

Short communication

## Do desiccation tolerances control the vertical distribution of intertidal seagrasses?

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### Abstract

Photosynthetic processes in *Zostera japonica*, an upper intertidal species, were found to be more severely affected by desiccation than *Z. marina*, a lower intertidal and subtidal species, at comparable levels of tissue water content. The data indicate that photosynthetic responses to desiccation at the level of the individual leaf are insufficient to explain observed patterns of intertidal seagrass zonation. Desiccation tolerance in seagrasses is more likely to involve a complex interaction of morphological traits and growth strategies at the level of the whole plant, such as downsizing (e.g. smaller, narrower leaves), reduced structural rigidity and increased rates of leaf abscission and leaf turnover.

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### 1. Introduction

Intertidal species zonation patterns and the mechanisms underlying them have been the focus of study by marine ecologists and phycologists for more than a century (Davison and Pearson, 1996). The lower limits of intertidal species distributions are thought to be controlled by biotic factors such as predation and competition (e.g. Schonbeck and Norton, 1980), whereas the upper limits are determined by physiological tolerances to exposure and desiccation (Zaneveld, 1969; Schonbeck and Norton, 1978). The desiccation tolerances of marine macroalgae are considered to be a major factor responsible for vertical zonation patterns in the intertidal zone.

The ability of intertidal algae to tolerate periodic exposure to air has been hypothesized to involve a number of different mechanisms, including specialized adaptations to reduce tissue water loss (Zaneveld, 1937), the ability to maintain high rates of photosynthesis in air (Dring and Brown, 1982) and rapid and complete recovery of photosynthesis during re-hydration (Dring and Brown, 1982; Beer and Kautsky, 1992). The first hypothesis has been refuted by subsequent studies that

concluded there was no relationship between rate of tissue water loss and the vertical position of the species within the intertidal zone (Schonbeck and Norton, 1979; Dromgoole, 1980; Lipkin et al., 1993). It has been demonstrated that fully hydrated intertidal algae are able to maintain high rates of photosynthesis in air; photosynthetic rates decline with decreasing water content, although the specific water content at which changes occur varies by species (Wiltens et al., 1978; Dring and Brown, 1982). However, it is the extent to which the photosynthetic apparatus can recover from water loss upon re-immersion that most clearly distinguishes desiccation-tolerant species from desiccation-sensitive species (Wiltens et al., 1978; Dring and Brown, 1982; Smith and Berry, 1986; Brown, 1987). Despite the considerable body of accumulated knowledge, there is still debate regarding the exact mechanisms of stress tolerance (Davison and Pearson, 1996).

Most seagrasses are intolerant of desiccation and do not grow in the intertidal zone (Koch, 2001). There are some exceptions, including a few temperate species in the genus *Zostera*, such as *Zostera japonica* (Bulthuis, 1995), *Z. marina*, *Z. noltii* (Leuschner and Rees, 1993; Pérez-Lloréns and Niell, 1993) and *Z. novazelandica* (Ramage and Schiel, 1998). In tropical and subtropical ecosystems, more seagrass species are able to grow in the intertidal (Björk et al., 1999), where they are often exposed to high irradiance levels and desiccating

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atmospheric conditions (Jupp et al., 1996). Tropical intertidal seagrass species include *Halodule uninervis*, *Halodule wrightii*, *Halophila ovalis*, *Cymodocea rotundata*, *Thalassia hemprichii* and *Enhalus acoroides* (Den Hartog, 1970; Jupp et al., 1996; Björk et al., 1999; Tanaka and Nakaoka, 2004).

Like for marine macroalgae, differences in desiccation tolerances have been hypothesized to explain zonation patterns in seagrasses (Harrison, 1982a; Jupp et al., 1996; Huong et al., 2003; Boese et al., 2005). A number of studies have investigated the photosynthetic responses of seagrasses to dehydration stress (Pérez-Lloréns and Niell, 1993; Leuschner and Rees, 1993; Adams and Bate, 1994; Leuschner et al., 1998; Björk et al., 1999; Seddon and Cheshire, 2001). Fewer have evaluated the photosynthetic recovery of seagrasses when re-hydrated (Adams and Bate, 1994; Björk et al., 1999; Seddon and Cheshire, 2001), despite its recognized importance in intertidal algae zonation. Others have reported alternative measures of desiccation stress, such as rates of tissue water loss (Björk et al., 1999; Tanaka and Nakaoka, 2004), and proportion of necrotic leaf tissue (Boese et al., 2003).

Of these, only three studies have evaluated desiccation responses of seagrasses with respect to their position in the intertidal zone. The results have been inconclusive. Leuschner et al. (1998) reported that photosynthesis rates of *Z. marina* were more sensitive to desiccation than *Z. noltii*, a finding which is consistent with the position of the species within the intertidal zone. Björk et al. (1999) described the photosynthetic responses to dehydration and re-hydration of eight tropical intertidal seagrasses. Contrary to what might be expected, they found that photosynthesis rates of tropical seagrass species growing highest in the intertidal zone were more sensitive to desiccation than deeper growing species. Tanaka and Nakaoka (2004) used a different approach, comparing desiccation stress tolerances among three subtropical seagrasses using reciprocal transplant experiments and rates of leaf tissue water loss expressed as desiccation coefficients. They reported statistically significant differences in the desiccation coefficients between species, but noted that they did not correspond to the observed intertidal distribution patterns. Therefore, the extent to which physiological responses to desiccation controls the intertidal distribution of seagrasses remains unclear.

The present study compares tissue water loss rates and photosynthetic responses to dehydration and re-hydration of two temperate *Zostera* species, *Z. japonica* and *Z. marina*, along the northern Pacific Coast of the United States. *Z. japonica* was first reported from the Pacific Coast of North America in 1957, and has rapidly expanded its distribution within its established range (Baldwin and Lovvorn, 1994). Factors controlling the distribution of *Z. japonica* are of particular interest to resource managers, since it often co-occurs with the native eelgrass, *Z. marina* (Thom, 1990; Dumbauld and Wyllie-Echeverria, 2003).

*Z. marina* occupies the lower intertidal to upper subtidal zones, and *Z. japonica* typically occupies the mid- to upper intertidal zone (Harrison, 1982b; Phillips, 1984; Thom, 1990; Bulthuis, 1995). Where *Z. marina* is found in the upper intertidal zone, it is often associated with depressions or

drainage channels that retain water during periods of tidal exposure (Harrison, 1982b; Thom, 1990). Harrison (1982b) suggested that differences in desiccation tolerances were responsible for the observed patterns of distribution of *Z. marina* and *Z. japonica* in the Pacific Northwest. However, desiccation responses of these two species were not measured; his inference was based on comparisons of growth rates under simulated intertidal conditions. Therefore, the objective of this study was to determine if the observed intertidal zonation patterns of these two seagrass species could be explained by differences in their physiological responses to dehydration and re-hydration.

## 2. Materials and methods

Whole *Z. japonica* and *Z. marina* plants were collected at low tide in July 2002 from the mid-intertidal zone in Padilla Bay, Washington (48° 34'N, 122° 32'W). Padilla Bay is a large, shallow bay, located at the southern end of the Straits of Georgia, with extensive intertidal flats occupied by the seagrasses *Z. marina* and *Z. japonica* (Bulthuis, 1995). Plants were maintained in the laboratory in aerated seawater at a temperature (22° C) and salinity (30 psu) typical of the site at the time of collection. All analyses were conducted within 2–4 h of collection.

### 2.1. Photosynthetic responses to desiccation

The effective quantum electron yield ( $Y$ ) of photosystem II was measured in ambient light (approximately 180  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) without dark adaptation using a pulse amplitude modulated (PAM) fluorometer (Diving-PAM, Waltz) according to the procedures described in Björk et al. (1999). The tip of the microfiber optics was placed at a distance of 5 mm and an angle of 60° to the samples using the leaf distance clip. Samples were irradiated with a photosynthetic photon flux (PPF) of 500  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at a temperature of 22° C. Effective yield ( $Y$ ) was calculated as  $(F'_m - F)/F'_m = \Delta F/F'_m$ , where  $F'_m$  is the maximum fluorescence during an 0.8 s saturating light pulse, and  $F$  is the steady state fluorescence at a given irradiance (Genty et al., 1989).

Dehydration responses were evaluated by first gently blotting 4–5 cm leaf sections of *Z. marina* and *Z. japonica* to remove excess water. Samples were then placed on a balance, and the fully hydrated wet weight (WW) was recorded. Simultaneous readings of effective yield ( $Y$ ) and tissue weight ( $W_t$ ) were recorded every 2 min for *Z. marina*. Due to a more rapid rate of tissue water loss, readings were made every minute for *Z. japonica*. Readings were continued until a zero value for yield was obtained. The relative water content (RWC) of each leaf was calculated according to the formula:  $\text{RWC} = (W_t - \text{Dry Weight (DW)}) / (\text{WW} - \text{DW})$  (Björk et al., 1999). This process was repeated for six replicate leaf sections of each species.

Non-linear curve-fitting techniques were used to fit standard sigmoidal curves to the dehydration response data for each species (Motulsky, 1995). In order to compare the dehydration

responses of the two *Zostera* species, the same curve was fitted to both datasets, and an *F*-test was used to determine whether the two datasets were significantly different (Origin, OriginLab, Version 7.5).

To evaluate the ability of leaves to recover from dehydration, three replicate leaf sections of each species were air-dried in the laboratory at a temperature 22–23 °C to a series of pre-determined water contents (Björk et al., 1999): 15%, 32% and 53% RWC. Leaf sections were then placed in the leaf distance clip and re-hydrated by submerging in 30 psu seawater at a temperature of 22 °C. The Diving PAM was set to automatically record values for effective yield (*Y*) every minute; readings were continued until stable values were obtained.

## 2.2. Water loss rates

Estimated rates of water loss by leaf tissue were also calculated as an indicator of desiccation potential. Using the dehydration response data described above, relative water content (RWC) of each leaf section was plotted against elapsed time. Exponential curves were fitted to each plot, using the formula:

$$I_t = I_0 e^{-kt}$$

where  $I_t$  is the RWC at time  $t$ ,  $I_0$  the RWC at time 0 and  $k$  is the desiccation coefficient (Tanaka and Nakaoka, 2004). A one-way analysis of variance (ANOVA) was used to compare the desiccation coefficients of the two seagrass species. The length of drying time necessary to achieve the specified levels of relative water content (15%, 32% and 53%) was also compared.

## 3. Results

The photosynthetic responses to desiccation of the two intertidal *Zostera* species were similar (Fig. 1a and b). Statistical analysis indicated that the two datasets were not significantly different ( $F = 0.016$ ,  $p = 0.99$ ). There were, however, marked differences in the ability of the two species to recover from dehydration, but these differences were contrary to what would be expected based on their intertidal distribution. When dried to a relative water content of 15%, neither species displayed an ability to resume photosynthesis (Fig. 2a and b). The photosynthetic responses of *Z. marina* leaves dried to a relative water content of 53% and subsequently re-hydrated were similar to those of fully hydrated leaves (Fig. 2b). In contrast, *Z. japonica* leaves dried to a relative water content of 53% exhibited a photosynthetic yield approximately half as great as fully hydrated leaves after 10 min, with only limited recovery after 18 min (Fig. 2a). The photosynthetic apparatus of *Z. japonica* appeared to be severely damaged after dehydrating to a relative water content of 32%, with little ability to recover after being re-submerged (Fig. 2a). *Z. marina* leaves also appeared stressed when dehydrated to a relative water content of 32%, but were able to recover much of their photosynthetic capacity after nearly 20 min of re-hydration (Fig. 2b). Under ambient conditions in the laboratory, water

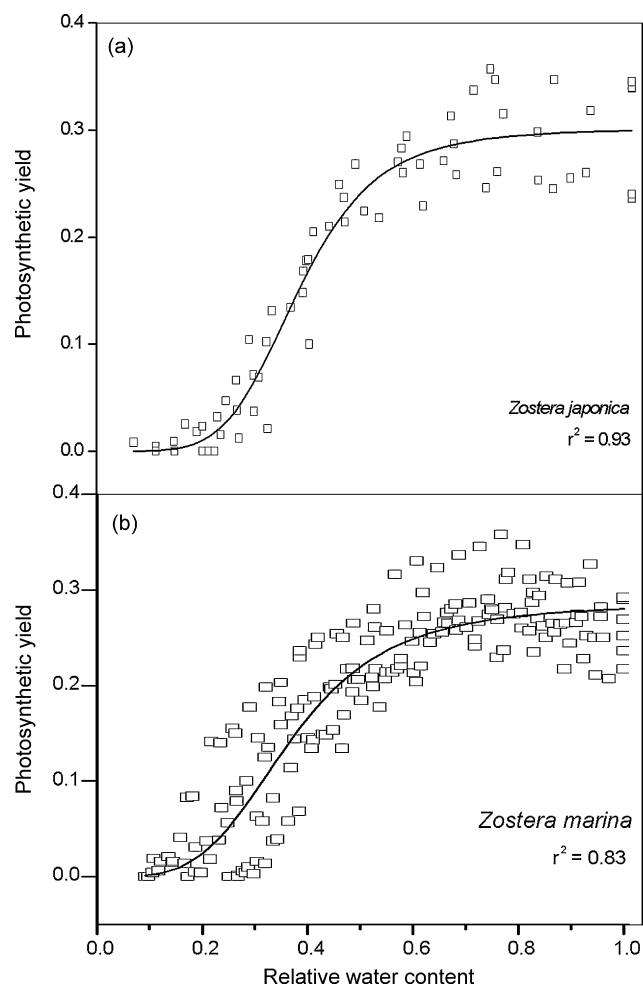


Fig. 1. Photosynthetic responses to dehydration in leaf sections of: (a) *Zostera japonica* and (b) *Zostera marina*. Leaves were exposed to air and allowed to dry. Simultaneous readings of weight and photosynthetic yield were made every 1–2 min.

loss rates from *Z. japonica* leaf tissue were 4–5 times faster than *Z. marina* (Table 1). Desiccation coefficients for *Z. marina* ranged between 0.030 and 0.036, with an average of 0.032 (Table 1). Desiccation coefficients for *Z. japonica* were much higher and more variable, ranging between 0.093 and 0.209, with an average of 0.134 (Table 1).

## 4. Discussion

Since *Z. japonica* and *Z. noltii* are morphologically similar and closely related genetically (Les et al., 2002), it might be expected that the dehydration responses of *Z. japonica* and *Z. marina* would be consistent with those reported by Leuschner et al. (1998) for *Z. noltii* and *Z. marina*. However, the results presented here contrast with those of Leuschner et al. (1998), since the dehydration and re-hydration responses of *Z. japonica* and *Z. marina* were not consistent with their relative position in the intertidal zone. Direct comparisons could not be made due to differences in approaches and metrics used. The desiccation coefficients determined for *Z. marina* in the present study are within the range of values (0.013–0.049) reported by Tanaka

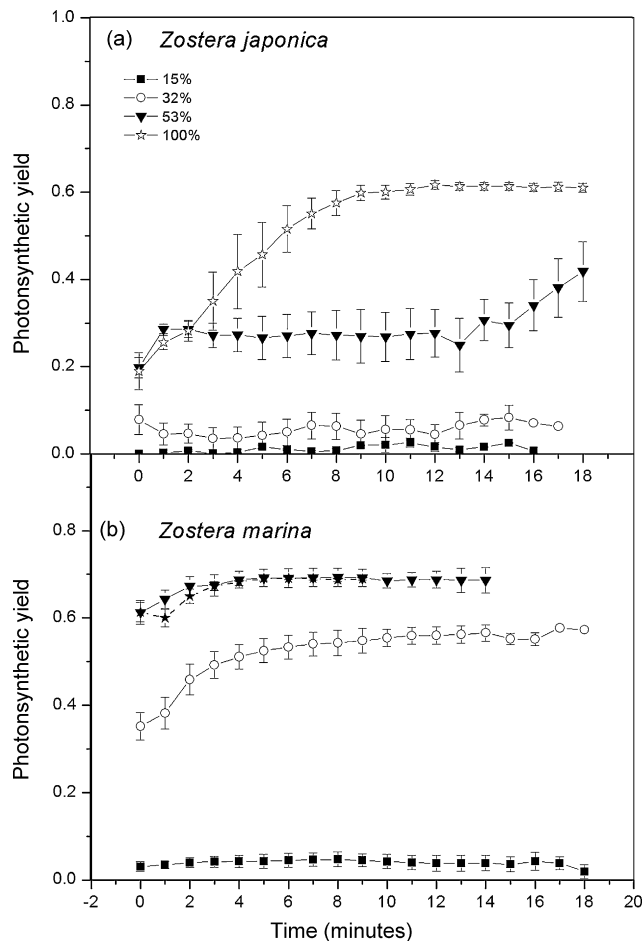


Fig. 2. Photosynthetic responses to re-hydration of desiccated leaf tissue in (a) *Zostera japonica* and (b) *Zostera marina*. Leaves were air-dried to defined relative water contents. These plants then were re-submerged in seawater to allow for re-hydration, and recovery of photosynthetic competence was measured.

and Nakaoka (2004) for subtropical seagrasses. Rates of water loss from *Z. japonica* observed in the present study were 4–5 times faster than *Z. marina*. The re-hydration responses also indicate that photosynthetic processes in *Z. japonica* are much more severely affected than those of *Z. marina* at comparable levels of tissue water content.

Although the ability to tolerate desiccation is undoubtedly a factor in the survival of intertidal seagrasses, the results of this study add to the growing body of knowledge that suggests that differences in physiological responses to desiccation are not sufficient to account for the observed patterns of intertidal distribution in some temperate and tropical seagrass species (Björk et al., 1999; Tanaka and Nakaoka, 2004). Like marine

Table 1  
Mean desiccation coefficients and time (in minutes) required to reach specified levels of RWC when air-dried in the laboratory at a temperature 22 °C

Species	Mean desiccation coefficient	RWC		
		53%	32%	15%
<i>Z. japonica</i>	0.134	4.3	7.3	9.7
<i>Z. marina</i>	0.032	18.6	33.8	48.0

macroalgae, upper intertidal seagrasses apparently do not possess any specialized adaptations to reduce rates of water loss from leaf tissue upon exposure to air (Björk et al., 1999; Tanaka and Nakaoka, 2004; this study). Seagrasses differ from marine macroalgae, however, in that the ability of intertidal seagrasses to resume photosynthesis upon re-immersion does not appear to be correlated with intertidal elevation.

Although these results may seem counter-intuitive, they indicate that we must consider alternative mechanisms if we hope to explain the observed zonation patterns of intertidal seagrasses. Björk et al. (1999) hypothesized that tolerance to high light conditions may be responsible for the observed zonation patterns. However, we suggest that the ability to tolerate periods of exposure to air may be more important, as it is a trait that results from a complex interaction of morphological features and plant growth strategies involving the entire plant, rather than physiological responses of individual leaves.

Intraspecific plasticity in leaf size and shape seems to be a characteristic associated with desiccation-tolerance in intertidal seagrasses. Plants with small, narrow leaves seem to be better adapted to air exposure (Pérez-Lloréns and Niell, 1993). Specimens of the temperate seagrasses *Z. marina*, *Z. noltii* and *Z. japonica* collected from the mid- to upper intertidal zones typically have smaller, narrower leaves than those from lower intertidal and subtidal zones (Drew, 1979; Harrison, 1982a; Pérez-Lloréns and Niell, 1993). Similar polymorphism in *Halodule* and *H. ovalis* was described by Den Hartog (1970). Until recently, the potential relationship between interspecific variation in leaf morphology and zonation of intertidal seagrass communities has been neglected (Tanaka and Nakaoka, 2004). However, since plants with small, narrow leaves may lose water more rapidly than plants with larger, wider leaves (Björk et al., 1999; Tanaka and Nakaoka, 2004; this study), this feature confers no clear advantage in terms of reducing rates of tissue water loss in upper intertidal seagrass species.

The selective advantage conferred by downsizing in response to emergence stress may instead be related to structural and mechanical properties of the plants. Björk et al. (1999) noted that the thin, flexible petioles of *H. ovalis* allowed the leaves to lie flat against the moist sand during periods of emergence. Species such as *H. wrightii* and *Z. japonica* lack petioles, but the narrow leaves grow densely enough to overlap, providing shade and protection from evaporation for those leaves not in direct contact with the wet sand (Björk et al., 1999; this study). Other characteristics such as vertical rhizome length, and sheath size and structure, also appear to influence vertical species zonation. Species with longer vertical rhizomes and inflexible sheaths, such as *T. hemprichii*, are exposed to air for longer periods than those species with shorter rhizomes and more flexible sheaths, such as *C. rotundata* (Tanaka and Nakaoka, 2004).

In spite of these morphological adaptations that might limit the exposure of intertidal seagrasses to drying conditions, significant damage to leaf tissue does occur as a result of desiccation (Erftemeijer and Herman, 1994; Boese et al., 2003). When leaves become damaged, another mechanism for coping

with desiccation stress may involve leaf-shedding. Leaf abscission in response to water deficit has been observed in both terrestrial and emergent wetland plants (McMichael et al., 1973; Saltmarsh et al., 2006). The extent to which this process occurs in intertidal seagrasses is unknown, although it could be important. Massive leaf loss as a result of exposure and desiccation has been reported in some tropical intertidal seagrasses (Stapel et al., 1997). Adams and Bate (1994) reported that recovery of *Ruppia cirrhosa* and *Zostera capensis* from desiccation was due to rapid re-growth of new leaves and not re-hydration of desiccated leaves. It may also be reflected in faster leaf turnover rates in those species occurring higher in the intertidal zone. The average lifetime of individual *Z. marina* leaves ( $69 \pm 8$  days) was more than 10 days longer than the average life of individual *Z. japonica* leaves (Lee et al., 2006). Leaf turnover rates also appear to be related to plant size, with smaller plants exhibiting more rapid leaf turnover than larger plants (Marba et al., 2006). The advantage of smaller leaves could also reflect the lower energetic costs associated with leaf production to offset the increased costs of more rapid turnover rates. The results presented here are consistent with the idea that intertidal seagrasses with smaller leaves have less invested in them, and may sacrifice those that are damaged and regenerate new ones rather than repair damage due to desiccation.

Increasing evidence suggests that photosynthetic responses to desiccation at the level of the individual leaf are insufficient to explain observed patterns of intertidal zonation. Desiccation tolerance in seagrasses is more likely to involve a combination of morphological traits and growth strategies, such as down-sizing (e.g. smaller, narrower leaves), reduced structural rigidity (Björk et al., 1999; Tanaka and Nakaoka, 2004) and increased rates of leaf abscission and leaf turnover. The relative importance of each may differ among species based on differences in genetic history or environmental conditions.

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## References

- Adams, J.B., Bate, G.C., 1994. The tolerance to desiccation of the submerged macrophytes *Ruppia cirrhosa* (Petagna) Grande and *Zostera capensis* Setchell. *J. Exp. Mar. Biol. Ecol.* 183, 53–62.
- Baldwin, J.R., Lovvorn, J.R., 1994. Expansion of seagrass habitat by the exotic *Zostera japonica*, and its use by dabbling ducks and brant in Boundary Bay, British Columbia. *Mar. Ecol. Prog. Ser.* 103, 119–127.
- Beer, S., Kautsky, L., 1992. The recovery of net photosynthesis during rehydration of three *Fucus* species from the Swedish west coast following exposure to air. *Bot. Mar.* 35, 487–491.
- Björk, M., Uku, J., Weil, A., Beer, S., 1999. Photosynthetic tolerances to desiccation of tropical intertidal seagrasses. *Mar. Ecol. Prog. Ser.* 191, 121–126.
- Boese, B.L., Alayan, K.E., Gooch, E.F., Robbins, B.D., 2003. Desiccation index: a measure of damage caused by adverse aerial exposure on intertidal eelgrass (*Zostera marina*) in an Oregon (USA) estuary. *Aquat. Bot.* 76, 329–337.
- Boese, B.L., Robbins, B.D., Thursby, G., 2005. Desiccation is a limiting factor for eelgrass (*Zostera marina* L.) distribution in the intertidal zone of a northeastern Pacific (USA) estuary. *Bot. Mar.* 48, 274–283.
- Brown, M.T., 1987. Effects of desiccation on photosynthesis on intertidal algae from a Southern New Zealand shore. *Bot. Mar.* 30, 121–127.
- Bulthuis, D.A., 1995. Distribution of seagrasses in a North Puget Sound estuary: Padilla Bay, Washington, USA. *Aquat. Bot.* 50, 99–105.
- Davison, I.R., Pearson, G.A., 1996. Stress tolerance in intertidal seaweeds. *J. Phycol.* 32, 197–211.
- den Hartog, C., 1970. *The Seagrasses of the World*. North-Holland Publishing Company, Amsterdam, Netherlands, 275 pp.
- Drew, E.D., 1979. Physiological aspects of primary production in seagrasses. *Aquat. Bot.* 7, 139–150.
- Dring, M.J., Brown, M.T., 1982. Photosynthesis of intertidal brown algae during and after periods of emersion: a renewed search for the causes of zonation. *Mar. Ecol. Prog. Ser.* 8, 301–308.
- Dromgoole, F.I., 1980. Desiccation resistance of intertidal and subtidal algae. *Bot. Mar.* 23, 149–159.
- Dumbauld, B.R., Wyllie-Echeverria, S., 2003. The influence of burrowing thalassinid shrimps on the distribution of intertidal seagrasses in Willapa Bay, Washington, USA. *Aquat. Bot.* 77, 27–42.
- Erfemeijer, P.L.A., Herman, P.M.J., 1994. Seasonal changes in environmental variables, biomass, production, and nutrient contents in two contrasting tropical intertidal seagrass beds in South Sulawesi, Indonesia. *Oecologia* 99, 45–59.
- Genty, B., Briantais, J.M., Baker, N.R., 1989. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *Biochim. Phys. Acta* 990, 87–92.
- Harrison, P.G., 1982a. Spatial and temporal patterns in abundance of two intertidal seagrasses, *Zostera americana* den Hartog and *Z. marina* L. *Aquat. Bot.* 12, 305–320.
- Harrison, P.G., 1982b. Comparative growth of *Zostera japonica* Aschers & Graebn. and *Z. marina* L. under simulated intertidal and subtidal conditions. *Aquat. Bot.* 14, 373–379.
- Huong, T.T.L., Vermaat, J.E., Terrados, J., Tien, N.V., Duarte, C.M., Borum, J., Tri, N.H., 2003. Seasonality and depth zonation of intertidal *Halophila ovalis* and *Zostera japonica* in Ha Long Bay (northern Vietnam). *Aquat. Bot.* 75, 147–157.
- Jupp, B.P., Durako, M.J., Kenworthy, W.J., Thayer, G.W., Schillak, L., 1996. Distribution, abundance, and species composition of seagrasses at several sites in Oman. *Aquat. Bot.* 53, 199–213.
- Koch, E.W., 2001. Beyond light: physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. *Estuaries* 24, 1–17.
- Lee, S.Y., Kim, J.B., Lee, S.M., 2006. Temporal dynamics of subtidal *Zostera marina* and intertidal *Zostera japonica* on the southern coast of Korea. *Mar. Ecol.* 27, 133–144.
- Les, D.H., Moody, M.L., Jacobs, S.W.L., Bayer, R.J., 2002. Systematics of seagrasses (Zosteraceae) in Australia and New Zealand. *Syst. Bot.* 27, 468–484.
- Leuschner, C., Rees, U., 1993. CO<sub>2</sub> gas exchange of two intertidal seagrass species, (*Zostera marina* L. and *Zostera noltii* Hornem. m during emersion. *Aquat. Bot.* 45, 53–62.
- Leuschner, C., Landwehr, S., Mehlig, U., 1998. Limitation of carbon assimilation of intertidal *Zostera noltii* and *Z. marina* by desiccation at low tide. *Aquat. Bot.* 62, 171–176.
- Lipkin, Y., Beer, S., Eshel, A., 1993. The ability of *Porphyra linearis* (Rhodophyta) to tolerate prolonged periods of desiccation. *Bot. Mar.* 36, 517–523.
- Marba, N., Hemminga, M.A., Duarte, C.M., 2006. Resource translocation within seagrass clones: allometric scaling to plant size and productivity. *Oecologia* 150, 362–372.
- McMichael, B.L., Jordan, W.R., Powell, R.D., 1973. Abscission processes in cotton: induction by plant water deficit. *Agron. J.* 65, 202–204.
- Motulsky, H., 1995. *Intuitive Biostatistics*. Oxford University Press, New York, New York, 408 pp.

- Pérez-Lloréns, J.L., Niell, F.X., 1993. Temperature and emergence effects on the net photosynthesis of two *Zostera noltii* Hornem. morphotypes. *Hydrobiologia* 254, 53–64.
- Phillips, R.C., 1984. The ecology of eelgrass meadows in the Pacific Northwest: a community profile. FWS/OBS-84/24. U.S. Dept. of the Interior, Washington, DC.
- Ramage, D.L., Schiel, D.R., 1998. Reproduction in the seagrass *Zostera novaezelandica* on intertidal platforms in southern New Zealand. *Mar. Biol.* 130, 479–489.
- Saltmarsh, A., Mauchamp, A., Rambal, S., 2006. Contrasted effects of water limitation on leaf functions and growth of two emergent co-occurring plant species, *Cladium mariscus* and *Phragmites australis*. *Aquat. Bot.* 84, 191–198.
- Schonbeck, M., Norton, T.A., 1978. Factors controlling the upper limits of furoid algae on the shore. *J. Exp. Mar. Biol. Ecol.* 31, 303–313.
- Schonbeck, M., Norton, T.A., 1979. An investigation of drought avoidance in intertidal furoid algae. *Bot. Mar.* 22, 133–144.
- Schonbeck, M., Norton, T.A., 1980. Factors controlling the lower limits of furoid algae on the shore. *J. Exp. Mar. Biol. Ecol.* 43, 131–150.
- Seddon, S., Cheshire, A.C., 2001. Photosynthetic response of *Amphibolis antarctica* and *Posidonia australis* to temperature and desiccation using chlorophyll fluorescence. *Mar. Ecol. Prog. Ser.* 220, 119–130.
- Smith, C.M., Berry, J.A., 1986. Recovery of photosynthesis after exposure of intertidal algae to osmotic and temperature stresses: comparative studies of species with differing distributional limits. *Oecologia* 70, 6–12.
- Stapel, J., Manuntun, R., Hemminga, M.A., 1997. Biomass loss and nutrient redistribution in an Indonesian *Thalassia hemprichii* seagrass bed following seasonal low tide exposure during daylight. *Mar. Ecol. Prog. Ser.* 148, 251–262.
- Tanaka, Y., Nakaoka, M., 2004. Emergence stress and morphological constraints affect the species distribution and growth of subtropical intertidal seagrasses. *Mar. Ecol. Prog. Ser.* 284, 117–131.
- Thom, R.M., 1990. Spatial and temporal patterns in plant standing stock and primary production in a temperate seagrass system. *Bot. Mar.* 33, 497–510.
- Wiltens, J., Schreiber, U., Vidaver, W., 1978. Chlorophyll fluorescence induction: an indicator of photosynthetic activity in marine algae undergoing desiccation. *Can. J. Bot.* 56, 2787–2794.
- Zaneveld, J.S., 1937. The littoral zonation of some Fucaceae in relation to desiccation. *J. Ecol.* 25, 431–468.
- Zaneveld, J.S., 1969. Factors controlling the delimitation of littoral benthic marine algal zonation. *Am. Zool.* 9, 367–391.