<0.05$).

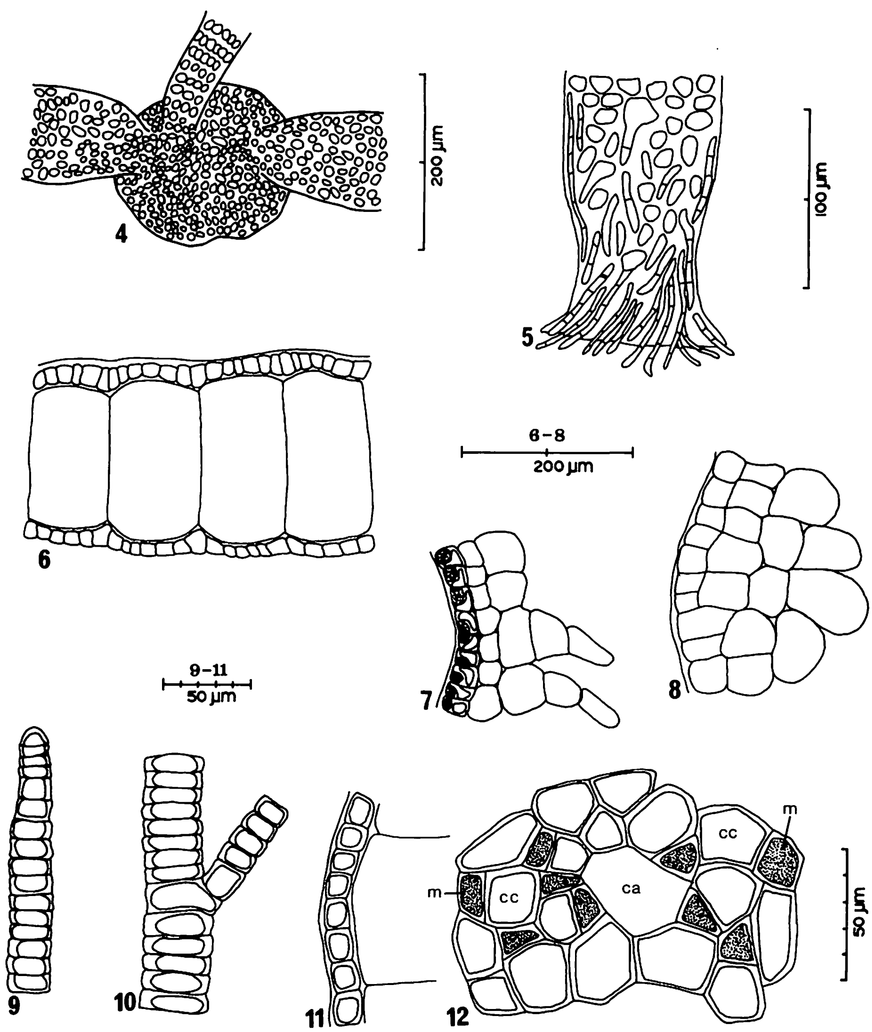
Number of erect branches was dependent on the type of basal system: plants fixed by



Figs. 2 & 3. *Compsopogon coeruleus*. Habit of dried plants. 2. Large plant with saccate (arrow) and normal (arrowheads) portions (July). 3. Large plant (July). Scale bars=5 cm.

rhizoids had always a single erect branch, whereas those fixed by basal disc always had more than one erect branch. This character was positively correlated with current velocity ($r=0.90$, $p<0.001$) and also with percentage of plants with basal disc ($r=0.75$, $p<0.01$) and negatively with percentage of plants without basal system ($r=-0.67$, $p<0.05$), height ($r=-0.61$, $p<0.05$) and diameter ($r=-0.59$, $p<0.05$).

Type of basal system was highly variable throughout the study period. The proportion of plants fixed by basal disc was high (45–85%) from December through June, low (0–25%) from July to October and high again (65–75%) in November and December. Plants without basal system were absent from December to April, fluctuated in their propor-



Figs. 4–12. *Compsopogon coeruleus*. 4. Basal disc with three erect branches (February). 5. Basal portion with rhizhoids (June). 6. Longitudinal section of a small plant showing axial cells and one cortical layer (February). 7. Cross section of a saccate plant showing monosporangia on outer cortical layer and short filaments growing towards the inner part of the thallus (September). 8. Cross section of a saccate plant showing three to four-layered cortex (July). 9. Apical portion of a uniseriate branch (July). 10. Basal portion (near cortication) of a uniseriate branch (February). 11. Longitudinal section of a small plant with one-layered cortex (February). 12. Surface cortex view of a saccate plant showing cortical cells (cc), monosporangia (m) and a cavity (ca) among the cortical cells (July).

Table 2. Taxonomic characters of *Compsopogon* species referred to in the literature and of the specimens presently studied. Data from the protologues and KRISHNAMURTHY (1962).

Species	Height (cm)	Basal system	Erect branches number	Diameter (µm)	Cortical cells size (µm)	Cortical layers number	Monosporangia size (µm)	Microsporangia	Spine-like branches	Axial cell size (µm)	Uniseriate branch size (µm)
C. coeruleus (BALBIS) MONTAGNE 1846	20–40	rhizoids	1	up to 2000	16–48 × 9–20	≥1	20–22	8–9 µm	(−)	100 × 48	16–26 × 9–19
C. hookeri MONTAGNE 1846	>50	rhizoids	1	up to 2000	18–24 × 12–18	≥1	13–18	(−)	(−)	—	14–22 × 8–10
C. aeruginosus (J. AGARDH) KÜTZING 1849	±20	—	1–2	up to 500	19–32 × 9–19	1–2	9–13	(−)	(+)	—	19–28 × 6–16
C. corinaldii (MENEGHINI) KÜTZING 1849	<5	basal disc 64–78 µm	few	±200	12–22 × 9–12	1	9–13	(−)	(−)	—	12–26 × 9–19
C. chalybeus KÜTZING 1849	5–10	basal disc 64–100 µm	2–4	—	16–28 × 12–19	1	12–16	(−)	(−)	—	32–38 × 16–22
C. iyengarii KRISHNAMURTHY 1957	up to 20	basal disc 450 µm	several	120–250	8–24 × 8–16	≥1	12–15	(−)	(−)	—	12–16 × 6–10
C. argentinensis PUJALS 1967	up to 26	disc rhizoids	1–6	up to 1200	10–30 × 13–46	1–3	10–23	(−)	(−)	56–85 × 30–36	13–36 × 3.3–22
C. lusitanicus REIS 1977	30–32	disc rhizoids	1–7	300–950	—	2–3	(−)	8–10 µm	(−)	30–255 × 180–225	30–35
C. occidentalis TRACANNA 1980	38	disc rhizoids	1 to several	up to 1450	13–58 × 10–45	1–3	10–18	(−)	(−)	20–530 × 23–450	—
C. corticrassus CHIHARA and NAKAMURA 1980	50–80	basal disc	several	2000–3000	14–36 × 7–20	3–4(−5)	16–22	(−)	(−)	—	—
C. prolificus YADAVA and KUMANO 1983	up to 42	disc rhizoids	1–2	up to 200	16–30 × 6–16	1–3	15–20	10–18 µm	(−)	44–50 × 58–70	—
Specimens studied	0.5–68	disc rhizoids	1–38	30–3000 (−10000)	7.5–55	1–4	7.5–27.5	(−)	(−)	(10−)50–330 × (5−)20–320	10–55(−165) × 3–15(−17.5)

tion from May to October (10-90%) and represented a small fraction of the population in November and December (10-15%). Proportion of plants fixed by rhizoids was relatively stable from December to May (15-25%), alternated with those without basal system from June to October (10-55%) and was stable in November and December (15-20%). Plants without basal system were found more abundantly in times of low current velocity (July to September) and a negative correlation was observed between percentage of plants without basal system and that variable ($r=-0.88$, $p<0.01$). In contrast, percentage of plants with basal disc was positively correlated with current velocity ($r=0.98$, $p<0.001$).

Dry weight ranged from 0.051 g m^{-2} (December 1988) to 5.519 g m^{-2} (August) with a yearly mean of 1.172 ± 1.716 g m^{-2} (Fig. 14). There was a positive correlation of dry weight with plant height ($r=0.81$, $p<0.001$) and diameter ($r=0.94$, $p<0.001$). Among stream variables dry weight was negatively correlated with temperature ($r=-0.70$, $p<0.05$) and current velocity ($r=-0.74$, $p<0.01$).

In general, we observed low values of dry weight (0.051-1.228 g m^{-2}) (Fig. 14), small plants (monthly mean 2.7-14.7 cm high, 116-202 μm in diameter) (Fig. 1), with one, rarely two cortical layers (Figs. 6 & 11) and relatively few monosporangia from October to June (spring to fall); high values of dry weight (2.033-5.519 g m^{-2}), large plants (22.8-32.5 cm high, 524-882 μm in diameter) (Fig. 3), with (1-)2-4 cortical layers (Fig. 8) and monosporangia covering corticated portions of the plants (Fig. 12) were found from July to September (winter). In addition, saccate plants (Figs. 2, 7 & 12) were encountered in winter. They were formed by degeneration of axial cells in old and large plants.

Taxonomic characters

The range of each character analysed for the population of *C. coeruleus* is summarized in Table 2. Monosporangia (Figs. 12 & 14) were the only reproductive structures observed. They were very variable in shape, being round, elliptical, ovoid, fusiform or irregularly polygonal (triangular to hexangular) in surface view. Cortical cells (Fig. 12) were irregularly polygonal or round, ranging from triangular to hexangular. Two morphological characters observed in the *C. coeruleus* population were never reported for the genus. Some short filaments growing towards the inner portion of the thallus were observed in some saccate plants of *Compsopogon* (Fig. 7). They are probably related to mechanical sustentation of the thallus, since these plants do not have axial cells. Some cavities situated among the cortical cells (Fig. 12) were often observed on the surface of saccate plants, which presumably resulted from release of contiguous monosporangia.

Discussion

Phenology of *C. coeruleus* in the stream studied was greatly influenced by current velocity and water temperature. Variation of characters such as plant height and diameter, type of basal system and number of erect branches on the basal system were highly and negatively correlated with current velocity. This observation could be considered in terms of mechanical adaptation of the thallus of *Compsopogon* to avoid effects provoked by high current velocities. Sheath and Hambrook (1988) found that the value of breaking stress of the *Compsopogon* thallus was one of the highest among freshwater red algae. They classified *Compsopogon* as a semi-erect, non mucilaginous filamentous form, which was accepted as more resistant to mechanical stress of flow than crustose, tufts or mucilaginous filamentous forms. Values of current velocities reported by them for *C. chalybeus* (14-59, mean of 36 cm s^{-1}) are comparatively lower than the present ones, however, our yearly mean fits within their values. They proposed that freshwater red algae have evolved different mechanisms to exist in moderate flow and suggested that the constant flow of stream environements has been a major evolutionary influence in determining thallus form of freshwater red algae. The strategy exhibited by the population of *C. coeruleus* is presumably an adaptation to current velocity: a small plant fixed by basal disc and with numerous erect filaments is supposedly more adapted to live under higher current velocities than a large plant fixed by rhizoids and with a single erect filament.

According to SHEATH (1984) most freshwater red algae exhibit maximum biomass and growth in the period from late fall to early summer in temperate regions. Our results of dry weight, plant height and diameter essentially agree with his statement but revealed a shorter period of maximum growth (winter). SHEATH and HAMBROOK (1988) pointed out that seasonal occurrence of freshwater rhodophytes in tropical regions is related to precipitation, in contrast with temperate regions where precipitation is not as seasonally related to rhodophyte occurrence. The present information reinforces this idea. In summary, rainfall altering seasonal stream current velocity is the key factor controlling phenology of *C. coeruleus* in the stream studied.

Temperature influcences latitude, altitude and drainage basin distribution, as well as seasonality of freshwater red algae (SHEATH 1984). *Compsopogon* is accepted as dominantly tropical or subtropical with occurrence at low altitudes. KREMER (1983) found that *Compsopogon hookeri* had the highest photosynthetic rates at 30 to 35°C. Paradoxically, dry weight, plant height and diameter (and presumably growth) here reported were negatively correlated with temperature, though water temperatures were relatively high throughout the year. In addition, during winter a higher proportion of plants were old (indicated mainly by the great quantity of monosporangia) than the ones of summer, whose population consisted essentially of young plants.

The variability of morphologic, morphometric and meristic characters exhibited by the population of *C. coeruleus* practically embraces the limits of most species of the genus. SHYAM and SARMA (1980) commented that *C. coeruleus, C. hookeri* and *C. corinaldii* come close to one another and it appears that *C. hookeri* is a more robust and well developed form, while *C. corinaldii* seems to be a juvenile or developmental stage of *C. coeruleus*. They concluded that there seems to be justification to merge *C. hookeri* and *C. corinaldii* in *C. coeruleus*. They raised the hypothesis that most species are probably ecophenes of the same alga. Following this view, *C. argentinensis, C. lusitanicus, C. occidentalis, C. corticrassus* and *C. prolificus* can be included in the group of well developed, large and more robust forms, while *C. chalybeus, C. aeruginosus* and *C. iyengarii* are identifiable with young or developmental stages of *C. coeruleus*.

KRISHNAMURTHY (1962) based his in-

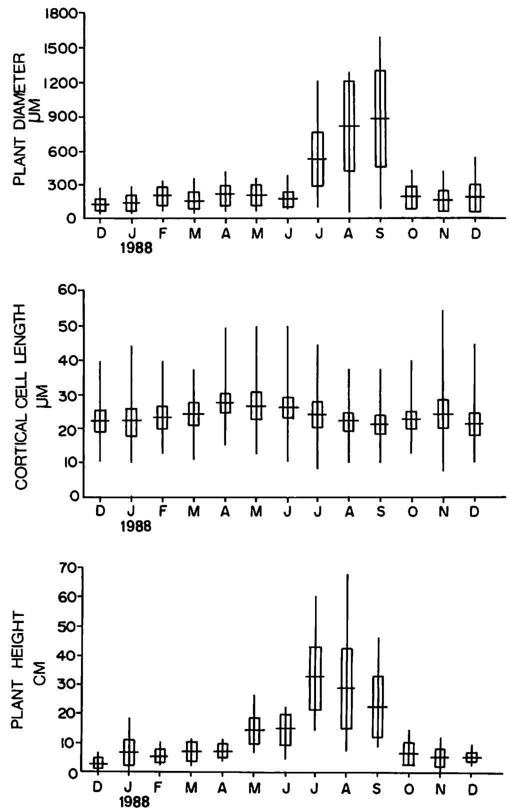


Fig. 13. Variation (mean, standard deviation, minimum and maximum values) in plant height, plant diameter and cortical cell length of *Compsopogon coeruleus* from December 1987 to December 1988.

frageneric system heavily on type of basal system, number of erect branches on basal system and plant dimensions (height and diameter). NICHOLS (1964) demonstrated the great plasticity of type of basal system, which is related to substrate and cultural conditions. Number of erect branches on the basal system was found to be related to and as variable as the type of basal system. It is shown here to be unreliable for species identification. SHYAM and SARMA (1980) found that the length and thickness of the mature plants were quite variable in nature as well as in cultures and, therefore, of no taxonomic value. ENTWISLE and KRAFT (1984) and NECCHI (1989) had difficulties in identifying, respectively, Australian and Brazilian specimens of *Compsopogon* and showed inconsistencies in Krishnamurthy's system. CHIHARA and NAKAMURA (1980) and R. SETO (pers. comm.) regard shape and size of cortical cells, number of cortical layers and size of monosporangia as important characters for species delineation. In the present study these characters were very variable or seasonally related. However, they could be retained as useful criterions if well defined limits among species could be established. NICHOLS (1964) and SHYAM and SARMA (1980) pointed out that if a wide variation was found in relatively restricted culture conditions a wider plasticity would be expected in nature where the conditions are more variable. The present findings are in complete agreement with this supposition and reinforce the recent tendency (SHYAM and SARMA 1980, ENTWISLE and KRAFT 1984, NECCHI 1989) of a drastic reduction of the number of species accepted within the genus. In addition, specimens collected at different times could be identified with distinct species on the basis of the currently accepted criterions.

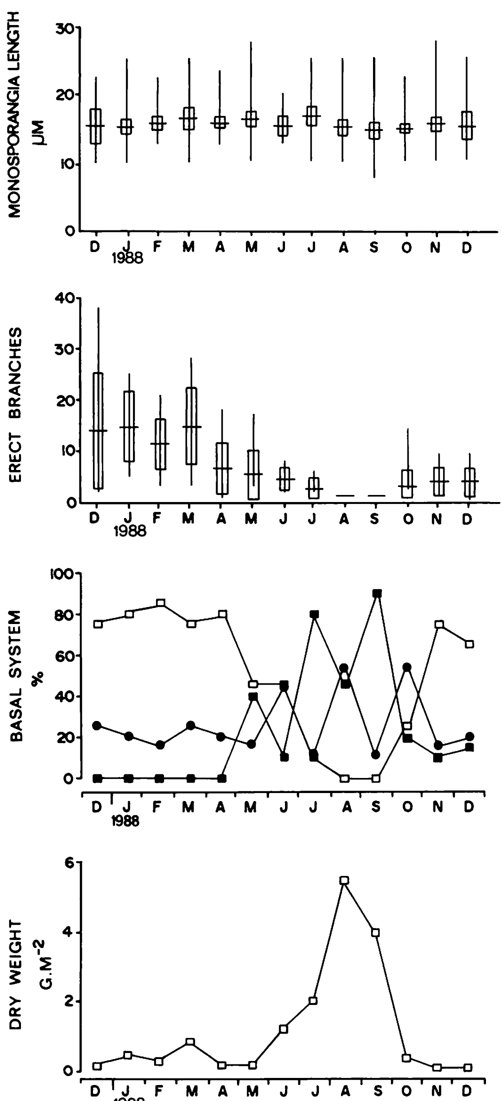


Fig. 14. Variation (mean, standard deviation, minimum and maximum values) in monosporangia length, number of erect branches on the basal system, percentage of the types of basal system (● rhizoids; □ disc-shaped holdfast; ■ without basal system) and dry weight of *Compsopogon coeruleus* from December 1987 to December 1988.

In this study the difficulties in recognizing reliable features for species identification and in establishing well defined circumscription for the species within the genus were clear. We suggest a review of the infrageneric taxonomy of *Compsopogon* in the light of the new information originating from culture and field studies.

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O. NECCHI, Jr.・R. M. GÓES・M. R. DIP：*Compsopogon coeruleus* (BALBIS) MONTAGNE（紅藻オオイシソウ科）の季節的変化とオオイシソウ属の分類形質の評価

Compsopogon coeruleus の季節的変化をブラジル南東部のサンパウロ州の1河川で1987年12月～1988年12月に調査した。現在用いられているこの属の全ての分類形質について，水温・流速・降水量との関連を調べた。藻体の長さと直径，単胞子嚢と皮層細胞の大きさは1年を通してかなり変化し，夏（1月～3月）と冬（7月～9月）とで明確な差が認められた。藻体の長さと直径は流速と水温にたいして負の相関をもち，単胞子嚢と皮層細胞の大きさは互いに正の相関を示した。基部の直立枝は基部の型に依存し，流速と正の相関を示した。盤状基部をもつ藻体の割合および基部系をもたない藻体の割合は，流速とそれぞれ正および負の相関を示した。河川の流速を季節的に変える降水量は，本種の季節的変化を制御している主要因であることが明らかになった。分類形質の変動範囲は，現在この属に含まれている大部分の種の両極端にまで及んでいる。この属の種の同定に使える有効な形質を決めることおよびこの属の種を明確に定義することは，極めて困難である。(Instituto de Biociências, Letras e Ciências Exatas, UNESP, Departamento de Botânica, Caixa Postal 136, 15001-São José do Rio Preto, SP, Brasil)