Coastal Dune Succession and the Reality of Dune Processes

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INTRODUCTION
Coastal dunes were one of the first ecological systems studied in some detail (e.g., Cowles, 1899; 1901), and observation of the distribution of vegetation on coastal dunes gave rise to the idea of succession, defined as the sequential replacement of dominant species over time in the absence of disturbance (Clements, 1916). The early studies of coastal dune vegetation, particularly of the Indiana Dunes of Lake Michigan (e.g., Cowles, 1899; Fuller, 1912; Downing, 1922), were some of the first to apply the chronosequence method based on the ergodic hypothesis of substituting spatial sequences of vegetation for the temporal sequences of vegetation development. This method was subsequently used for the study of other types of
succession, such as on glacial till following glacial retreat (Cooper, 1923; 1931; 1939; Crocker and Major, 1955) and on abandoned agricultural land (Billings, 1938; 1941). It is still used extensively today to study succession (e.g., Thuille and Schulze, 2006; Merila et al., 2006). However, as discussed in Chapter 1 and in more detail later in this chapter, the chronosequence-based successional sequences encounter problems as soon as we begin to examine the assumptions of this space-for-time substitution. For example, for primary succession on the Indiana Dunes (Fig. 1), cottonwoods (*Populus deltoides* Bartr. ex Marsh.) are typically shown growing on the second dune ridge behind the foredunes that are dominated by the pioneer dune grass *Ammophila breviligulata* Fernald, leading to the chronosequence interpretation that *P. deltoides* is a seral species that establishes after the dune has been built and stabilized by *A. breviligulata* (e.g., McNaughton and Wolf, 1973). However, several studies (Fuller, 1912; Downing, 1922; Olson, 1958a; Poulson, 1999) have noted that the extremely small-seeded *P. deltoides* establishes only on moist germination beds, such as low pannes, swales, or recently in-filled runnels with surfaces close to the water table (Fig. 2); the margins of beaches or blowout ponds; or depressions on the beach, such as those caused by wheel ruts. No studies have shown evidence of successful establishment of these tree seedlings on the crests or slopes of dunes previously built up by the establishment of grasses. Furthermore, well-established seedlings of *P. deltoides* have been found to be very tolerant of sand deposition because of their rapid vertical growth and adventitious roots (Fuller, 1912; Poulson, 1999). Thus, these

![FIG. 1](image-url) Traditional dune successional sequence of plant communities attributed to Cowles (1898). (From McNaughton and Wolf (1973), redrawn with permission from Holt, Rinehart & Winston.)
FIG. 2 Establishment of cottonwoods (*Populus deltoides*) at Long Point on Lake Erie, Ontario, Canada. (A) Runnel developed during longshore sandwave migration by the onshore migration, emergence, and welding of a nearshore sand bar. (B) *Populus* seedlings 1 year after recession of the runnel. (C) Established *Populus* saplings in a former runnel. (Photographs by R. G. D. Davidson-Arnott.)
trees, once established, can survive subsequent establishment of *A. breviligulata* and the growth of a dune. This would explain how mature *P. deltoides* can be found growing on the dunes despite their inability to establish on such dry sites.

This example clearly illustrates how the chronosequence-based spatial pattern of vegetation can lead to an incorrect interpretation of the temporal sequence of plant species establishment. It also shows the importance of the contemporary understanding of aeolian sand transport processes, together with the ecological requirements of plant species for germination, establishment, growth, and survival. In fact, sand erosion and deposition have been widely recognized as a principal cause of plant species distribution in the coastal dune environment (Martin, 1959; Ayyad, 1973; Moreno-Casasola, 1986; Maun and Perumal, 1999; Poulson, 1999; Maun, 2004). Marsh (1987) proposed the relationship between sand mobility and dune species distribution illustrated in Fig. 3.

Therefore, rather than invoking the developmental argument of dune succession based on flawed chronosequence evidence, in this chapter we will use the concept of sediment budgets and the processes of coastal and aeolian sediment transport on beaches and dunes to largely explain the spatial and temporal distribution of coastal dune vegetation. However, before presenting this alternative explanation of dune vegetation dynamics and patterns, we first look at the traditional hypothesis of dune plant succession and review the major problems with this hypothesis. We then provide some basic explanation of sand budgets and transport on beaches and foredunes and show how an understanding of sand movement can be used to explain the observed distribution and abundance of dune vegetation. While the previous chapter (Chapter 7) and this chapter provide an introduction to some of the relevant geomorphic literature on coastal processes, we would encourage anyone interested in dune vegetation dynamics to use this as a mere starting point for any substantial understanding of sediment transport and coastal processes.

**TRADITIONAL DUNE SUCCESSION HYPOTHESIS**

The standard textbook diagram of dune succession on the Indiana dunes along the southern shores of Lake Michigan (Fig. 1) shows a linear sequence from bare sand to dune grasses (primarily *Ammophila breviligulata*), then cottonwood (*Populus deltoides*), pines (*Pinus strobus* L. and *P. banksiana* Lamb.), and black oak (*Quercus velutina* Lam.). Each of these dominant species is accompanied by its associated subordinate species.
(various graminoids, forbs, and shrubs). At times the sequence that has been proposed includes a stage of annuals (e.g., *Cakile edentula* (Bigel.) Hook.) preceding the dune grass stage (McNaughton and Wolf, 1973) or a climax beech-maple (*Fagus grandifolia* Ehrh.-*Acer saccharum* Marsh.) community following the black oak stage (Cowles, 1901; Clements, 1916). This vegetation sequence was derived from observations by Cowles (1899), as well as other early ecologists (e.g., Fuller, 1912; Downing, 1922), of the spatial distributions of these dominants on dune sequences along transects moving inland from the lake edge. This spatial pattern was interpreted as representing the temporal sequence of vegetation development that occurs on each dune, based on the reasonable assumption that the dune nearest

FIG. 3 Ranges of tolerance to sand erosion and deposition for six dune species and their corresponding distribution on the lee slope of an active sand dune in the Great Lakes region of the United States. (From Marsh (1987), redrawn with permission from John Wiley & Sons.)
the lakeshore is the youngest and the dune furthest inland is the oldest. This assumption was based on evidence of the long-term drop in water level of Lake Michigan during the Holocene. Thus, the hypothesis was that (1) the oldest dunes currently covered by a black oak–dominated community had undergone temporal changes in vegetation cover that essentially followed the observed spatial sequence and (2) all dunes in this area would trace this same sequence of communities in their development. Similar sequences but with different species [e.g., *Ammophila arenaria* (L.) Link instead of *A. breviligulata* (Hewett, 1970), *Cakile maritima* Scop. instead of *C. edentula* (Barbour, 1972)] have been postulated for marine and coastal dunes in various locations around the world.

The explanation that was given for the succession of plant communities on sand dunes (as well as on other substrates) was Clements’ (1916) theory of habitat alteration and facilitation, in which each dominant species alters the habitat in a way that facilitates the establishment of the next-dominant species in the sequence and inhibits or prevents its own regeneration. The “evidence” for this theory provided by various studies (e.g., Morrison, 1973) typically involved showing significant differences in soil properties (e.g., pH, organic matter content, field capacity, cation exchange capacity, and nitrogen) along the spatial dune sequence. The soil properties found associated with each dominant were interpreted as an indication of the soil conditions necessary for the establishment of each dominant species. [Note that Colinvaux (1993) used Crocker and Major’s (1955) similar chronosequence study of soil properties as solid evidence for the facilitation theory of plant succession on glacial till, although this conclusion was subsequently shown by Chapin *et al.* (1994) and Fastie (1995) to be flawed.]

According to Clements’ theory, the endpoint of succession was the climax community, which was stable since the dominant of this community was believed to alter the habitat such that it allowed no further invasions. Thus, in the absence of any major disturbance that might destroy the climax dominant, there would be no further change in species composition. According to Clements (1928), the species composition of the climax community was determined by the regional climate alone since any other factors (such as the characteristics of the initial substrate) would be altered sufficiently by the seral dominants to become irrelevant. For the Indiana dunes along Lake Michigan, the climatic climax was presumed to be mesic beech-maple forest. There was some subsequent disagreement on whether the final stage in the sequence was a black oak or beech-maple community, perhaps because of the lack of widespread beech-maple communities.
PROBLEMS WITH THE DUNE SUCCESSION HYPOTHESIS

Chronosequence Assumptions

The first problem with the traditional dune succession sequence of plant communities is that it is based on the results of chronosequence studies. This approach has many critical assumptions that must be valid in order to infer that the observed spatial sequence of plant communities represents the temporal sequence that each of the dunes has followed and will follow. The basic assumption is that the dune sites along the spatial sequence differ only in age and that, regardless of the spatial location, they have all traced exactly the same sequence of species and environment. However, in order to conclude that all dunes have followed and will follow the same developmental sequence, one must assume that (1) the conditions that influence successful establishment of the dominant species of each seral
community has been the same and are determined only by the previous
dominant species and (2) the establishment of species is not significantly
influenced by temporal variation in environmental factors, such as temper-
ature or precipitation. In other words, the climate at the time of dune initi-
ation or any other seral stage plays little or no role in selecting which
species can successfully establish; all that matters is the seral stage of dune
development.

There is little, if any, evidence for the validity of either of these two
assumptions. First, there is now abundant and conclusive evidence that sig-
nificant climatic variation occurs at all time scales and that environmental
conditions, such as temperature and precipitation, are therefore not con-
stant over the time span represented by the ages of the Indiana dunes or any
dune system (i.e., centuries to millennia). Furthermore, such climatic varia-
tion is not primarily controlled by the vegetation. Second, plant history
studies generally show that the most vulnerable stages in a plant’s life are
seed germination and seedling establishment (e.g., Laing, 1958; Sharitz and
McCormick, 1973; Houle, 1995; Clark et al., 1999; Rey and Alcántera,
2000; also see Grubb, 1977; Harper, 1977; Grime, 1979), and most mor-
tality in dune plant populations occurs within the first year (Lichter, 2000)
or even the first few days or weeks (Maun, 1994). Many, if not most, plant
species have a relatively narrow window of conditions that allow successful
establishment and survival of seedlings. As a result, many plant species
show episodic establishment in response to environmental variability; for
example, establishment of the dune grass, *Ammophila arenaria* (L.) Link
(Huiskes, 1977), and the pines, *Pinus strobus* and *P. resinosa* Ait. (Lichter,
2000), is episodic because of high desiccation mortality of seedlings. Thus,
plant species may encounter variable establishment success on dunes at dif-
ferent times and locations, depending on the prevailing environmental con-
ditions and regardless of the age of the dune. The environment encountered
by so-called later successional species as their propagules arrive is not
determined only by the dominant species that have established before them.

An additional assumption of the chronosequence-based succession
argument is that propagules of the species appropriate for each stage are
always available (i.e., that establishment of species is limited by environ-
mental conditions and not by species availability). However, numerous
studies have concluded that distance to seed source and propagule avail-
ability are significant limiting factors in species recruitment on a wide range
of substrates, including sand dunes (Olson, 1958a; Saunders and Davidson-
Arnott, 1991; Lichter, 2000), glacial till, (Chapin et al., 1994; Fastie,
1995), alluvium (Walker and Chapin, 1986; Walker et al., 1986), and
volcanic deposits (Wood and del Moral, 1987; del Moral and Bliss, 1993). The importance of species availability was a key component of Gleason’s (1939) individualistic view of community development and composition. This individualistic view was supported by Raup (1975), who observed that because of the stochastic nature of such species availability, no two communities in similar environments have identical species composition.

**Data Collection Techniques**

A second problem is that the traditional dune succession sequence was originally based on casual observations rather than systematic data collection. In subsequent years, it has often been obtained by averaging relative abundance data from several transects across a dune system. The pattern obtained by such averaging does not necessarily represent the sequence found for any individual transect. However, if the sequence of dune communities illustrated by Cowles (1899) actually represented a temporal sequence, one should expect most, if not all, transects to show this consistent pattern. Johnson and Muller (1992) and Stallins and Parker (2003) did not find consistent sequences of similar vegetation across transects on a marine coastline. Stallins and Parker’s explanation for this inconsistency was that the vegetation was responding not only to environmental gradients along transects but also to disturbances that did not occur simultaneously along the coast. Similarly, when Olson (1958a) arranged plant communities on the basis of the radiocarbon ages of the dunes on which they were found, he found much variation in the dominant species for any particular age or stage of dune development, depending on the particular location and disturbance history of the site (Fig. 4). Olson noted that the usual ordering of dune communities into a temporal sequence was a fiction, derived from patching together what appears to be the pattern for the region; he dubbed such a sequence a “synthetic succession” since communities at one end are not actually likely to be transformed into those at the other end.

**Species Replacement**

A third problem concerns the position in the dune succession sequence of annuals and cottonwoods (*Populus deltoides*) on the Indiana dunes (Fig. 1). McNaughton and Wolf (1973) described how the “grasses replace the annuals and then in about 20 years they are invaded by cottonwood tree seedlings.” However, as we will explain here, grasses do not replace
annuals and cottonwoods do not invade areas previously colonized by grasses. Annuals (e.g., *Cakile edentula*) are primarily found on bare sandy areas at the driftline and midbeach, which are kept bare in the fall and early spring months by high waves (Payne and Maun, 1981). Their habitat is largely segregated from the upper beach and dune habitat of the perennial grasses (e.g., *Ammophila breviligulata*) by seasonal wave disturbance. Any *A. breviligulata* that may advance by rhizomatous growth during the summer months into the driftline beach habitat of *C. edentula* are subsequently destroyed by high waves. Furthermore, while some individual annual plants may be found within the grass populations on the upper beach and dunes, this is not their normal habitat; seeds of *C. edentula* are primarily dispersed by the action of high waves that cast the fruits onto the driftline during autumn and winter (Payne and Maun, 1981). Similarly, Barbour (1972) noted that *Cakile maritima* is not found in the coastal dunes of California because the seeds are not carried inland beyond the reach of the water.

As previously discussed in this chapter, the dunes on which cottonwoods are found would have been initiated by the establishment of *Ammophila breviligulata* after the cottonwood trees had already successfully established on a moist surface close to the water table. Similarly, studies of dunes in northern Canada concluded that small seeded woody plants,
such as *Salix* and *Betula*, could not germinating on dunes since their seedlings were known only from moist to wet dune slacks (e.g., Raup and Argus, 1982), although *Salix* also appears to establish from branches/cuttings that wash up onto the driftline (A. M. Maun, personal communication). If a dune invades an area where these woody species have already established, these shrubs and trees may be found occupying the lee slope of the dune because they can withstand and thrive with sand burial (Fuller, 1912; Olson, 1958b; Raup and Argus, 1982; Poulson, 1999). This explanation of how nonxerophytic species establish and are maintained on dunes would help to explain the observation by McLeod and Murphy (1977) that, although the Lake Michigan sand dune vegetation has been described as xerophytic, it includes many species and genera that are not typically considered xerophytic and are primarily distributed along waterways (e.g., *Cornus stolonifera* Michx., *Populus deltoides*, *Salix glaucophylloides* Fern.).

**Soil Development and Colonization Constraints**

A fourth problem with the traditional dune succession hypothesis is the facilitation argument that mid- and late-successional species can establish only after habitat alteration (primarily soil development and nitrogen fixation) by early successional species (Clements, 1916). However, several studies have not found soil development or soil nutrient status to be a significant factor in explaining species distribution on dunes (Chadwick and Dalke, 1965; Lichter, 2000). Furthermore, through seed addition and seedling transplant studies, Lichter (2000) showed that tree species traditionally considered to be mid- to late-successional on dunes (e.g., *Juniperus communis* L., *Pinus strobus*, *Quercus rubra* L.) were capable of germinating and establishing seedlings on young dunes (30 years old) still dominated by *Ammophila breviligulata* where soil development would have been minimal. Olson (1958a) also found that the tree species *Tilia americana* L. can establish on steep lee slopes and protected pockets of young dunes along with grasses and shrubs. Furthermore, where *T. americana* has established, other hardwood trees can also establish without the dune going through any pine or oak stages. Thus, abundant evidence suggests that most, if not all, of the dominant species on dune systems can establish without the changes in pH or the addition of organic matter or nitrogen brought about by plants considered to be pioneers or early seral species. In fact, Baldwin and Maun (1983) found no significant differences in organic matter content within the top 5 cm of soil taken from the high beach, first dune ridge, slack, and second dune ridge on the Lake Huron sand dunes in
Ontario, Canada. Similarly, Poulson (1999) found that depth of A-horizon, amount of humus, cation exchange capacity, and levels of K and P on the Miller dunes were not statistically different than in a beech-sugar maple old-growth forest on sandy soil at Warren Woods in Michigan. Thus, Lichter (2000) concluded that, on his study dunes, successful establishment of “later successional” species depends not on facilitation by previous dominant species but on interacting constraints of chance seed dispersal, stochastic weather conditions, and fluctuating populations of rodent seed predators.

Physical and Biotic Disturbances

Probably the most important problem or limitation with the traditional view of dune succession is the lack of incorporating disturbance as an influential factor in the establishment and survival of plants on all of the dunes, regardless of their position relative to the shoreline and regardless of their age. For example, the common explanation that was given for the role of the dune grasses, such as Ammophila breviligulata or A. arenaria, was that of dune stabilization. As explained in one textbook (Strahler and Strahler, 1978), “the shoots of dune grass act to form a baffle that suppresses movement of sand, and thus the dune becomes more stable. With increasing stabilization, plants that are adapted to the dry, extreme environment but cannot withstand much burial begin to colonize the dune.” The assumption here appears to be that sand accumulation on the dune is somehow reduced by the establishment of the sand-binding dune grass. However, while the dune grasses do certainly act in reducing the windflow (e.g., Arens et al., 2001), thus trapping sand and resulting in vertical growth of the dune, they cannot stop the continued influx of sand from the beach. Neither can the establishment of trees stop such influx, as indicated by the sand burial of some established forests on dunes, resulting in reduced growth or even death of the trees (Wolfe, 1932; Kumler, 1969; Marin and Filion, 1992).

Established dunes may experience repeated episodes of sand deposition. For example, studies of the large (>30 m) perched dunes on the eastern shores of Lake Superior and Lake Michigan have found buried soil horizons beneath pine forests, indicating repeated episodes of dune-building over the past several millennia linked to changing lake levels and changing sand supply (Anderton and Loope, 1995; Loope and Arborgast, 2000). As a result of these repeated burials, the surfaces of these dunes are actually much younger than expected. In fact, buried organic horizons in
dunes indicating episodic aeolian sand movement and dune building are not limited to dunes along the Great Lakes but have been found elsewhere (e.g., Farrow, 1919; Filion, 1984). The implication of these buried organic horizons in dunes is that stability of the dune surface is determined not just by vegetation cover but also by sand supply (this is discussed in more detail in the later section on sand budgets). Furthermore, sand movement is not the only disturbance affecting dune vegetation; other disturbances include windstorms, fire, grazing, insect outbreaks and trampling. Thus, the plant community patterns observed on any dune system at any given time reflect not only environmental gradients of abiotic and biotic factors but also disturbance history (Downing, 1922; Olson, 1958a; Hobbs and Grace, 1981; Reice, 1994; Saunders and Davidson-Arnott, 1991; Stallins and Parker, 2003). Chapter 7 provides more greater details on the coastal processes and disturbances prevalent in coastal dune environments.

**PROCESS-RESPONSE ALTERNATIVE TO TRADITIONAL SUCCESSION HYPOTHESIS**

While most ecology textbook authors have indicated an awareness of some of the above-mentioned issues and arguments against the traditional dune successional sequence, probably a major reason that this interpretation of dune vegetation persists has been the lack of an alternative conceptual framework to replace it. We propose a framework based on a process-response approach that links plant population processes of birth and death to the principal physical processes operating.

Because of the low field capacity and limited capillarity of sand (especially in medium to coarse sand) and the resultant rapid drying of sandy surfaces, as well as the wind exposure of most coastal environments, the principal disturbance of coastal dunes is aeolian sand transport, which both creates and modifies the dunes. Although coastal dune ecosystems are also influenced by natural disturbances and processes other than sand transport (e.g., overwash, salt spray, herbivory), we would argue that the movement of sand is the principal filter for species selection on the backbeach, foredunes, and second dune ridge. Therefore, this section will briefly explain some background on budgets and transport of sand and then show how these can be used to explain the distribution of dune vegetation. Processes and disturbances, such as competition, grazing, and fire, that become more important on the stabilized dunes with more thorough vegetation cover will not be discussed in this chapter.
SAND TRANSPORT AND SAND BUDGETS

“Dunes are rarely stable landforms . . . and are liable to migration (by aeolian transport of sand-grains from the windward to the leeward slopes) and severe erosion” (Small and Witherick, 1986). Thus, the essential feature of most sand dune systems is the movement of sand by wind and a key element of such sand movement is the sand budget (i.e., the availability of sand for transport). As noted by Psuty (1988), “All variations of beach/dune forms are tied to sediment availability, the relative input to the dunes and to the beach, and whether these inputs are decreasing or increasing over some duration.” Thus, Fig. 5 presents Psuty’s ideas on morphologic development of the beach-dune system under varying combinations of sand budgets for the two components.

When sediment (sand) inputs exceed outputs, the system is described as having a positive budget; a negative budget indicates the reverse (i.e., outputs exceed inputs). Each component of the coastal beach/dune system (beach, foredunes, and so forth) has its sediment budget and can react in relatively short time frames to imbalances between inputs and outputs, producing changes in the coastal topography. For example, coastal dunes can grow in elevation by as much as 58 to 90 cm in a year (Ranwell, 1958; Tyndall et al., 1986; Costa et al., 1991) or can deflate by 60 to 75 cm in a blowout over 3 to 14 days (Gares, 1992). Note that within a beach-dune system that may have an overall positive sediment budget, there may be localized areas of deflation/erosion.

For coastal dunes to be in a stable state (neither growing nor deflating), three conditions are required: (1) that the dune be far enough from the shoreline to be unaffected by erosive wave action; (2) that the dune have complete vegetation cover such that the surface sand is not exposed to erosive wind action; and (3) that there be no external source of sand for deposition.

The first condition is obviously affected by beach width; factors and processes influencing spatial and temporal variation in beach width are discussed later. However, in general, embryo dunes and first dune ridges on beaches are subject to erosion during storm surges or longer-term cycles of high water (Saunders and Davidson-Arnott, 1991) and are therefore rarely stable while the dunes landward of landward of and protected by the foredunes are more likely to be stable. If close to the water, even high-cliffed dunes along the coastline are vulnerable to undercutting by wave action, subsequently exposing the cliff sand to transport by wind (Anderton and Loope, 1995; Arbogast et al., 2002).
FIG. 5 Development of various beach and dune morphologies under various sediment budget combinations. (From Psuty (1988), redrawn with permission from Coastal Education and Research Foundation, Inc.)
Concerning the second condition, parts of dunes that lack complete plant cover (either through initial patchiness of plant establishment or subsequent disturbance such as grazing, fire or trampling) have sand exposed to aeolian transport, particularly when the sand is dry and wind speeds are sufficient to initiate saltation (e.g., blowouts). Plants obviously play an important role in dune sand budgets by acting as sediment traps (extracting momentum from the wind and acting as obstacles to airflow), thus causing the deposition of incoming sand and preventing sand from continuing to move downwind (Lancaster and Baas, 1998; Arens et al., 2001). Plant cover also inhibits loss of sand from surfaces on which they occur by protecting the sand grains from the action of wind. However, plant cover of a dune by itself cannot stabilize a dune surface since it cannot control the input of sand from upwind sources. Thus, establishment of Ammophila may facilitate dune growth by trapping incoming sand, but the dunes stop growing and their surfaces stabilize only when the sand supply is removed (e.g., by the development of another dune upwind that robs it of its sand supply or by rising water levels that reduce the beach width and hence area of sand exposed to wind). Growth of a stabilized dune may be reinitiated if sand again became available (e.g., by destruction of the upwind dune).

Finally, if the availability of sand from external source areas increases (e.g., when falling lake levels expose a greater area of dry beach sand), then even previously stable, completely vegetated dunes downwind from this increased sand supply may become buried in sand. For example, buried soils in the perched Grand Sable Dunes near the east end of Lake Superior have been explained by Anderton and Loope (1995) as a result of episodic changes in sand supply. Although in general increased sand supply and foredune progradation occur during falling lake levels (Olson, 1958c), in the case of the perched Grand Sable Dunes, Anderton and Loope argued that sand supply increased during periods of rising lake levels. At such times, the bluffs were destabilized through basal erosion, producing actively eroding slopes that provided a fresh source of sediments for aeolian transport to these perched dunes.

Determination of sand budgets (i.e., changes in mass flux of sand) over the surface of a beach-dune system requires knowledge of the process by which sand is transported. Numerous models of aeolian sediment transport have been proposed (Bagnold, 1936; Kawamura, 1951; Zingg, 1953; Owen, 1964; Kadib, 1965; Hsu, 1971; Lettau and Lettau, 1978; Nakashima, 1979; Horikawa et al., 1984, Anderson and Haff, 1991; McEwan and Willetts, 1993; Spies and McEwan, 2000). In these mechanistic models of saltation, sediment transport is a function of wind speed.
Most of these models consider transport under the near-ideal conditions of a uniform wind field, dry uniform sand particles, and a horizontal, flat, unobstructed surface, even though field conditions are rarely, if ever, ideal (Namikas and Sherman, 1998). The presence of moisture in the sand or a sloping surface (upward or downward) would have a significant effect on the transport rate. Namikas and Sherman listed several moisture correction models (Belly, 1964; Kawata and Tsuchiya, 1976; Hotta et al., 1984; Gregory and Darwish, 1990) and slope correction models (Bagnold, 1956; Allen, 1982; Dyer, 1986; Hardisty and Whitehouse, 1988; Zeman and Jensen, 1988) that account for these factors. They then presented a computer program (AEOLUS II) that allows iterative selection of combinations of appropriate models to simulate aeolian transport on a complex surface with varying grain size, slope, and moisture content. Since the sand budgets of the various components of the dune-beach system are necessarily connected as sand is transported across the system, AEOLUS II calculates different transport rates and resulting mass flux within each spatially explicit component or “bin.”

Furthermore, wind flow is strongly affected by topography (Namikas and Sherman, 1998; van Boxel et al., 1999; van Dijk et al., 1999), creating a positive feedback situation. For example, studies of wind flow in blowouts show that once a blowout is initiated, the structure of the blowout influences subsequent wind flow patterns (Landsberg and Riley, 1943; Olson, 1958b; Hesp, 1996; Hesp and Hyde, 1996; Pringle et al., 1999; Hesp, 2002). Any wind flow approaching a trough blowout from a seaward or alongshore direction in an arc of at least 180° to the entrance orientation is directed into the blowout. Thus, the direction that sand is transported within the blowout is determined by the topography created by the blowout. Besides changes in wind direction, the morphology of the blowout creates jets in the deflation basin and depositional lobe, flow deceleration and expansion up the depositional lobe, further jets over the crest of the depositional lobe, and finally flow separation and corkscrew vortices over the crests of the erosional walls (Hesp and Hyde, 1996). AEOLUS II attempts to account for some of the feedback effect of topography on wind flow by iteratively adjusting the topography as a result of the mass flux at each time step (Namikas and Sherman, 1998).

The output of this model gives simulated topographic change on a three-dimensional landscape (Fig. 6). While this model is the only three-dimensional spatially explicit distributed model of sand transport and
topographic change that we could find in the literature, it has the major limitation of applying only to unvegetated surfaces and does not allow for changes in windflow and deposition due to the presence of plants.

An alternative approach that does include vegetation is the model by van Dijk et al. (1999) that uses published deterministic and empirical relationships describing the influence of meteorological conditions, topography, sediment characteristics, and vegetation to determine sediment transport. Their model produced two-dimensional simulated dunes whose morphology is consistent with those of natural dunes, both unvegetated and vegetated. As indicated in Fig. 7, model simulations showed that the height of vegetation influenced the morphology of the developing dune and empirical studies appear to support these model results (Olson, 1958b; Oertel and Larsen, 1976). However, this influence of vegetation height on dune morphology may be a temporary depositional phenomenon and may not be detectable as the dune evolves over several decades.

Arens et al. (2001) used the model by van Dijk et al. (1999) to investigate the influence of experimentally planted reed stem density on sediment transport and on the resulting dune forms and found that vegetation density also influenced the shape of the dune, both in the empirical and simulated results (Fig. 8). The highest stem density produced a steeper dune because most of the sand was trapped by the first row of planted stems.
The lowest stem density produced a smoother wider dune since sand was deposited more evenly throughout the planted area. Despite these differences in sand transport and deposition, the total amount of sand that accumulated was not affected by stem density. This indicates that the mass flux was limited by the amount of sediment transported to the planted area from the upwind beach.

**FIG. 7** Simulated two-dimensional dune development on an initially flat partly vegetated surface during 4 days of a constant wind (0.4 m·s\(^{-1}\)) for three different vegetation heights (0.2 m, 0.5 m, and 0.8 m). Vegetation is present downwind (i.e., to the right) of \(x = 0\). (From van Dijk et al. (1999), redrawn with permission from Wiley.)
FIG. 8 Simulated two-dimensional dune development resulting from a high-density (plot N4) and a low-density (plot N1) of reed stems planted in rows on the windward bare slope of a foredune. (From Arens et al. (2001), redrawn with permission from Wiley.)
Thus, what is required here is a model to quantify the rate of sediment supply from the beach to the first zone of net deposition (typically where vegetation acts as an obstacle to windflow and extracts momentum from the wind and saltating sand). Bauer and Davidson-Arnott (2002) developed a model of sand transport processes operating on the beach to predict sand supply to the dunes. A problem they addressed was that none of the equilibrium sediment transport models account for the fact that sediment transport may be less than the maximum for any given windspeed and set of sand characteristics because of the fetch effect. As the wind begins to entrain sand and cause saltation of individual grains, there is a cascading effect of the impact of saltating grains dislodging more grains from the surface. As a result, the number of saltating particles increases exponentially and asymptotically downwind to a limiting maximum (saturation) condition (Chepil, 1957; Anderson et al., 1991; Gillette et al., 1996). Whether the sand transport rate is at equilibrium upon reaching the vegetation depends on the beach geometry, angle of the wind approach relative to shorenormal, and any “end effects” (since the beach is not indefinitely long and would have limiting lateral barriers to alongshore transport with an oblique wind). These barriers may include both natural and artificial features, such as rivers, vegetated zones, and seawalls. Bauer and Davidson-Arnott’s model could be useful in explaining some of the alongshore differences in dune formation.

While Bauer and Davidson-Arnott’s (2002) model provides a more realistic approach to determining sand supply from the beach to the dunes, there is still the issue of sand supply to the beach. In van Dijk et al.’s (1999) model of sand transport and dune formation, the beach lost sand but had no mechanism for replenishment. As a result, the researchers had to artificially replenish the beach with sand in order to allow the model to continue. Certainly, if sand supply to the beach is a limiting factor as on eroding shorelines, it would be necessary to incorporate a model of sediment transport from longshore drift cells and wave action that would determine sand supply to the beach. Thus, Bauer and Davidson-Arnott suggested coupling their model to a littoral sediment budget model (e.g., Bowen and Inman, 1966) for a more comprehensive model of beach-dune interaction.

Beaches may vary in their sand budgets over varying temporal scales because of short-term changes in water levels (e.g., storm surges), cyclic changes in water level (e.g., seasonal as well as quasi-periodic lake level fluctuations; see Figure 3 in Davidson-Arnott and van Heyningen, 2003), and long-term trends in water levels (e.g., sea level change resulting from
global warming or cooling). As water levels rise, beach widths decrease and vice versa. Beach width acts as a major control on sediment supply to the foredunes as well as on the extent of dune erosion during storms (Davidson-Arnott, 1988). As previously discussed, these changes in beach width result in increased availability of sand for aeolian transport and dune formation/growth or scarping/erosion of established dunes.

Besides changes in water levels, beach width and onshore sediment movement are also affected by the alongshore migration of sandwaves (where they occur) on a temporal scale of years to decades (Stewart and Davidson-Arnott, 1988). Stewart and Davidson-Arnott describe sandwaves as local beach protuberances with lengths of 500 to 2500 m, maximum widths of 50 to 90 m, and lifespans of 10 years or more, which migrate alongshore at 150 to 300 m•y⁻¹. These sandwaves migrate through the onshore migration and attachment of a nearshore bar, after which the bar becomes emergent, thus extending the width of the beach. As a result, the beaches are very narrow between the sandwaves (Davidson-Arnott, 1988). Because they influence onshore sediment transport and beach width, these migrating sandwaves affect erosion and accretion of dunes (Davidson-Arnott and Stewart, 1987), particularly during storms that occur during high water levels (Davidson-Arnott and Stewart, 1987; Saunders and Davidson-Arnott, 1991). Ruessink and Jeuken (2002) also found evidence of migrating sand units that traveled along sections of the coast of Holland. As with the sandwaves along the Lake Erie coast in Canada studied by Davidson-Arnott and coworkers, these sandwaves in Holland were found to play an important role in foredune dynamics through temporal changes in beach width and resulting sand budgets.

**Coupling Sand Budgets and Vegetation Distribution**

Although past studies examining the distribution of coastal dune vegetation have cited influential factors such as desiccation (De Jong and Klinkhamer, 1988), nutrient shortage, and salt spray or soil salinity (Barbour *et al.*, 1976; Barbour and De Jong, 1977; Barbour, 1978; Barbour *et al.*, 1987; Olff *et al.*, 1993), as well as herbivory and seed predation (Boyd, 1988a; 1988b; 1991; Klinkhamer *et al.*, 1988), sand burial has generally been considered the most important factor (Ranwell, 1958; Hewett, 1970; van der Valk, 1974; Moreno-Casasola, 1986; Harris and Davy, 1987; Sykes and Wilson, 1990; Zhang and Maun, 1990a; Martínez and Moreno-Casasola, 1996; Maun and Perumal, 1999; Kent *et al.*, 2001; Maun, 2004). Since aeolian sand transport is the principal factor creating
and modifying the dune surface on which plants are establishing and growing, it acts as a primary filter in determining which plants can successfully establish and survive.

Species differ in their tolerance of sand burial (positive sand budget) or erosion (negative sand budget) (Fig. 2). Numerous studies have investigated the responses of various species to varying rates and amounts of sand burial (Maun and Riach, 1981; Maun, 1985; Maun and Lapierre, 1984; 1986; Harris and Davy, 1987; Sykes and Wilson, 1990; Zhang and Maun, 1990a; 1990b; Yuan et al., 1993; Maun, 1996; Chen and Maun, 1999; Martinez and Maun, 1999; Maun and Perumal, 1999). This variation results in selection for those species that tolerate the particular sand budget of a surface (Moreno-Casasola, 1986; Maun and Perumal, 1999; Dech and Maun, 2005), thus influencing or determining species composition of dune plant communities (Owen et al., 2004; Kent et al., 2005). For example, Tyndall et al. (1986) proposed that the restriction of species distributions on the beach and foredunes of the North Carolina Outer Banks could be explained by the differential ability of species to establish seedlings from buried seeds. Of six species occupying the foredunes, Cakile edentula, which was able to emerge from the greatest depths of experimental sand burial, was the only species occurring on the open beach. More recently, Dech and Maun (2005) showed clearly that the distribution and abundance of both woody and herbaceous species on the Lake Huron dunes in Ontario followed a gradient of sand burial, independent of any other environmental factors. Furthermore, species’ tolerance of varying rates of sand deposition or erosion may change through their life cycle. Thus, while the extremely small seedlings of cottonwood (Populus deltoides) cannot survive sand burial, once well-established on a stable deflation panne with roots below the water table, the saplings can tolerate a considerable positive sand budget (Downing, 1922).

The first important implication of recognizing the key role that the sand budget plays in vegetation dynamics and vegetation patterns on dunes is the necessity to understand the spatial pattern of sand budgets resulting from aeolian sediment transport processes. As the sediment transport models mentioned in the previous section indicate, the beach-dune environment (and particularly the beach and foredune components) has a very dynamic surface over relatively short time periods. Thus, a change in the wind speed at the surface (e.g., a decrease resulting from planting sand reeds at any density) on the bare windward slope of a foredune resulted in a change from a negative sand budget to a positive one and vertical growth of the surface (Arens et al., 2001). Changes in any of the factors that influence
and determine aeolian sediment transport, such as wind speed, sand moisture content, or slope, have impacts on the transport rate and resulting mass flux. Furthermore, such transport produces topographic changes that, in turn, affect windflow and result in a feedback effect on subsequent transport and topographic changes. Once we understand the dynamic nature of the surface of the beach-dune environment, we can begin to relate this to the tolerances of various species for the various sand budget environments they would encounter. These conditions determine the subset of species that can establish in different parts of the beach-dune system (e.g., on the crests, lee slopes and bases of foredunes).

The second implication is the recognition of the temporal instability of the sand budgets at varying time scales. In other words, the sand budget of any surface in the coastal environment can, and does, switch between positive, negative, or zero over time. At Great South Beach, New York, Clark (1986) found evidence of sand deposition sufficient to destroy all vegetation occurring at irregular intervals but at least once every 100 years over the past 340 years. This means that the particular species that have an advantage in terms of improved establishment and decreased mortality in response to the sand budget conditions will also change over time. For example, an area that was deflated to the water table following a period of negative sand budget may allow establishment of species that require wet surfaces for seed germination and seedling survival (e.g., *Populus deltoides*). Other species with similar requirements for establishment may also invade. However, if the sand budget changed subsequently to a positive one as a sand supply became available and the established plants began to act as sand traps, many of these species may become buried and die while *P. deltoides*, which can tolerate and continue to grow vertically when subjected to sand deposition, will continue to flourish. Other species that can establish and survive with a positive sand budget may then cohabit the area with *P. deltoides*. Thus, the composition of the community would change as the changing conditions affect species differentially and individualistically (Gleason, 1939).

Furthermore, because different areas of coastal environments will have different histories of changing sand budgets with different subsets of species available to them as the sand budgets changed, they would not be expected to follow any deterministic temporal pattern of community composition change. In other words, dunes that may be a similar distance from the shoreline and may be considered to have originated from the same dune-building event at some time in the past would not be expected to have the identical species composition of plant community, as Olson’s (1958a) study
showed (see Fig. 3). A good example of this is the beach topography resulting from the passage of an alongshore sandwave as described earlier. The attachment and emergence of a nearshore bar during sandwave migration can result in the formation of a runnel between the emergent bar and the beach (Davidson-Arnott, 1988; Stewart and Davidson-Arnott, 1988). The subsequently infilled runnel can provide the seedbed conditions for successful establishment of *Populus deltoides*. If the beach continues to prograde and the area is invaded by dune-building grasses such as *Ammophila breviligulata*, the foredune community that develops will include *P. deltoides*. On the other hand, a foredune that did not originate in this manner and did not involve successful *P. deltoides* establishment before establishment by *A. breviligulata* would not have *P. deltoides* as a component of the plant community.

**CONCLUSION**

Sand dune succession is not a fact or a phenomenon but a hypothesis of vegetation development on dunes that is based on chronosequence studies. A chronosequence is a series of spatially distinct sites of varying ages that is assumed to represent a temporal sequence of vegetation. Thus, the chronosequence assumes that the spatially distinct sites are identical in all aspects other than age and that all sites in the spatial sequence have followed or will follow the same temporal sequence. The validity of this assumption has not proven to be valid for many reasons. Empirical evidence has shown that sites are rarely, if ever, stable (i.e., constant climate and disturbance free) over the time period represented by the age of the oldest site. Because of a constantly changing climate, sites of different ages would have initiated under very different climatic conditions that would affect seedling establishment. As a result of other factors, such as changing water levels and migration of alongshore sandwaves, the history of foredune development would vary both spatially and temporally, affecting the sequence of species establishment. Also, because of disturbance regimes changing over time, the sites would have been subject not only to different types of disturbances but also to different disturbance regimes. In other words, not all sites would share a common disturbance history. Finally, the ubiquity of disturbance regardless of the age of the dune substrate would mean that the vegetation in all sites in the sequence, not just the youngest site, would be expected to have arisen from some disturbance.

In fact, the traditional hypothesis of dune succession (and of plant succession in general) assumes the development of vegetation in the absence of
disturbance. That most coastal dune communities are subject to different disturbances (e.g., sand movement, overwash/inundation, hurricanes, fires, trampling, overgrazing) at rates frequent enough to play a significant role in the establishment and survival of plant species is undeniable and therefore, this point alone should be sufficient argument against the stability of vegetation on even “fixed” dunes and their development to a stable climax community. As noted by Carter (1990), “[m]any dunes systems are a mosaic of stable and unstable surfaces”; they do not consist simply of a growing dune inland of which are dunes stabilized for increasing lengths of time.

Whether the vegetation reflects the dominant influence of sand movement or one of the other disturbances, such as fire, depends on the relative frequency of these disturbances. For example, on the embryo and foredunes where vegetation is often too sparse to propagate fires and where sand transport is significant enough to be measurable at short time scales (<1 year), the vegetation would obviously reflect species’ tolerances to sand erosion/deposition rather than to fire. On the other hand, on dunes further inland where the sand budget is neither significantly positive nor negative and where continuous ground cover by vegetation allows fires to spread, the vegetation would more likely reflect species’ tolerances to the fire regime (frequency and intensity).

Much of the dune succession studies have focused on vegetation development on the first few dune ridges, where the stability of the surface is an issue. Despite this, there is a surprising lack of recognition of the geomorphological literature on sediment transport in coastal environments that provides an understanding of the temporal and spatial dynamics of the dune surfaces upon which vegetation must establish. Lacking such understanding, the succession argument (and particularly the facilitation explanation for community replacement) assumes that it is the establishment of the “pioneer” dune grasses that stabilizes the sand surface, thus allowing seral species that are intolerant of sand deposition to establish and replace the grasses that not only tolerate but require continued sand deposition for survival. While plants do influence the rates of sediment mobilization and deposition through their influence on windflow, they cannot prevent sand movement which depends on the availability of sand for transport (i.e., the sand budget).

Sand budgets are important in determining whether the surface of a particular site is accreting or deflating. The changes in surface morphology resulting from changes in sand availability and the aeolian processes of sand transport have been modeled relatively successfully for both bare and vegetated surfaces (e.g., van Dijk et al., 1999; Arens et al., 2001). Furthermore,
such models can be used to explain and predict dune growth or deflation under changing conditions. The next step would be to couple these sediment transport and sand budget models with the ecological tolerances of species for varying rates of sand deposition or erosion in order to explain the distribution of species on actively accreting or deflating surfaces.

However, other factors are also recognized as playing a role in successful plant establishment and thus explaining species distribution in coastal dune environments. For short-lived species, the current environmental conditions of a particular site (e.g., the current sand budget, temperature and precipitation, distribution of seed predators and herbivores) may best explain the distribution of species. For old long-lived species within the community such as trees, it would be necessary to know the developmental history of the site since the time of establishment of the population in order to account for its presence. Thus, Clark (1986) concluded that “[p]resent distributions [of the barrier-beach vegetation] are largely the product of historical events acting together with existing conditions.”

The above proposed framework points out the importance of integrating the work of coastal and aeolian geomorphologists with that of physiological and population ecologists to develop a better and more realistic understanding of the spatial and temporal distribution of plant species populations in coastal dune environments (e.g., Hayden et al., 1995). Without such integration, ecologists tend either to correlate current environmental conditions with population or community distribution patterns, assuming some kind of equilibrium state between the two without considering the dynamic nature of the dune environment, or to invoke a “synthetic successional” argument (sensu Olson 1958a) based on an invalid chronosequence.

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REFERENCES


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Author Queries:

[Au1] Pls. check cross reference
[Au2] Pls. check cross reference
[Au3] CEC defined correctly? Pls. spell out K and P (potassium and phosphate?).
[Au4] Pls. check cross reference
[Au5] Should the “E” be a degree symbol?
[Au6] Okay to keep unpublished report in reference list?
[Au7] Pls. supply page range