

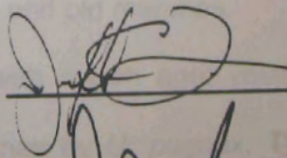
LOW MARSH SUCCESSION ALONG AN OVER-WASH SALT
MARSH CHRONOSEQUENCE

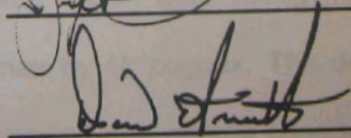
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Chicago, Illinois

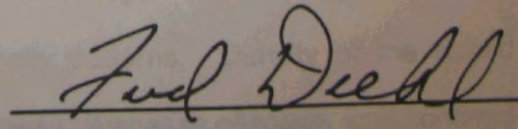
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M.S., Florida State University, 1972

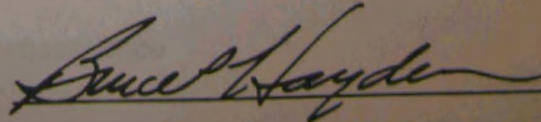
A Dissertation presented to the Graduate Faculty of the University of
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Department of Environmental Sciences
University of Virginia
May, 1998









ABSTRACT

Young marshes of the Hog Island marsh chronosequence possessed well aerated sediment that was composed mainly of sand grains, and also showed high pore-water redox levels, but low sulfide, and ammonium concentrations. With age, these variables changed in a monotonic way, until the mature marsh, 150Y, demonstrated poorly oxidized sediments, composed mainly of fine grains, and low pore-water redox, with high nutrient levels. Distinct physico-chemical stages were described using correspondence analysis (CA). CA also showed that temporal stability in physico-chemical characteristics of these marshes generally increased with marsh age.

Spartina alterniflora end of season biomass was greatest in marshes of intermediate age and lowest in very young and old marshes.

Uca spp. composition changed with marsh age: young marshes were inhabited by *U. pugilator* and older marshes by *U. pugnax*. The density of the marsh periwinkle, *Littorina irrorata*, also showed age related changes that were related to *Spartina alterniflora* stem density patterns. Density of the ribbed mussel decreased with age, and the mud snail, *Ilyanassa obsoleta*, was confined solely to the two older marshes of the chronosequence.

Each community was best described by the composition of its snails. Young marshes were characterized by greater periwinkle (*Littorina irrorata*) densities, while older marshes contained more mud snails (*Ilyanassa obsoleta*) than periwinkles. Community inter-annual stability, like physico-chemical stability mentioned above, generally increased with marsh age.

A species-poor ecosystem, these low marshes of the Hog Island chronosequence, underwent succession that tended toward a climax ecosystem or attractor. The important aspects of this process were summarized by the variables on correspondence analysis vector one, entitled 'bio-aeration'. Factor scores of vector one generally proceeded from values associated with low levels of pore-water sulfide, ammonium, redox and high *Uca* spp. density in young marshes to the opposite variable values in 150Y, the mature marsh of the chronosequence. As was the case for physico-chemical stage and biological community, young marsh ecosystems showed much greater inter-annual instability than marshes older than about 21 years.

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Graduate degrees are awarded to individuals, but the effort involves a community. I wish to thank but some members of my graduate community.

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Finally, eternal thanks to my family who supported me in my many trips to 'the Shore'. Thanks to my mother-in-law, Beth Tucker, who fed my body with her wonderful cakes, and my soul with her kindness and courage. I wish that my father-in-law, Robbie Tucker, could be here to witness the fruition of my labors. He would be proud. A most special appreciation to my wife, Mary Lee. I am grateful to have had a partner who understood my need to go away to do field work. She has always been an inspiration to live life to the fullest.

I am dedicating this dissertation to the memory of Antoinette Walsh Lord,

a mia madre

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INTRODUCTION TO SUCCESSION THEORY WITH SPECIAL
REFERENCE TO COASTAL SALT MARSHES

4 Introduction to succession theory with special reference to coastal marshes

1.4 General succession theory

Although the term 'succession' was first used in 1906 by Clements (later by Clements, 1916) to describe his studies in Germany, research into ecological succession is largely a 20th century enterprise, and one that has been dominated by ideas generated from terrestrial ecosystems, not wetlands.

The work of Clements and especially Clements (1916) under the century laid the foundation for a theory of succession and provided justification for the

CHAPTER ONE

employment of a 'climax' concept. In 1935, as the director of sand dune communities at the southern end of Lake Michigan, he found that long-term trends were controlled more by large-scale climatic events that drastically

INTRODUCTION TO SUCCESSION THEORY WITH SPECIAL REFERENCE TO COASTAL SALT MARSHES

disturb succession as an autogenic process along which each plant community or seral stage, when the local environment is that it is less favorable than the next seral stage, but unfavorable to itself. Clements called this process 'facilitation'. So as seral stages pass through a succession, a community that terminates as a 'climax community'. The principle that Clements established for ecological succession was that of directional growth and maturity to a 'climax' (Clements, 1916). Gleason (1917) immediately took issue with Clements' explanation. In his view, communities do not show trends to more

1. Introduction to succession theory with special reference to coastal marshes

1.1 *General succession theory*

Although the term 'succession' was first used in 1806 by DeLuc (cited by Clements, 1916) to describe hydroseres in Germany, research into ecological succession is largely a 20th century enterprise, and one that has been dominated by ideas generated from terrestrial ecosystems, not wetlands.

The work of Cowles and especially Clements earlier this century laid the foundation for a theory of succession and provided ammunition for the controversy that would follow. Cowles (1899) studied the dynamics of sand dune communities at the southern end of Lake Michigan. He found that long-term trends were controlled mainly by large-scale climatic events that drastically altered dunes, but that community dynamics in the time between these events was auto-regulated by the biota. The Clementsian model (Clements, 1916) describes succession as an autogenic process during which each plant community, or seral stage, alters the local environment so that it is less harsh and more favorable to the next seral stage, but unfavorable to itself; Clements called this process 'facilitation'. Seral stages also pass through a predictable series (a sere) that terminates in a 'climax community'. The analogue that Clements envisioned for ecological succession was that of organismal growth and maturity to an adult stage (Clements, 1916). Gleason (1917) immediately took issue with Clements' symbolism. In his view, ecosystems do not show 'juvenile to adult'

developmental tendencies. Rather succession depends on the sum of interactions between individual plants with the environment and each other. Gleason broadened the spectrum of allowable developmental paths to include successional reversals. He weakened Clements' notion of a fixed final stage of succession, calling it instead a 'tentative climax'.

Important enhancements in successional theory arose from mid-20th century efforts that were a reaction to the inflexibility of the Clements (1916) model. Clements (1936) himself was forced to concede that ecosystem development was not as predictable as he had once proposed. His reaction to criticism, however, was to obscure the notion of multiple climaxes with jargon. 'Sub-climax', 'pre-climax', and 'dis-climax' were all born from Clements' efforts to reconcile the reality of poly-climaxes with his original mono-climax theory. Whittaker (1953) recognized that climax communities were highly site-specific, and that many paths (seres) could lead to the same climax community, as well as different climaxes emerging from the same sere. Whittaker's climax was a system characterized by a steady-state with a self-maintaining population, a high level of complexity and species diversity, and maximum sustained utilization of environmental resources. He also included successional reversals in his model, calling these, 'deflected development' (Whittaker, 1953). One of the most provocative papers of this century on ecosystem development was the 1969 work of E.P. Odum entitled, 'The Strategy of Ecosystem Development', wherein he defined ecological succession as:

'an orderly process of community development, that is reasonably directional, and therefore, predictable. It results from modification of the physical environment by the community; that is, succession is community-controlled even though the physical environment determines the pattern, the rate of change, and often sets limits as to how far development can go.'

He goes on to suggest that the process culminates in a stable ecosystem, one which has come to be called the 'climax community'. To Odum, the major goal of succession is increased system homeostasis, that is maximal protection from environmental disturbance. In the process of becoming better buffered from the environment, ecosystems travel through a predictable series of changes that demonstrate increased organic matter storage, species diversity, spatial heterogeneity, stability, and nutrient conservation. Like Odum (1969), Vitousek and Reiners (1975) predicted that mature ecosystems are better able to sequester nutrients than younger ones. Connell and Slatyer (1977) represented the first major departure from facilitation as the only successional mechanism. Their facilitation was termed a Type I model of succession. The Type II model, their 'tolerance' model, proposed that a successional sere constitutes a predictable sequence of plant species based on different resource utilization patterns of individual species. Their 'inhibition' model (Type III) predicted that early colonizers garner all the space in a system and are displaced only if disturbance events provide gaps in which pioneer species could be replaced.

More recent efforts to unify successional theories only stress the divergence of views that 'seem to spring largely from an unachievable search for an ecological Shangri-La' (Miles, 1987). Bormann and Likens (1979), adhering to Margalef's dictum that 'biomass is the keeper of organization' (Margalef, 1968), focused on biomass changes during forest succession at Hubbard Brook Valley in the White Mountains of New Hampshire. They discovered a three-stage process of re-growth after clear-cutting within a second-growth northern hardwood forest. Biomass accumulates during the first or 'aggradation' phase, decreases slightly during the 'transition' phase, and finally fluctuates about a somewhat lower mean value during the 'steady state' phase. During this final phase, species composition and relative importance of species remain constant. In his 'resource-ratio hypothesis', Tilman (1985 and 1988) describes succession as a response of plant communities to a combination of increasing soil nutrients and decreasing light availability over time. Succession therefore involves a progression of plant strategies ranging from efficient nutrient sequestration in the early stages to greater light efficiency with ecosystem age. His model also allows for seral reversion and multiple climaxes (steady states). Most models have emphasized a steady state climax that maximizes stability and species diversity. Kaufman (1993 and 1995), however, proposed a climax model that maximizes the flexibility of ecosystems in the face of disturbance. Using Boolean networks of two variables, species number and degree of species interconnectedness, he found that computer models progress to a 'self-organized critical state' that is on

