

Diurnal Pattern of Salt Secretion in Leaves of the Black Mangrove, *Avicennia marina*, on the Sinai Coast of the Red Sea¹

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ABSTRACT: *Avicennia marina* (Forsk.) Vierh has a typical diurnal pattern of salt gland activity, with high secretion rate during the day, a peak at noon, declining after sunset, and remaining low throughout the night. The main factor affecting the daily secretion rhythm was radiation, with a 2-hr time lag between the radiation level and the corresponding secretion. This lag might be a result of a salt accumulation phase, or of the time needed to build up photosynthetic product pools, needed to generate ATP through the respiration process, for active salt secretion. Differences between daily secretion patterns of young and mature leaves were not significant, and temperature had little effect on controlling the secretion rhythm.

Avicennia marina (Forsk.) Vierh (Avicenniaceae) is a coastal-swamp halophyte, common in subtropical and tropical regions such as North America, Vietnam, the Pacific region of India, eastern and southern Africa, eastern and southern Australia, and southern New Zealand (Chapman 1960, 1976, Teas 1984, Odum and McIvor 1990). The natural distribution of the species reflects its wide salt tolerance, and previous studies have shown that under laboratory conditions *A. marina* can survive in a wide range of salinities, from 175‰ seawater (Clarke and Hannon 1970) to distilled water (Drennan and Pammenter 1982). The species is sensitive to low temperature (West 1956), but is the only mangrove that can thrive under desert conditions like those found along the Red Sea shores. It forms monospecific stands along the southern shores of the Sinai Peninsula, from Ras Muhamad to Shurat el Arwashie in the Nabq area, the northernmost boundary of the mangrove formation. Elaborate mechanisms allow the survival of *A. marina* in this metahaline environment. First, simple non-metabolic ultrafiltration through selective permeable membranes rejects from 80% (Waisel et al. 1986) to 95% (Scholander 1968)

of the salts in seawater. Second, accumulating salts (the 5–20% that enter the roots) are actively and efficiently secreted through salt glands (Berjak 1978, Fahn 1979, Ish-Shalom-Gordon and Dubinsky 1990).

The aim of the study reported here is to describe the diurnal secretion activity of the salt glands of *A. marina* and the way this pattern is affected by environmental factors and leaf age.

MATERIALS AND METHODS

Site Description

The study was conducted on *A. marina* plants from Shurat el Gharqana, in the Nabq area, on the Sinai coast of the Red Sea. The mangrove stands of the Nabq area have been studied by several authors (Leshem and Levison 1972, Por and Dor 1975, 1984, Por et al. 1977, Evenari et al. 1985, Gara et al. 1986). These stands of *A. marina* are growing on Pliocene fossil reefs and associated deposits, as well as on recent subfossil coral reefs. The salinity in this habitat can be as high as 4.7‰ (Por et al. 1977), above that of the adjacent open sea, which reaches a maximum of 4.1‰ (Reiss and Hottinger 1984). The *A. marina* plants are rooted in the tidal zone, exposed to fluctuations in water levels (50–70 cm

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according to Por et al. 1977), and flushed with seawater by the tides. The diurnal pattern of the wind shows a maximum intensity at midday and low intensity during the morning and afternoon, with velocity usually ranging from 0 to 7 km/h. The winds are an important environmental factor because they blow salty sea spray onto the *A. marina* stems and leaves.

Measurements

Young (2–3 cm long) and mature (6–7 cm long) leaves were rinsed at 2-hr intervals, and the rinse water was collected for salinity analysis. Each leaf was rinsed with 100 ml of distilled water and was left intact, attached to the tree during the whole experiment. The total salt concentration of the solution was determined using a Y.S.I. conductometer (TH-27B). The results were converted to excretion rates in mg salt cm⁻² hr⁻¹ after determination of the leaf area.

It is possible that removal of the secreted product from the leaf surface might have depressed or stimulated glandular activity to a level significantly different from that occurring in a leaf where the secreted product continued to accumulate naturally. However, we believe this disturbance was minor, because the rate of salt secretion is probably determined by the accumulation of excess salts in the plant itself, not on the leaf surface (Ish-Shalom-Gordon and Dubinsky 1990). Furthermore, in nature salt is occasionally removed from the leaf surface by winds.

To elucidate the relationship between salt secretion rates and the diurnal pattern of temperature and light, all parameters were measured at the same time. Each secretion measurement was followed by measurements of temperature and irradiance using a mercury air thermometer (shielded against direct radiation) and a light meter (Li-Cor 185 equipped with a LI-190SB quantum sensor). The same measurements were also done of leaves covered with black plastic bags and clear plastic bags to investigate the relative importance of irradiance and temperature, respectively, by mimicking secretion and temperature change in darkness. The temperature in those plastic bags was also measured. The

contribution of wind-borne sea spray to salt accumulation on the leaves was estimated using abraded glass slides that were placed vertically, close to the experimental leaves. The slides and leaves were treated by the same procedure. The role of these slides was to enable us to estimate the amount of sea-spray salt deposited on the leaf by the wind. By subtracting this amount from the total salt found on the leaves, we calculated the net amount of secreted salt. In the case of the leaves covered with plastic bags, the salt in the rinse water was the net salt secretion, as those leaves were protected from wind-borne salt.

RESULTS AND DISCUSSION

Daily Pattern of Salt Secretion

Figure 1 presents the daily course of salt secretion of young and mature leaves of *A. marina*, and of the temperature and irradiance. The results reveal the typical pattern of gland activity: high levels of secretion during the day, a peak at noon, a decline after sunset, and low levels throughout the night.

The low levels of secretion in darkness found in our work were previously reported in *A. marina* and *Aeluropus litoralis* (Willd.) Parl. (Pollak and Waisel 1979). We suggest that the ability to secrete ions in darkness allows the plant to empty leaf reservoirs that accumulate during the previous day, before a new supply of salt arrives through the transpiration stream. Night secretion is also an advantage because of the prevailing high air humidity and the decrease in water stress. However, Drennan and Pammenter (1982) described a diurnal secretion pattern in *A. marina* with a midday depression and relatively high secretion levels in the morning and afternoon. The contrast between the two studies might result from differences in experimental conditions.

Differences between Salt Secretion of Young and Mature Leaves

Berjak (1977, 1978) was the first to describe a shift from salt secretion through both sur-

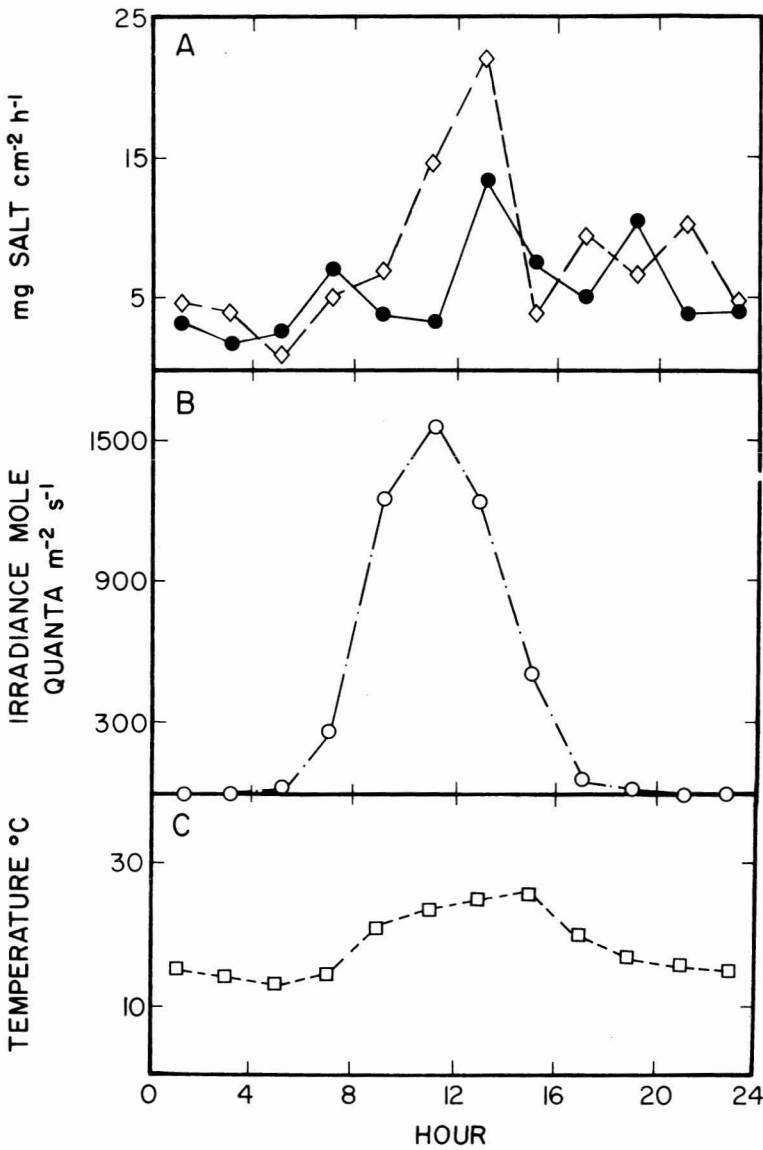


FIGURE 1. Environmental effects on the diurnal pattern of salt secretion of *Avicennia marina*: \diamond , young leaf; \bullet , mature leaf; \circ , radiation; \square , temperature. Each data point represents the mean of 12 replicates, three leaves on every day, on four experimental days.

faces in young leaves to exclusively abaxial secretion in mature leaves, coincident with stomatal development in *A. marina*. Drennan and Berjak (1979, 1980, 1982) described a degenerative decrease in glandular density as the leaf matured, from 8 per mm² in young

leaves to 0.5 per mm² in mature ones, on both sides of the leaf. They believed that secretion in mature leaves occurs only through abaxial stomata. However, according to Drennan et al. (1985), abaxial salt glands of mature leaves continue to secrete. Our results (Figure 1)

show that rates of salt secretion in mature leaves were slower than those in young ones, but this difference occurs mainly at midday and was not significant. Drennan and Berjak (1979) reported that the density of salt glands in mature leaves was only 1/16 that of the young ones. We found that mature leaves secreted at about the same rate as young leaves, which was much more than the 1/16 that was expected if secretion takes place only through the salt glands. It is, therefore, possible that the secretion has another pathway, in addition to the glands, and this may well be through the stomata, as suggested by Drennan and Berjak (1979, 1980, 1982). However, the significantly higher salt gland density ($32.47 \pm 3.27 \text{ mm}^2$) observed in the young leaves in our study site (Ish-Shalom-Gordon and Dubinsky 1990), and different leaves' behavior are also possible explanations for the differences between the two studies. The fact that the salt secretion of mature leaves has a similar diurnal pattern to that of the young ones might imply that salt secretion through stomata is also affected by light.

Relation between Salt Secretion and Photosynthesis

Glandular salt secretion in *A. marina* is thought to be an active process and, as such, requires metabolic energy. This energy cost might be one of the reasons why *A. marina* plants located far from the shore, where salt concentration is higher than in the sea, are smaller and less developed than those growing in the sea. However, there may be other reasons why these plants might grow less, such as lower water supply.

Because the most important metabolic process in plants is photosynthesis, and because salt secretion requires energy, a correlation between these two processes was expected. In *Limonium latifolium* (Sm.) Ktze. (Arisz et al. 1955), *Atriplex* sp. (Luttge 1971), *Aegiceris* sp., and *Aegialitis* sp. (Scholander et al. 1962), salt secretion was light-dependent. Those authors and Raines (1972) suggested that this light-dependence is a result of the effect of light on photophosphorylation or on the

photosynthetic production of respiratory substances. However, salt secretion in *Aeluropus litoralis* (Pollak and Waisel 1979) and in *Aegialitis annulata* R. Br. (Atkinson et al. 1967) was unaffected by light.

The relative importance of irradiance and temperature was examined by measuring the salt secretion of young leaves covered with black plastic bags and with clear plastic bags (Figure 2). Temperatures measured inside those bags are shown in Figure 3. Only small differences were found between air temperatures (18–22°C), temperatures in black plastic bags (19–23°C), and temperatures in clear plastic bags (20–22°C).

Our results clearly show that salt secretion in *A. marina* is a light-dependent process. The secretion rate during the night (Figure 1) and in leaves covered with black plastic was about one-fourth (26.6%) of the rate in daytime. Leaves covered with clear plastic (Figure 2) secreted slightly less salt (82%) than uncovered ones but showed the same diurnal pattern.

The highest correlation coefficient ($R^2 = 0.6$) between salt secretion and irradiance was found when a 2-hr lag between the data sets was introduced (Figure 4). The 2-hr lag might be explained in two ways. One possible explanation is physiological: the time lag is needed to build up salt concentration to a threshold needed for salt secretion. Another possible explanation is metabolic: the observed lag might be a result of the time needed to build up photosynthate pools subsequently utilized to generate ATP through the respiration process.

Salt secretion was more affected by irradiance than by temperature, and there was no significant temperature effect on salt secretion (Figure 1), confirming the results reported by Waisel et al. (1986). However, the correlation coefficient of 0.6 between salt secretion and previous light intensity implies the presence of other minor influences on salt secretion, and temperature might be one of them. Possibly, *A. marina* cannot survive in a cool climate because low temperatures lower salt secretion. Indeed, Shimony (1972) reported that *A. marina* plants kept for 18 hr at 5°C did not secrete at all.

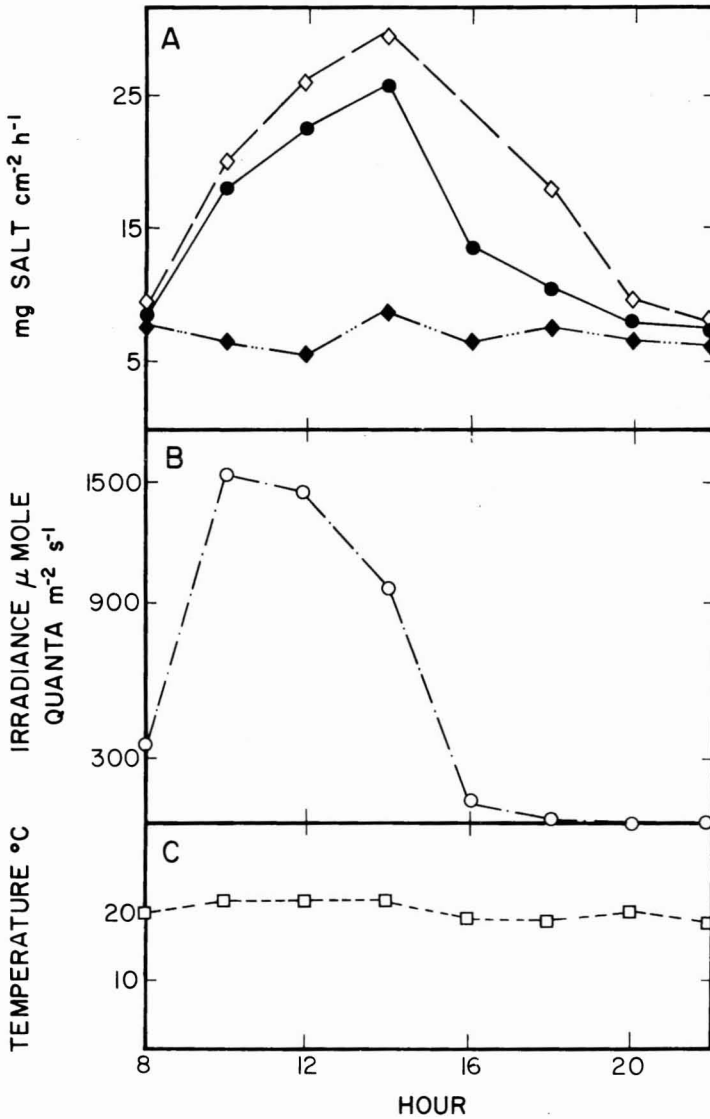


FIGURE 2. Radiation and the diurnal pattern of salt secretion of young *Avicennia marina* leaves: ○, radiation; □, temperature; ◇, control leaf; ◆, leaf covered with black plastic; ●, leaf covered with clear plastic. Each data point represents the mean of 12 replicates, three leaves on every day, on four experimental days.

CONCLUSIONS

Young leaves of *A. marina* have a diurnal salt secretion pattern, peaking at noon. This constant secretion is a light-dependent process, but continues at a slow rate during the night. Mature leaves have the same secretion pattern, but at a lower rate. The 2-hr time lag

between irradiance and secretion might be the result of a salt-accumulation phase before secretion, or of time needed to build up photosynthate pools, subsequently utilized to generate ATP through the respiration process, for active salt secretion. We believe that in the Red Sea stands the first explanation seems more likely.

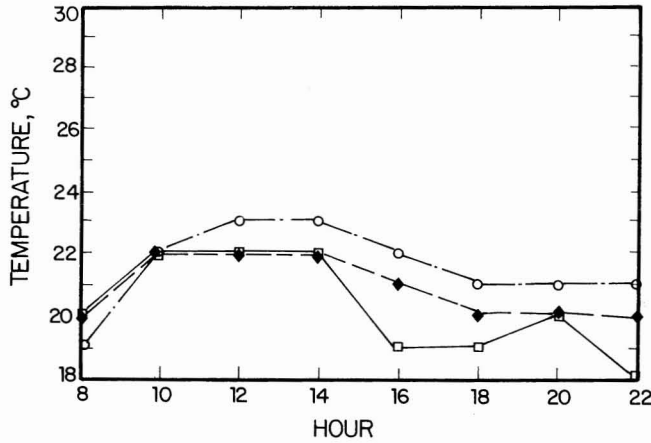


FIGURE 3. Diurnal course of temperature: □, open air, among *Avicennia marina* leaves; ○, in black plastic bag; ◆, in clear plastic bag.

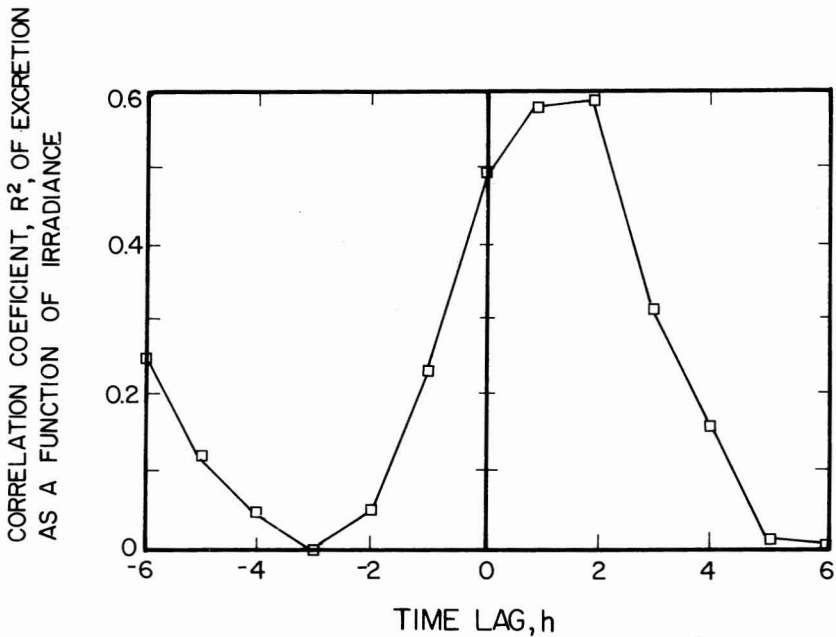


FIGURE 4. Effect of irradiance time lag on R^2 .

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