

Underestimation of *Spartina* productivity in western Atlantic marshes: marsh invertebrates eat more than just detritus

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Silliman, B. R. and Bortolus, A. 2003. Underestimation of *Spartina* productivity in western Atlantic marshes: marsh invertebrates eat more than just detritus. – *Oikos* 101: 549–554.

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The problem

Quantifying primary productivity and understanding the factors that control plant growth are primary goals of ecosystem ecology. Although some methods have been very successful in providing accurate measurements of plant growth and elucidating the importance of both physical and biological factors in regulating primary production (e.g. terrestrial systems: Smith 1996; marine communities: Bertness et al. 2001), many techniques are still hampered by methodological biases that greatly affect productivity estimates and overall experimental results. For example, a recent review of tropical seagrass systems suggests that past experiments investigating seagrass productivity may have been compromised because they did not control for the confounding effects of grazing (i.e. monitoring and/or excluding fish and invertebrate grazers – Valentine and Heck 1999). The authors argue that the probable consequences of not accounting for herbivore effects are: (1) inaccurate estimates of both net and gross primary production and (2) an intellectual bias concerning the relative roles of bottom-up (i.e. nutrients and nutrient regulating factors) and top-down (e.g. herbivory) forces in controlling seagrass growth. In this paper, we argue that these conclusions also apply broadly to salt marshes along the East Coast of both North and South America. Specifically, we suggest that past studies of plant productivity in Western Atlantic marshes, by not accounting for the confounding effects of grazing (i.e. excluding herbivorous crabs and snails), are likely to have significantly underestimated plant growth and

overestimated the relative importance of bottom-up factors in regulating marsh primary production. We contend that current methods of measuring marsh grass growth must be amended to include grazer exclusions in carefully controlled field experiments. Only then will we be able to obtain accurate measurements of marsh plant productivity and assess the relative importance of top-down effects in controlling marsh grass growth.

The importance of marsh primary productivity to ecological studies

Ecosystem science and modeling were in large part born out of research conducted in North American salt marshes during the 1950's, 60's and 70's (Odum and Smalley 1959, Wiegert and Evans 1967, Wiegert and Owen 1971, Wetzel 1975, Wiegert 1975). Models of energy flow within the salt marsh/estuarine food-web (Teal 1962, Odum and de la Cruz 1967) have formed the intellectual framework for modeling trophic interactions in many marine communities dominated by macrophytes (e.g. mangroves – Odum and Heald 1975; seagrasses – Ogden 1980; and kelp forests – Dunton and Schell 1987). In addition, salt marsh trophic models have been widely cited in reviews of food-web theory (Pomeroy and Albert 1988, Polis and Winemiller 1996), and in text-books as examples of methods for ecosystem analyses (Valiela 1995, Smith 1996, Bertness et al. 2001). Because the central goal of these marsh-based food-web models is tracing carbon flow through

Accepted 23 September 2002

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ISSN 0030-1299

trophic levels (Hopkinson and Day 1977), measuring marsh primary productivity correctly has long been fundamental to their predictive success and overall applicability to other natural communities. In addition, a keystone element of marsh ecosystem models is that they minimize the role of grazers in affecting primary productivity (Mitsch and Gosselink 1993).

Marsh-grazer dogma

Salt marshes are among the most productive in the world, with annual rates of primary productivity as high as that in coral reefs and tropical rain forests (e.g. up to 3900 g dry wt C/m²/yr – Mitsch and Gosselink 1993). Over the past 40 years, most marsh research has been devoted to obtaining accurate estimates of primary productivity (Lomnicki et al. 1967, Singh et al. 1984, Dai and Wiegert 1996) and understanding the factors that influence the success of the dominant grasses in the community, *Spartina* spp. (Weinstein and Kreeger 2001). Due to strong tidal influences, most investigations of the controls of *Spartina* growth have emphasized the primacy of edaphic conditions (Valiela and Teal 1974, Mendelssohn et al. 1981, King et al. 1982, Bradley and Morris 1990, 1991). Early salt marsh studies that did investigate top-down controls concluded that plant-herbivore interactions were of little consequence to both energy transfer and regulation of plant productivity (Smalley 1959, 1960, Teal 1962, Marples 1966). Recent studies have challenged this conclusion by demonstrating direct consumption of *Spartina* plants by a variety of herbivores (e.g. geese: Smith and Odum 1981; horses: Furbish and Albano 1994; nutria: Taylor and Grace 1995; insects: Daehler and Strong 1995). Nonetheless, the relative importance of these grazers is diminished because their individual effects are often restricted to small spatial scales (10's of m² – Pennings and Bertness 2001). Thus, an overwhelming consensus remains that bottom-up effects are the primary determinants of marsh grass productivity (Mendelssohn and Morris 2001).

Counter evidence

Recent work in salt marshes in both the United States (Silliman 1999, Silliman and Zieman 2001, Silliman and Bertness 2002) and Argentina (Bortolus and Iribarne 1999, Bortolus 2001) has challenged current marsh dogma and demonstrated that grazing by abundant invertebrates is also important in regulating marsh plant production. In both instances, the most abundant and widespread grazer in each system, long classified as a detritivore, was shown to routinely graze live *Spartina* and in the process exert strong control over plant

growth. For example, in an experiment examining the relative impacts of nitrogen (N) enrichment and periwinkle grazing on *Spartina alterniflora* (salt marsh cordgrass) growth in a Virginia (USA) salt marsh, snail removal (density = 48 snails/m²) from unfertilized stands of cordgrass increased aboveground biomass by 49%, whereas in N addition plots, snail removal increased cordgrass growth by 86% (Silliman and Zieman 2001). By the end of this experiment, the marsh canopy in snail addition treatments (144 snails/m²) was almost completely destroyed, regardless of nitrogen level, and standing crop was reduced by nearly 85% in comparison to ungrazed treatments. Below ground plant reserves were also negatively affected by *L. irrorata*, as snail grazing reduced rhizome biomass by ~ 25% (Silliman 1999). Additional exclusion experiments in marshes in both Georgia (n = 16 marshes) and Virginia (n = 4 marshes) showed that removal of snails from the marsh canopy at commonly occurring high densities (400–800 snails/m²) results in a striking 400–700% increase in end-of-season standing crop (Silliman 1999, Silliman and Bertness 2002).

In Argentinean marshes, removal of the most abundant grapsid crab, *Chasmagnathus granulata*, which commonly occurs at densities between 60 and 100 ind./m², yielded similar results, as cordgrass standing crop increased by nearly 350% (Bortolus and Iribarne 1999). Additional experiments showed that: (1) grazing by grapsid crabs at relatively low densities (~ 16 ind./m²) can reduce *Spartina* standing crop by up to 87% in less than a month (Bortolus 2001), and (2) crabs prefer to consume soft, young parts of the plant (i.e. young leaves and shoots; Bortolus and Iribarne 1999) over both older leaves and *Spartina* detritus.

Both the marsh periwinkle, *Littoraria irrorata*, and the burrowing crab, *C. granulata*, are locally abundant and widespread over their natural distribution range and thus, like bottom-up effects, may commonly exert control over cordgrass productivity across large geographic areas (Table 1). In the United States, *L. irrorata* is found in abundance (50–800 ind./m²) in marshes on the mid-Atlantic, Southeast and Gulf coasts and, in certain areas, can reach densities up to 2,000 ind/m² (Table 1). *C. granulata* is equally abundant in marshes from Brazil to Argentina, where its natural range spans nearly 45 latitudinal degrees of coastline (Boschi et al. 1992). In these coastal environments, burrowing crabs routinely reach densities of 60 ind./m², but often occur at densities an order of magnitude greater (Spivak et al. 1994, Bortolus and Iribarne 1999, Bortolus et al. 1999). Importantly, large-scale marsh surveys in both North (from Maryland to Georgia; n = 32 marshes – Table 1; Silliman 1999; Silliman and Zieman 2001) and South (from Buenos Aires to Trelew; n = 16 marshes – A. Bortolus unpubl.) America reveal that grazing by snails and crabs on live *Spartina* is, like their densities, widespread and locally intense.

Table 1. Reported densities of *L. irrorata* and *C. granulata* in Western Atlantic salt marshes, and corresponding grazing intensity where available. Data are means.

Species	Site	Grazer density (ind./m ²)	Grazing intensity (cm radulation/stem)	Reference
<i>L. irrorata</i> :	Hog Island, Virginia	48	9.2	Silliman and Zieman 2001
	Raccoon Island, Virginia	158	19.9	Silliman and Zieman 2001
	Cobb Island, Virginia	88	11.9	B. R. Silliman, pers. obs.
	Tar landing, North Carolina	194	22.3	Silliman and Zieman 2001
	North Carolina	> 100		Stiven and Kuenzler 1979
	Sapelo Island, Georgia	3342	234.5	B. R. Silliman, pers. obs.
	Sapelo Island, Georgia	348	33.7	B. R. Silliman, pers. obs.
	Sapelo Island, Georgia	605	44.5	Silliman and Bertness 2002
	Sapelo Island, Georgia	700		Pomeroy and Wiegert 1981
	Tybee Island, Georgia	243	25.4	B. R. Silliman, pers. obs.
	Florida	300		Warren 1985
	Alabama	145		West and Williams 1985
	Texas	> 100		Vaughn and Fisher 1982
	Louisiana	323	41.6	B. R. Silliman, pers. obs.
				(% leaves grazed/m ²)
<i>C. granulata</i> :	El Cangrejito, Argentina	> 100	> 95	Bortolus and Iribarne 1999
	Boca Marsh, Argentina	61	> 95	Bortolus 2001
	CELPA Marsh, Argentina	> 125	> 95	Bortolus 2001
	Bahia Blanca, Argentina	25		A. Bortolus, pers. obs.
	Brazil	60	> 90	Cesar Costa, pers. com.

Consequences of snail and crab grazing to past studies of *Spartina* growth

Previous studies which measured cordgrass productivity and/or investigated the role of physico-chemical factors in controlling *Spartina* spp. growth within the natural range of *L. irrorata* and *C. granulata* have not excluded snails or crabs from experimental areas (e.g. North America: Smalley 1959, Hopkinson et al. 1980, Morris and Haskin 1990; Dai and Wiegert 1996, 1997; South America: Lana et al. 1991, Perazzolo and Pineiro 1991, Panitz 1992, Bonnet et al. 1994, Nasca et al. 2001). Although these studies rarely mention whether periwinkles or grapsid crabs were present at the experimental site, the likelihood is high, since a primary focus was investigating cordgrass productivity in the short and intermediate *Spartina* zones, the areas where snails and herbivorous crabs are most abundant (snails: Pomeroy and Wiegert 1981; crabs: Bortolus 2001). A recent

survey of periwinkle abundance and grazing intensity in southeast marshes provides even stronger support for this contention (Table 2). At 8 former sites of *S. alterniflora* growth studies, we found *L. irrorata* abundance and grazing intensity to be comparable to or much greater than that in recent caging experiments, where snail radular activity reduced plant growth by up to 85% (Silliman and Zieman 2001). Given the large effect that *L. irrorata* and *C. granulata* can have on the growth of *Spartina*, and that these grazers were likely present and grazing at past growth experiments at moderate to high densities (Table 1 and 2), we argue that the potential productivity of *Spartina* spp. has been greatly underestimated. Additionally, because many studies in North America have investigated the role of physical factors in maintaining height-form *S. alterniflora* by comparing edaphic conditions in high-marsh habitats, where plants are short and snails

Table 2. Present day snail density and grazing intensity at former sites of studies investigating *S. alterniflora* growth and/or height-form differentiation. Data were collected using the survey method of Silliman and Zieman (2001). Data are means.

Site	Snail Density in tall zone (ind./m ²)	Snail density in short zone (ind./m ²)	Grazing intensity in short zone (radualtions/stem)	Study focus	Reference
Virginia	4	231	21.3	b	Walsh 1998
Virginia	2	287	39.8	b	Osgood and Zieman 1993
Virginia	5	85	9.8	b	Osgood and Zieman 1993
North Carolina	3	183	19.8	b	Mendelssohn 1979
North Carolina	0	74	13.9	a	Broome et al. 1975
South Carolina		65	10.5	a	Morris and Haskin 1990
Georgia	1	348	35.9	b	Dai and Wiegert 1996
Georgia		378	26.3	b	Gallagher 1975
Georgia		458	44.3	a	Chalmers 1979

a = measuring short-form cordgrass growth; b = comparing growth between short- and tall-form *Spartina alterniflora*.

Table 3. Effects of nitrogen fertilization on *S. alterniflora* standing crop in mid-Atlantic and Southeast salt marshes, and present day snail density and grazing intensity at respective study sites. Data are means.

Site	Fertilizer (g N m ⁻² yr ⁻¹)	Control (g m ⁻² yr ⁻¹)	Fertilized (g m ⁻² yr ⁻¹)	Standing crop increase (%)	Snail density (ind./m ²)	Radulations (\bar{x} cm/stem)	Reference
Virginia	43	221	1340	505	0	0	Silliman and Zieman 2001
	43	155	726	368	48	9.5	Silliman and Zieman 2001
	43	51	147	188	144	18.2	Silliman and Zieman 2001
North Carolina	112	348	948	172	183	19.8	Mendelssohn 1979
North Carolina	67	450	1800	300	74	13.9	Broome et al. 1975
Georgia	112	404	892	121	348	35.9	Dai and Wiegert 1996
Georgia	20	471	803	70	378	26.3	Gallagher 1975
Georgia	100	396	650	64	258	24.3	Chalmers 1979
Louisiana	20	1666	1916	15	NA	NA	Patrick and Delaune 1977

abundant, with those in creek–bank habitats, where plants are tall and snails virtually absent (Pomeroy and Wiegert 1981, Mitsch and Gosselink 1993) the role of abiotic stressors (e.g. porewater salinity and sulfides) in suppressing cordgrass growth has been overestimated (Table 2). Essentially, the negative effects of snail grazing have been inaccurately included in the estimated effects of physical stressors in suppressing cordgrass production. Importantly, this conclusion does not suggest that short-form *S. alterniflora* is short solely because of snail grazing; rather that both abiotic and biotic factors play significant roles in its maintenance.

The results of snail grazing experiments in North America also show that the potential yield response of *S. alterniflora* to N enrichment has been underestimated because of the grazing effects of the marsh periwinkle (Silliman and Zieman 2001). The magnitude of *S. alterniflora* yield response to N enrichment in Silliman and Zieman's study is, to our knowledge, the highest in the literature (Table 3). In treatments without snails, N fertilization increased end-of-experiment standing crop by 505%. The next highest yield response in the literature was reported by Broome et al. (1975) – 300%. In neither Broome et al.'s (1975) study, nor in any other of the fertilization studies, was *L. irrorata* excluded from experimental stands of *S. alterniflora* (Table 3). Our survey shows that at 5 of these former study sites, the abundance of *L. irrorata* presently ranges from 70–500 snails/m² and that the intensity of grazing corresponds to these densities (Table 3). Given the large, negative effect that low densities of *L. irrorata* can have on the nitrogen-*S. alterniflora* interaction (Silliman and Zieman 2001 – see Table 3), it is highly probable that the yield response of *S. alterniflora* to N enrichment has been greatly underestimated.

Conclusions

Primary productivity in salt marshes has been studied for decades, yet the role of unobtrusive mesograzers (crabs and snails) in mediating productivity was only

appreciated when these grazers were experimentally manipulated. By employing grazer-exclusion cages, our recent field experiments demonstrate that one of the most productive systems in the world is much more productive than currently envisioned. In addition, the finding that these previously discounted mesograzers can elicit strong control of marsh plant productivity suggests that other small herbivores in salt marshes (e.g. grasshoppers and leaf hoppers) may also be exerting similar, yet undetected, control over plant production. We contend that herbivore exclusions need to be included in all future investigations of marsh grass growth where grazers (invertebrates and vertebrates) are present (almost all marshes). Without employing such measures, we will not be able to obtain accurate measurements of marsh plant growth or effectively compare primary productivity between marshes, as grazer densities vary considerably from marsh to marsh. Moreover, this methodological addition will improve: (1) estimates of marsh plant yield response to N eutrophication, (2) the overall accuracy of energy transfers in marsh-based food-web models, and (3) our current understanding of the relative importance of bottom-up and top-down processes in controlling plant productivity in salt marsh communities.

Acknowledgements – We thank A. Altieri, M. Bertness, C. Layman, E. Schwindt and S. Pennings for their comments on the manuscript. While writing this paper, we were supported by grants from the National Science Foundation, the Mellon foundation, CONICET, Fundacion Antorchas, International Foundation for Science (IFS), EPA-STAR fellowship, and NOAA-NERRS program.

References

- Bertness, M. D., Gaines, S. D. and Hay, M. E. 2001. Marine community ecology. – Sinauer Associates Inc.
- Bonnet, B. R. P., Lana, P., da, C. and Guiss, C. 1994. Influencia da gramínea *Spartina alterniflora* sobre a distribuição de *Neritina virginea* (Gasteropoda: Neritidae) em marismas da Baía de Paranaguá (Paraná, Brasil), *Neritica*. – Curitiba 8: 99–108.
- Bortolus, A. 2001. Interacciones ecológicas entre el cangrejo cavadador *Chasmagnathus granulata* Dana (1851) y los espar-

- tillares de *Spartina densiflora* Brongniarti (1829), meiofauna asociada y características del sustrato en la laguna costera Mar Chiquita (Buenos Aires, Argentina). – Dissertation. Univ. Nacional de Mar del Plata, Argentina.
- Bortolus, A. and Iribarne, O. 1999. The effect of the south-western Atlantic burrowing crab *Chasmagnathus granulata* on a *Spartina* salt-marsh. – Marine Ecol. Progr. Ser. 178: 79–88.
- Bortolus, A., Laterra, P. and Iribarne, O. 1999. Manejo sustentable en las marismas del Atlántico Sud Occidental. Segundas Jornadas Iberoamericanas sobre Diversidad Biológica. – San Luis, Argentina.
- Bortolus, A., Schwindt, E. and Iribarne, O. 2002. Physical stress and positive plant–animal interactions in the high marsh. – Ecology 83(3): 733–742.
- Boschi, E. E., Fischbach, C. E. and Iorio, M. I. 1992. Catálogo ilustrado de los crustáceos estomatopodos y decápodos marinos de Argentina. – Frente Marítimo 10: 7–94.
- Bradley, P. M. and Morris, J. T. 1990. Influence of oxygen and sulfide concentration on nitrogen uptake kinetics in *Spartina alterniflora*. – Ecology 71: 282–287.
- Bradley, P. M. and Morris, J. T. 1991. The influence of salinity on the kinetics of NH_4^+ uptake in *Spartina alterniflora*. – Oecologia 85: 373–380.
- Broome, S. W., Woodhouse, W. W. Jr. and Seneca, E. D. 1975. The relationship of mineral nutrients to growth of *Spartina alterniflora* in North Carolina: II. The effects of N, P, and Fe fertilizers. – Soil Sci. Soc. 39: 301–307.
- Chalmers, A. G. 1979. The effects of fertilization on nitrogen distribution in a *Spartina alterniflora* salt marsh. – Estuarine Coastal Marine Sci. 8: 327–337.
- Daehler, C. C. and Strong, D. R. 1995. Impact of high herbivore densities on introduced smooth cordgrass, *Spartina alterniflora*, invading San Francisco Bay, California. – Estuaries 18: 409–417.
- Dai, T. and Wiegert, R. G. 1996. Ramet population dynamics and net aerial primary productivity of *Spartina alterniflora*. – Ecology 77: 276–288.
- Dai, T. and Wiegert, R. G. 1997. A field study of photosynthetic capacity and its response to nitrogen fertilization in *Spartina alterniflora*. – Estuarine, Coastal Shelf Sci. 45: 273–283.
- Dunton, K. and Schell, D. M. 1987. Dependence of consumers and macroalgal (*Laminaria solidungula*) carbon in an arctic kelp community: ^{13}C evidence. – Marine Biol. 93: 615–625.
- Furbish, C. E. and Albano, M. 1994. Selective herbivory and plant community structure in a mid-Atlantic salt marsh. – Ecology 75: 1015–1022.
- Gallagher, J. L. 1975. Effect of an ammonium nitrate pulse on the growth and elemental composition of natural stands of *Spartina alterniflora* and *Juncus roemerianus*. – Am. J. Bot. 62: 644–648.
- Hopkinson, C. S., Gosselink, J. G. and Parrondo, R. T. 1980. Production of Louisiana marsh plants calculated from phenometric techniques. – Ecology 61: 1091–1098.
- King, G. M., Klug, M. J., Wiegert, R. G. and Chalmers, A. G. 1982. Relation of soil water movement and sulfide concentration to *Spartina alterniflora* production in a Georgia salt marsh. – Science 218: 61–63.
- Lana, P. C., Guiss, C. and Disaró, S. T. 1991. Seasonal variation of biomass and production dynamics for above- and belowground components of a *Spartina alterniflora* marsh in the euhaline sector of Paranaguá Bay (SE Brasil). – Estuarine Coastal Shelf Sci. 32: 231–241.
- Lomnicki, A., Bandola, E. and Jankowska, K. 1967. Modification of the Weigert–Evans method for estimation of net primary production. – Ecology 49: 147–149.
- Marples, T. G. 1966. A radionuclide tracer study of arthropod food chains in a *Spartina* salt marsh ecosystem. – Ecology 47: 270–277.
- Mendelssohn, I. A. 1979. The influence of nitrogen level, form, and application method on the growth response of *Spartina alterniflora* in North Carolina. – Estuaries 2: 106–112.
- Mendelssohn, I. A., Mckee, K. L. and Patrick, W. H. Jr. 1981. Oxygen deficiency in *Spartina alterniflora* roots: metabolic adaptation to anoxia. – Science 214: 439–441.
- Mendelssohn, I. A. and Morris, J. T. 2001. Eco-physiological constraints on the primary productivity of *Spartina alterniflora*. – In: Weinstein, M. P. and Kreeger, D. A. (eds), Concepts and controversies in tidal marsh ecology. Kluwer.
- Mitsch, W. J. and Gosselink, J. G. 1993. Wetlands. – Van Nostrand Reinhold.
- Morris, J. T. and Haskin, B. 1990. A 5-yr record of aerial primary production and stand characteristics of *Spartina alterniflora*. – Ecology 71: 2209–2217.
- Nasca, P., Cagnoni, M., Vila, A. et al. 2001. Efecto del fuego prescrito sobre la biomasa y productividad primaria neta de un espartillar de *Spartina densiflora* de la reserva de vida silvestre Campos del Tuyú.
- Odum, E. P. and Smalley, A. E. 1959. Comparison of population energy flow of a herbivorous and a deposit-feeding invertebrate in a salt marsh ecosystem. – Proc. Natl. Acad. Sci. USA 45: 617–622.
- Odum, E. P. and de la Cruz 1967. Particulate organic detritus in a Georgia salt-marsh estuarine system. – In: Lauff G. H. (ed.), Estuaries, AAAS Publication 83, Washington, DC, pp. 383–385.
- Odum, W. E. and Heald, E. J. 1975. The detritus food-web of an estuarine mangrove community. – In: Cronin, L. (ed.), Estuarine research. Academic Press, pp. 265–286.
- Ogden, J. C. 1980. Faunal relationships in Caribbean seagrass beds. – In: Philips, R. C. and McRoy, C. P. (eds), A handbook of seagrass biology: an ecosystem perspective. Garland STPM Press, pp. 173–198.
- Osgood, D. T. and Zieman, J. C. 1993. Factors controlling aboveground *Spartina alterniflora* (smooth cordgrass) tissue element composition and production in different-age barrier island marshes. – Estuaries 16: 815–826.
- Panitz, C. M. N. 1992. Ecological aspects of a salt marsh ecosystem in Santa Catarina Island, Brazil. – In: Seeliger, U. (ed.), Coastal plant communities of Latin America. Academic Press.
- Patrick, W. H. Jr. and Delaune, R. D. 1977. Chemical and biological redox systems affecting nutrient availability in the coastal wetlands. – Geosci. Man 19: 131–137.
- Perazzolo, M. and Pineiro, F. 1991. Aspectos anatómicos e adaptativos das partes vegetativas de *Spartina densiflora* Brons. (Gramineae) da marisma do estuário da Lagoa dos Patos-RS. – Acta Bot. Bras. 5: 3–16.
- Pennings, S. and Bertness, M. D. 2001. Salt marsh communities. – In: Bertness, M. D., Gaines, S. D. and Hay, M. E. (eds), Marine community ecology. Sinauer Associates Inc, pp. 289–316.
- Polis, G. A. and Winemiller, K. O. 1996. Food-webs. – Chapman and Hall.
- Pomeroy, L. R. and Wiegert, R. G. 1981. The ecology of a salt marsh. – Springer-Verlag.
- Pomeroy, L. R. and Albert, J. J. (eds) 1988. Concepts of ecosystem ecology: a comparative view. – Springer-Verlag.
- Silliman B. R. 1999. Effects of nutrient enrichment and periwinkle grazing on *Spartina alterniflora* growth. – Masters thesis. Univ. of Virginia.
- Silliman, B. R. and Zieman, J. C. 2001. Top-down control of *Spartina alterniflora* production by periwinkle grazing in a Virginia marsh. – Ecology 82: 2830–2843.
- Silliman, B. R. and Bertness, M. D. 2002. A trophic cascade regulates salt marsh primary production. – Proc. Natl. Acad. Sci. USA 99: 10500–10505.
- Singh, J. S., Lauenroth, W. K., Hunt, H. W. and Swift, D. M. 1984. Bias and random errors in estimators of net root production: a simulation approach. – Ecology 65: 1760–1764.

- Smalley, A. E. 1959. The role of two invertebrate populations *Littorina irrorata* and *Orchelimum fidicinium*, in the energy flow of a salt marsh ecosystem. – Univ. Microfilms 59-5687, Ann Arbor, MI.
- Smalley, A. E. 1960. Energy flow of a salt marsh grasshopper population. – Ecology 41: 672–677.
- Smith, T. J. III and Odum, W. E. 1981. The effects of grazing by snow geese on coastal salt marshes. – Ecology 62: 98–106.
- Smith, R. L. 1996. Ecology and field biology. – HarperCollins College Publishers.
- Spivak, E., Anger, K., Luppi, T. et al. 1994. Distribution and habitat preferences of two grapsid crab species in Mar Chiquita Lagoon (Province of Buenos Aires, Argentina). – Helgoländer Meeresunters 48: 59–78.
- Stiven, A. E. and Kuenzler, E. J. 1979. The response of two salt marsh molluscs, *Littorina irrorata* and *Geukensia demissa*, to field manipulations of density and *Spartina* litter. – Ecol. Monogr. 49: 151–171.
- Taylor, K. L. and Grace, J. B. 1995. The effects of vertebrate herbivory on plant community structure in the coastal marshes of the Pearl River, Louisiana, USA. – Wetlands 15: 68–73.
- Teal, J. M. 1962. Energy flow in the salt marsh ecosystem of Georgia. – Ecology 43: 614–624.
- Valentine, J. F. and Heck, K. L. Jr. 1999. Seagrass herbivory: evidence for the continued grazing of marine grasses. – Marine Ecol. Progr. Ser. 176: 291–302.
- Valiela, I. 1995. Marine ecological processes. – Springer-Verlag.
- Valiela, I. and Teal, J. M. 1974. Nutrient limitation in salt marsh vegetation. – In: Reimold, R. J. and Queen, W. H. (eds), Ecology of halophytes. Academic Press, pp. 547–565.
- Vaughn, C. C. and Fisher, F. M. 1982. Dispersion of the salt marsh periwinkle *Littoraria irrorata*: effects of water level, size, and season. – Estuaries 15: 246–250.
- Walsh, J. 1998. Low marsh succession along an over-wash salt marsh chronosequence. Dissertation. University of Virginia. Charlottesville, VA, USA.
- Warren, J. H. 1985. Climbing as an avoidance behavior in the salt marsh periwinkle, *Littorina irrorata* (Say). – J. Exp. Marine Biol. Ecol. 89: 11–28.
- Weinstein, M. P. and Kreeger, D. A. 2001. Concepts and controversies in tidal marsh ecology. – Kluwer Academic Publishers.
- West, D. L. and Williams, A. H. 1985. Predation by *Callinectes sapidus* (Rathbum) within *Spartina alterniflora* (Loisel) marshes. – J. Exp. Marine Biol. Ecol. 100: 75–95.
- Wetzel, R. L. 1975. An experimental study of detrital carbon utilization in a Georgia salt marsh. – PhD thesis. Univ. of Georgia.
- Wiegert, R. G. 1975. Simulation model of ecosystems. – Annu. Rev. Ecol. Syst. 6: 311–338.
- Wiegert, R. G. 1979. Population models: experimental tools for the analysis of ecosystems. – In: Hain, D., Stairs, G. and R. Mitchell (eds), Ecosystem analysis, pp. 233–279.
- Wiegert, R. G. and Evans, F. C. 1967. Investigations of secondary productivity in grasslands. – In: Petruszewicz, K. (ed.), Secondary productivity in terrestrial ecosystems. Polish Academy of Science, Krakow, pp. 499–518.
- Wiegert, R. G. and Owen, D. F. 1971. Trophic structure, available resources and population density in terrestrial and aquatic ecosystems. – J. Theor. Biol. 30: 69–81.