

Drought Tolerance and Light Requirements of High and Low Sublittoral Species of Mediterranean Macroalgae of the Genus *Cystoseira* C. Agardh (Fucales, Phaeophyceae)

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A comparative study of two Mediterranean macroalgae, the high growing sublittoral *Cystoseira mediterranea* and the low growing sublittoral *Cystoseira zosteroides* was made to evaluate their ability to resist desiccation, their drought tolerance and their photosynthetic light requirements. Desiccation resistance and drought tolerance were markedly higher for the high sublittoral *C. mediterranea*. *Cystoseira mediterranea* lost 50% of its relative water content (RWC) after 3.3 h, whereas *C. zosteroides* lost the same amount of moisture in only 1.1 h of exposure to air in controlled laboratory conditions (20 °C and 75% of relative air humidity). After complete desiccation, only the high sublittoral species was able to rehydrate fully by re-wetting. *Cystoseira mediterranea* was able to maintain its full photosynthetic rate to a RWC as low as 44%, whereas photosynthesis of *C. zosteroides* was reduced in plants with an 80% RWC. Photosynthetic rate was zero in plants of *C. mediterranea* and *C. zosteroides* with a RWC of 18% and 34%, respectively. Photosynthesis-irradiance (P/I) curves of *C. mediterranea* were characteristic of sun adapted species, with high saturating irradiance ($I_k > 1600 \mu\text{mol photon m}^{-2} \text{s}^{-1}$), high irradiance at the compensation point ($I_c = 21 \mu\text{mol photon m}^{-2} \text{s}^{-1}$), and high maximum photosynthetic rate ($P_{\text{max}} = 12.3 \text{ mg C g ash free dw}^{-1} \text{ h}^{-1}$). Conversely, *C. zosteroides* photosynthetic response to light was typical of shade adapted species, exhibiting photoinhibition at irradiances above $800 \mu\text{mol photon m}^{-2} \text{s}^{-1}$, and having comparatively lower I_k ($375 \mu\text{mol photon m}^{-2} \text{s}^{-1}$), I_c ($9 \mu\text{mol photon m}^{-2} \text{s}^{-1}$), and P_{max} ($6.0 \text{ mg C g ash free dw}^{-1} \text{ h}^{-1}$). Our results show that taxonomically and morphologically related plants display marked differences in desiccation resistance, drought tolerance and light requirements, in accordance with the environmental conditions prevailing in their respective habitats.

Introduction

Although the tidal amplitude of the Western Mediterranean Sea is small (Flos 1985), different seaweed belts can be distinguished above and below the mean sea water level (Feldmann 1937, Ballesteros and Romero 1988). *Cystoseira mediterranea* Sauvageau forms a conspicuous belt in exposed and unpolluted sites between the mean seawater level and half a meter depth (Feldmann 1937), while *Cystoseira zosteroides* (Turner) C. Agardh is a deep-water species, developing on pristine rocky substrata from 15 to 60 m depth.

The perennial thalli of *C. mediterranea* encounter regular emersion caused by wave movements. Occasionally (0–3 times per year) 'neap tides', caused by high atmospheric pressure and occurring mainly during the winter until the beginning of spring, can lead to the majority of the community being exposed to air for long periods of time (from 2–3 days to 4 weeks) (Rodríguez-Prieto 1992). Branch production

of *C. mediterranea* shows a strong seasonality, being highest in early spring and lowest in the summer and autumn (Ballesteros 1988, Rull and Gómez 1990, Delgado *et al.* 1994). On the contrary, the also perennial thalli of *Cystoseira zosteroides* are never exposed to air. Branch production also shows a strong seasonality, being highest during late spring (Ballesteros 1990).

Since the distribution of *C. mediterranea* is restricted to the upper levels of the sublittoral zone, this species may be ecophysiologicaly adapted to resist desiccation and high irradiances, while the deep-water species *C. zosteroides* may not possess such adaptation. As both species are taxonomically and morphologically very close, a comparative study was designed to test the capacity of *C. mediterranea* and *C. zosteroides* to resist desiccation, to tolerate drought, and to photosynthesize at different irradiances. This was done in order to evaluate the possible ecophysiological significance of air exposure and irradiance on the distribution of these two species.

Materials and Methods

Study site and species selection

Plants of *Cystoseira mediterranea* were hand collected in exposed zones at the cove of Sant Francesc (Blanes, Spain) (lat. 41°41' N, long. 2°48' E). Plants of *C. zosteroides* were collected by SCUBA diving at 23 m depth off the shore at Sant Elm (Sant Feliu de Guíxols, Spain) (lat 41°46' N, long. 3°02' E). Plants were collected during their respective high branch production period: late February for *C. mediterranea* and the beginning of July for *C. zosteroides*. Special care was taken with *C. zosteroides* to avoid direct sun exposure, placing them in dark plastic bags during transportation to the surface. All plants were carried to the laboratory in insulated and aerated tanks within 1 h. Only terminal healthy branches (2–3 cm long) cleaned of epiphytes were used for the experiments, which were carried out approximately 24 h after collection and sectioning.

Dehydration and rehydration

Six thalli sections were allowed to dehydrate in the laboratory after exposure to air for different periods of time under a controlled temperature of 20 °C (± 1) and a relative air humidity of 75% (± 5). Relative water content of the plant samples (RWC) was calculated as indicated in equation 1, where the intermediate weight was the weight of the dehydrated sample and the dry weight the weight after drying to constant weight at 60 °C for 24 h. In rehydration experiments, six completely desiccated thalli sections were weighed and subsequently submersed in seawater at 20 °C for various periods of time. Relative water content of rehydrated samples was calculated as in dehydration experiments using equation 1.

$$\frac{(\text{intermediate weight} - \text{dry weight})}{(\text{fresh weight} - \text{dry weight})} \times 100 = \text{RWC} \quad (1)$$

Plant incubations

Thalli sections were incubated in seawater for the determination of the photosynthesis/irradiance (P/I) curves and the photosynthetic responses to different degrees of dehydration. In the incubations, filtered seawater (Whatman GFF) was used in 250 mL Winkler bottles provided with magnetic stirrers. Indoor incubators with a controlled temperature of 20 °C (± 1 °C), and cool-white fluorescent tubes (Osram L 40 W), were used for irradiances below 400 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$. For higher irradiances, plant incubations were performed outdoors under direct sunlight, using neutral density fiberglass screens to obtain the desired irradiances. Magnetic stirrers and a thermostatic bath to keep the temperature controlled at 20 °C (± 1 °C) were used in the outdoor

incubations (between 12:00 and 14:00 h). Irradiance was monitored continuously with a Li-cor Li-1000 provided with a spherical Li-cor SPQA quantum sensor. Photosynthetic rate and respiration were measured as variations in the dissolved oxygen concentration, determined to within 0.01 mg L⁻¹ with an Orbisphere Model 2610 oxygen measurement system, after 2 h (productivity) and 4 h (respiration) of incubation. Concerning the amount of sample to be incubated, we followed the recommendations of Littler and Arnold (1982). Carbon productivity values were calculated from oxygen data using a photosynthetic quotient of 1. Photosynthesis/irradiance curves were obtained with fully hydrated thalli sections. Net photosynthetic rate and dark respiration were assayed in 3 replicates at irradiances ranging from 0 to 1700 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ and at 20 °C. Photosynthetic response to different degrees of dehydration was tested in 6 replicates by means of oxygen evolution rates at 330 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ and 20 °C. Desiccated thalli sections were submersed in seawater for 24 h prior to the incubation to provide the incubations with plants rehydrated at the maximum level possible.

Provided that seasonal variability of ash content of the different parts of the thallus of *C. mediterranea* and *Cystoseira zosteroides* were small (Ballesteros 1992), constant values of 32.5% and 51.3% ash contents, respectively, have been used to report rates per ash free dry weight (af dw).

Statistical analyses

The mean squares method was used to adjust the linear part of the P/I curves and the linear part of the photosynthetic responses of dehydrated plants (RWC < 60%). Parameters describing the P/I curves, irradiance at the compensation point (I_c), irradiance at light-saturated photosynthesis (I_k), maximum photosynthetic rate (P_{max}) and slope (α) were calculated as described in Littler and Littler (1992). Differences between regression lines were tested using ANCOVA. The curves describing the time-course dehydration of thalli sections of the two species studied were fitted to negative exponential functions. Tukey's significant difference test was used to locate pairwise differences in photosynthetic rates of plants with different degree of dehydration when ANOVAs were significant (Neter *et al.* 1990). The selected significance level for all statistical treatments, unless otherwise noted, was $p < 0.05$.

Results

Dehydration and rehydration

The process of dehydration of both species fitted negative exponential functions (Fig. 1). Dehydration of *Cystoseira mediterranea* proceeded more than two-

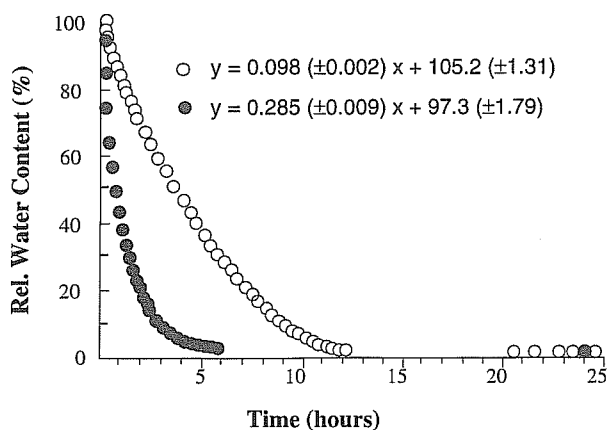


Fig. 1. Time-course of dehydration of *Cystoseira mediterranea* (empty circles) and *Cystoseira zosteroides* (dark circles) at 20 °C and 75% relative air humidity. Each plotted point is the mean of 6 replicates; standard deviations are too small for representation. Determination coefficients for the negative exponential functions fitted were 0.99 for both species ($p < 0.001$; $N = 50$ and 26 , for *C. mediterranea* and *C. zosteroides*, respectively).

fold slower than that of *C. zosteroides*. Plants of *C. mediterranea* lost 50% of their RWC in less than 3.3 h of exposure to air, while it took only a little more than 1 h for plants of *C. zosteroides* to dehydrate to the same extent. Rehydration rates of both species were 2–3 fold higher than their respective dehydration rates (Fig. 2). The highest rehydration levels were two-fold higher in *C. mediterranea* plants compared to *C. zosteroides*. Desiccated plants of *C. mediterranea* rehydrated almost completely after 5 h of immersion, recovering about 93% of their lost water, while after 5 h *C. zosteroides* thalli had not regained more than a 50% of their original water content, a level which was reached by about 2 h after submersion.

Photosynthesis/Irradiance curves

Photosynthesis/irradiance curves of *Cystoseira mediterranea* and *C. zosteroides* were markedly different (Fig. 3). Irradiance at the compensation point (I_c), irradiance at light-saturated photosynthesis (I_k) and maximum photosynthetic rate measured (P_{max}) for *C. mediterranea* were markedly higher than those of *C. zosteroides* ($p < 0.05$; Table I). Photosynthesis of *C. mediterranea* was not saturated at irradiances as high as $1600 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ ($12.3 \text{ mg C g ash free dw}^{-1} \text{ h}^{-1}$), contrasting to the photosynthetic rate of *C. zosteroides* that reached its highest rate at $300 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ while experiencing a reduction at irradiances above $800 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ ($6.0 \text{ mg C g ash free dw}^{-1} \text{ h}^{-1}$). The slope (α) of both P/I adjusted linear regressions were very similar, 0.03 compared to 0.04 (Table I).

Photosynthetic responses to different periods of dehydration

The photosynthetic rate of plants that had been exposed to air was related to their previous degree of dehydration (Fig. 4). *Cystoseira mediterranea* was less affected by desiccation than *C. zosteroides*, based on their photosynthetic responses. Rates began to decrease significantly compared to controls in dehydrated plants of *C. mediterranea* with a relative water content of 44%, and in plants of *C. zosteroides* with a 80% relative water content, though a decrease could have taken place at higher RWC and was not tested. From the linear relationship found for photosynthetic responses of plants with $\text{RWC} < 60\%$, zero photosynthetic rate ($y = 0$) was estimated to occur in dehydrated plants with 18% and 34% RWC, for *C. mediterranea* and *C. zosteroides*, respectively (Fig. 5).

Discussion

Cystoseira mediterranea, the high sublittoral species, appears to be better adapted to the conditions prevailing in the upper sublittoral zone than the low sublittoral species, *C. zosteroides*. Desiccation resistance

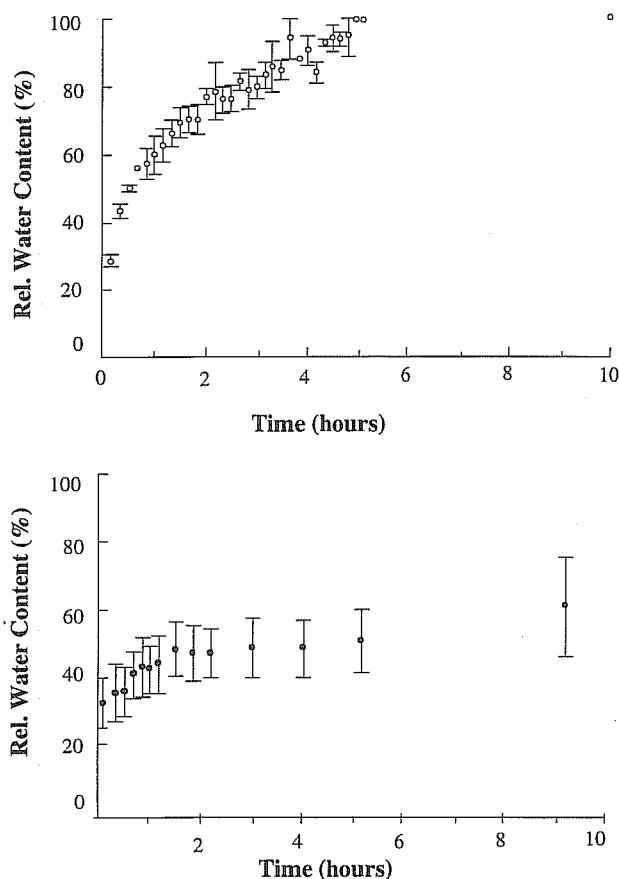


Fig. 2. Time-course of rehydration of *Cystoseira mediterranea* (top) and *Cystoseira zosteroides* (bottom). Plotted points are the mean \pm SD of 6 replicates.

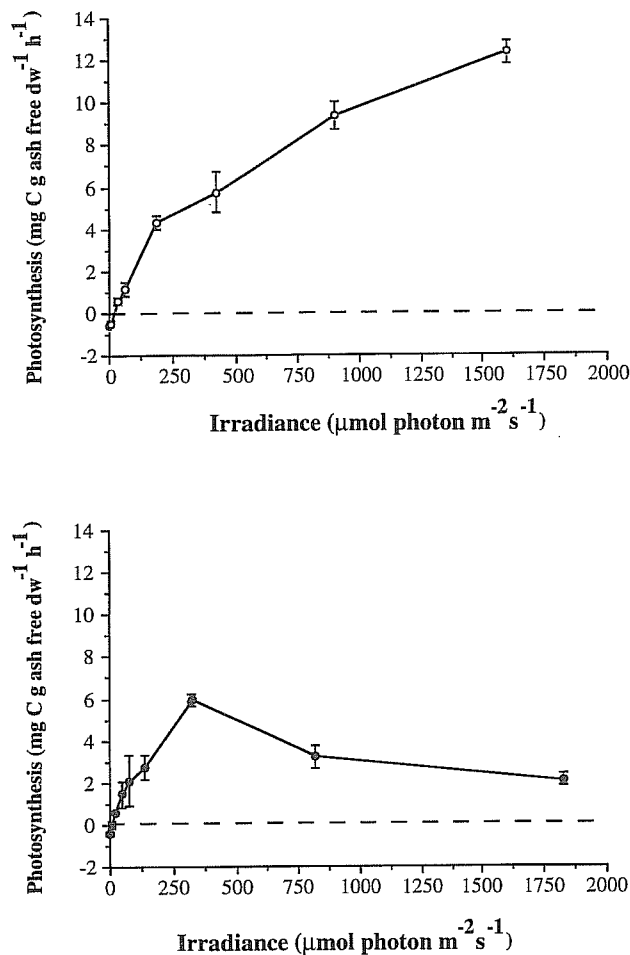


Fig. 3. Photosynthesis/irradiance curves of *Cystoseira mediterranea* (top) and *Cystoseira zosteroides* (bottom). Means \pm SD of 3 replicates.

and drought tolerance (*sensu* Brown 1987, Lüning 1990) were markedly higher for *C. mediterranea*. Plants of *C. mediterranea* dehydrated at a much slower rate than those of *C. zosteroides*. A high desiccation resistance has also been shown for numerous intertidal benthic macroalgae (Oates and Murray 1983, Beer and Kautsky 1992, Lipkin *et al.* 1993). After complete desiccation, restoration of the initial hydration was only achieved by plants of *C. mediterranea*, whereas plants of *C. zosteroides* could only regain approximately half of their initial moisture.

Photosynthetic rates of plants that had undergone drying depended on species and degree of dehydration. Differences in tissue composition could explain the higher capability of *C. mediterranea* for resisting desiccation (slower dehydration rates) compared with *C. zosteroides*. Species of the genus *Cystoseira* contain alginates in high amounts (from 10 to 30% dry weight) (Pellegrini 1970, Baghdadli *et al.* 1990) and it has been shown for many intertidal macroalgae that water-retaining substances and resistance to desiccation are related (Levitt 1972, Schonbeck and Norton 1979 a, 1979 b, Kloareg and Quatrano 1988, Jacob *et al.* 1992). Ash contents of 32 and 51% dw, for *C. mediterranea* and *C. zosteroides*, respectively, suggest different tissue composition. Not only the compounds themselves, but their stereochemistry, along with the structure of cell membranes, cell walls, and matrix, may be important factors accounting for the physiological resistance to exposure to air in macroalgae (Kloareg and Quatrano 1988, Jacob *et al.* 1992). The effect of environmental conditions may also play an important role, *e.g.* in the polysaccharide mercerization in the relatively saltier surface waters, or in determining the ultrastructural changes of the cell membranes following desiccation (Wiltens *et al.* 1978). Conversely, as thallus morphology of both species of *Cystoseira* are similar, it is most unlikely that the surface to volume ratio *sensu* Dromgoole (1980) could explain the differences observed in their respective drought resistances.

The high sublittoral *C. mediterranea* showed photosynthetic characteristics of sun adapted species *sensu* Ramus (1981), as has been pointed out for other medium-sublittoral species of the genus (Coudret and Jupin 1985), whereas the low-sublittoral *C. zosteroides* is considered light-shade adapted *sensu* Lüning (1990). In a comparative study of the P/I curves of *Cystoseira stricta* (Mont.) Sauvageau and *Cystoseira crinita* (Desf.) Bory, a high- and medium-sublittoral species of the southwestern Mediterranean, similar trends were observed (Tremblin *et al.* 1986). Nevertheless, *C. mediterranea* and *C. zosteroides* showed a similar initial slope of their P/I curves below 400 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$, suggesting a similar photosynthetic efficiency for both species at low irradiances.

Table I. Parameters of *Cystoseira mediterranea* and *Cystoseira zosteroides*: Respiration (R), maximum photosynthetic rate (P_{max}), slope (α), irradiance at the compensation point (I_c), and irradiance at saturated photosynthesis (I_k), obtained from the photosynthesis/irradiance mean squares adjustment.

	R mg C g af dw ⁻¹ h ⁻¹	α mg C g af dw ⁻¹ h ⁻¹ / $\mu\text{mol m}^{-2} \text{s}^{-1}$	I_c $\mu\text{mol m}^{-2} \text{s}^{-1}$	I_k $\mu\text{mol m}^{-2} \text{s}^{-1}$	P_{max} mg C g af dw ⁻¹ h ⁻¹
<i>Cystoseira mediterranea</i>	$-0.64 \pm (0.12)$	$0.031 \pm (0.004)$	21	>1600	12.3
<i>Cystoseira zosteroides</i>	$-0.35 \pm (0.08)$	$0.040 \pm (0.003)$	9	375	6.0

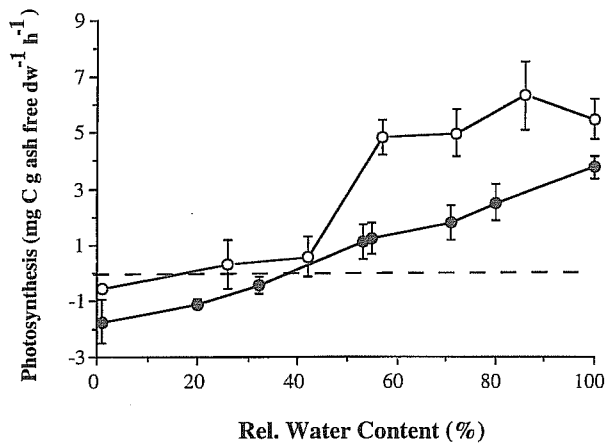


Fig. 4. Photosynthetic rate of thalli sections of *Cystoseira mediterranea* (empty circles) and *Cystoseira zosteroides* (dark circles) dehydrated to different degrees. Measurements were done at $330 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ irradiance and 20°C . Plotted points are means \pm SD of 6 replicates.

The adaptations of the high sublittoral species *C. mediterranea* are of ecological significance to overcome the effect of 'neap tides', after which the succession of the community is reset. The extent to which the community of *C. mediterranea* is pruned back depends on the time and duration of the 'neap tides' (up to 4 weeks) (Rodríguez-Prieto 1992). Field observations have shown a very variable degree of thalli desiccation through the *C. mediterranea* community during 'neap tides' (Rodríguez-Prieto 1992, Frigola-Gironés 1993). In nature, desiccation is minimized by the proper arrangement of the plants in the community. Overlapping of *C. mediterranea* thalli ensures moisture in the inner plants, though frequently at the expense of some of the most exposed plants. The community self-protection effect is specially important during summer 'neap tides', at a time when the community has reached its biomass maximum (Ballesteros 1988), and therefore the higher amount of plants can reduce the deleterious effects of combined emersion and direct sun exposure. These characteristics help to explain why survival possibilities of *C. mediterranea* are much greater in nature

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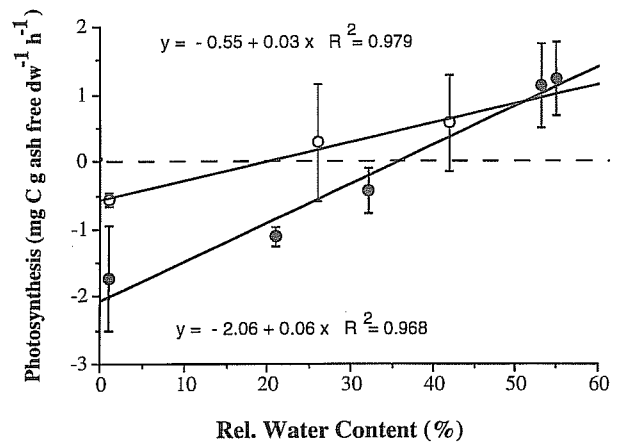


Fig. 5. Mean squares adjust of photosynthetic responses of thalli sections of *Cystoseira mediterranea* (empty circles) and *Cystoseira zosteroides* (dark circles) with relative water contents below 60%. Plotted points are mean \pm SD of 6 replicates.

than predicted on the basis of laboratory experiments.

The above mentioned special adaptations of *C. mediterranea* to air exposure and high irradiances, are coupled to patterns in seasonal growth (Ballesteros 1988) and nutrient dynamics (Delgado *et al.* 1994). All together they allow *C. mediterranea* to take advantage of the high energy and environmental unpredictability associated with the Mediterranean upper sublittoral zone and help to explain the high success of *Cystoseira mediterranea*, one of the most productive seaweeds of the Northwestern Mediterranean Sea (Ballesteros 1989). On the contrary, the low capability to resist desiccation and the light shade adaptation displayed by *C. zosteroides* are in agreement with its deep water habitat and with its light-limited productivity as suggested by Ballesteros (1990).

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