The Ecological Significance of Burial to Trees and Shrubs on Coastal Sand Dunes at Pinery Provincial Park

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Abstract

Coastal dunes of the Great Lakes are dynamic environments, where plants are stressed by recurrent sand burial. The unique plant communities of these systems consist of species adapted to withstand various amounts of burial, including several important trees. At the Pinery, burial of trees occurs largely on the lee slopes of blowouts. The encroachment of sand onto lee slopes and nearby savannas buries entire plant communities (retrogression), creating a bare area that is eventually populated by dune building grasses and shrubs (colonization). Burial activity varies amongst dunes and tolerance to burial varies amongst species, thus, lee slope communities (including trees and shrubs) exhibit zonation related to burial. Specialized dune-builders can also affect sand movement by colonizing bare areas and consolidating the substrate. The main adaptations that determine burial tolerance in trees and shrubs are the production of adventitious roots on a buried stem and allocation of resources to support growth out of the sand. Species that lack these traits eventually become extirpated in high burial habitats, while the sand-dependent species that possess these traits proliferate. Overall, burial is an important selective force that influences the landscape, community, and physiological ecology of trees in this globally unique habitat.

Keywords: *coastal sand dunes, tree burial, Pinery Provincial Park*

Introduction

On coastal sand dunes, burial is a recurrent abiotic stress that is universally imposed upon the vegetation. The objective of this paper is to present a

synthetic conceptual model of the importance of burial to the ecology of woody plants by integrating studies on coastal dunes of the Pinery Provincial Park from the landscape, community, and species levels of biological organization. Previous models of burial responses in plants have focused on the individual or species level (Antos and Zobel, 1987; Maun, 1998). Here we seek to build upon this foundation to provide a complete view of burial as a driving force in dune systems and provide valuable information for the management and conservation of these unique habitats.

Conceptual Model of the Ecological Significance of Burial

Burial at the Landscape Level: Retrogression and Colonization

Burial is a geomorphic process that operates at scales associated with levels of organization that span from landscapes to individual plants. The first element of a conceptual burial model for woody plants is the determination of the magnitude and distribution of burial as a selective force in the coastal dune environment, which can be viewed as a summation of its total spatial extent in a given ecosystem for a given time period. Determination of this information requires a quantitative approach to coastal dune dynamics (Jungerius and Schoonderbeek, 1992).

Several studies have produced estimates of rates of sand movement onto stands of woody species based on short-term observations of surface depth on pins (Ranwell, 1958), or dendrochronological sequences (Marin and Filion, 1992); however, these data give little indication of either the spatial extent or pattern of burial and, therefore, lack an important component of the burial context over a long period of time.

At the Pinery, a change-detection analysis of airphotos comparing the spatial coverage of bare sand, herbaceous and woody vegetation within ten blowouts from 1973 to 1998 was conducted. This analysis indicated that burial (retrogression) of dune lee slopes and adjacent savanna habitats, which supported plant communities with a significant cover of woody plants, comprised about 20% of the total area sampled over the 25 year period (Dech *et al.*, 2005). While this proportion comes from a selectively sampled area and is likely to vary among systems over both space and time, it does establish an important benchmark that quantifies the natural level of burial imposed upon woody plants in a coastal dune ecosystem. Such a benchmark would be useful in assessing how tree communities could be indirectly affected by

global changes, such as climate change and sea-level rise (Loope and Arbogast, 2000; Hesp, 2002). However, one must also consider the counteractive influence of stabilizing forces, mainly due to colonization by dune-building grasses and shrubs, when attempting to determine the net impact of sand movement.

The results from the change-detection analysis of the undisturbed system at the Pinery (Dech *et al.*, 2005) indicated that the process of colonization, or establishment of plants on bare areas, was approximately balanced with the level of burial (also at 20% of the sample area). Tight coupling of blowout activity and vegetation is well known (Jungerius *et al.*, 1981; Jungerius and van der Meulen, 1989; Hesp, 2002); however, the Pinery data suggest a relative balance of the co-occurring processes of retrogression and colonization at any given time, which produces high spatial variability of burial and a mosaic of patches of various activity levels at a broad range of sizes and shapes amongst different blowouts. Dunes are by nature dynamic systems, and the appreciation of sand movement as an important source of habitat variation that promotes biodiversity is beginning to increase (Martinez *et al.*, 2004). Clearly, the habitat patch diversity generated by burial has the potential to affect community composition.

Burial of Plant Communities: Zonation Related to Tolerance

Various environmental filters create habitat patches in coastal dunes. One of the most important filters on coastal dunes is sand movement (van der Valk, 1974; Moreno-Casasola, 1986; Maun, 1998), and this filter is known to produce a strong zonation of herbaceous plant communities on the open dune ridges close to the shoreline (Maun and Perumal, 1999). The spatial extent and variability of burial activity in plant communities behind blowouts creates an identical scenario in which strong zonation could develop, and results of vegetation surveys of the lee slopes of various dunes at the Pinery indicate that variable blowout activity does produce zonation in plant communities. Plant communities from nine stands on the lee slopes of parabolic dunes showed that patterns in composition were strongly related to burial (Dech and Maun, 2005).

Three general community types occurred along the burial gradient created by variable blowout activity: i) active dune communities, ii) semi-active dune communities, and iii) stabilized dune or savanna communities. In the understorey, there was an increase in species richness and diversity (Shannon's Diversity Index) from high to low burial activity, as well as a shift

in dominant species from sand-reed/broom-beard grass (*Calamovilfa longifolia/Schyzichirium scoparium)* in active stands to sand-reed/ivory sedge (*Calamovilfa longifolia/Carex eburnea)* in stable ones. The pattern in the overstorey trees was different. Species richness and diversity decreased in stable stands, and *Juniperus virginiana* remained dominant over the entire gradient.

The sub-dominants black oak (*Quercus velutina)* and white pine (*Pinus strobus)* showed a strong response to burial activity and increased markedly in stable dune communities. This zonation of woody species was not as strong as that of the herbaceous species, likely because the relatively large size and longevity of woody plants dampens their responses to burial (Dech and Maun, 2005). However, it was clear that the variability generated by landscape level geomorphological processes in dunes was incorporated into the community composition of woody plants. This indicates that there exists a wide variation in burial tolerance amongst woody species; however, the inherent differences between woody and herbaceous plants make it unclear if this intraspecific variability was produced by the same mechanisms.

Adaptations to Burial in Woody Plants: Adventitious Roots and Flexible Allocation

Few experimental studies have examined the effects of burial of woody plants on coastal sand dunes. Previous attempts to determine differences in species tolerance have been largely based on field observations. Experimental burial studies of woody plant species typical of central Canadian coastal sand dunes were conducted at the Pinery (Dech, 2004) and indicated that the predictions of Maun's (1998; 2004) conceptual model of burial stress in plants were confirmed, with representatives of negative, neutral, and stimulatory responses occurring in the pool of species studied.

Tree species that are not typical of active sand dune communities may germinate and grow for some length of time; however, they lack the traits necessary to survive recurrent sand deposition and are eventually restricted to patches of low burial activity or removed from the system completely (Maun, 2004). Species such as white pine and black spruce (*Picea mariana*)exhibited reduced growth and were categorized as intolerant (Dech, 2004). This corresponded well to their observed distributions as important components of wooded inland dunes on the Laurentian Great Lakes and Hudson Bay respectively, which are killed by burial in active areas of the dune system (Cowles, 1899; Olson, 1958; Marin and Filion, 1992).

White cedar *(Thuja occidentalis)* and red cedar (*Juniperus virginiana)* survive in the open dunes, but reach maximum importance in the transitional habitat between the dunes and the inland savanna. These species tolerated moderate levels of burial but became stressed or died at high burial (Dech, 2004). The dune building shrubs of the Laurentian Great Lakes, balsam poplar (*Populus balsamifera)* and heart-shaped willow (*Salix cordata*) were clearly stimulated by burial and achieved maximum growth in the highest burial treatments (Dech, 2004). The strategy of burial specialization well known for beach grasses such as marram grass (*Ammophila breviligulata*) appears to have also evolved in these species.

The traits that determined membership in the three response groupings proved to be the same for woody plants (Dech, 2004) as for herbaceous plants (Maun, 1998). The production of adventitious roots on buried stems allowed the tolerant woody species to survive burial, and this ability has emerged as a convergent trait possessed by virtually all species tolerant of burial on coastal sand dunes (Maun, 1998). The sand-dependent species also produced copious adventitious roots; however, their additional ability to alter resource allocation to biomass in a way that favoured the upward growth of stems and new leaf production allowed for these species to be stimulated by burial (Dech, 2004).

Synthesis

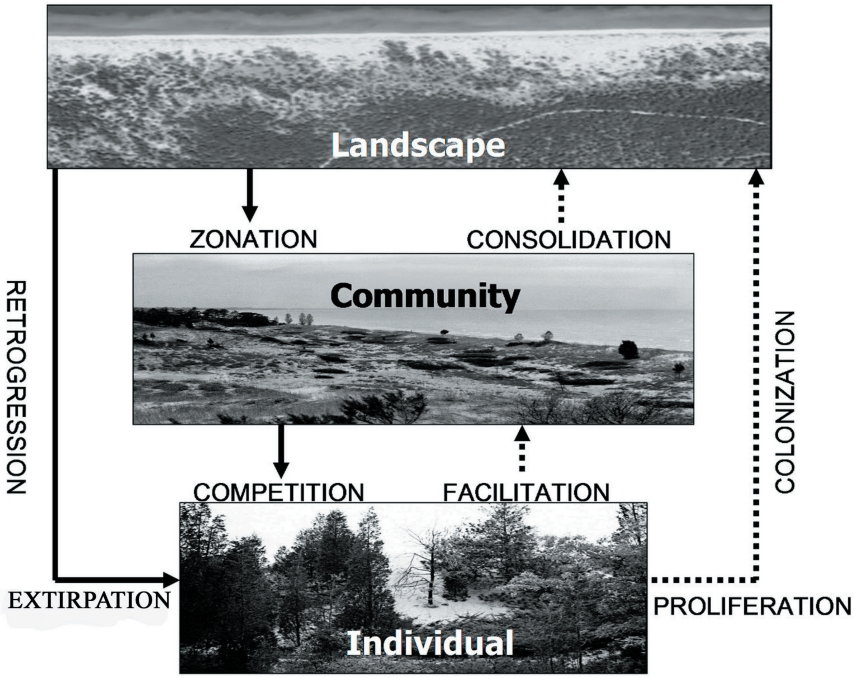
The three scales and levels of organization covered by this model are nested and therefore integrated in two directions (Figure 1). From the top down, sand movement through blowouts covers vegetation (retrogression) and produces a predictable assemblages of plants (zonation) by acting as a filter and removing species that are incapable of altering resource allocation and producing adventitious roots in order to survive (extirpation), or stressing/stimulating plants and altering their abilities to grow and capture resources (competition). Heavy burial can produce completely barren areas. From the bottom up, tolerant plants colonize or persist following burial, grow vigorously and gain dominance of the local plant community (proliferation), and eventually can provide an obstacle to wind currents that stabilizes sand movement and leads to the eventual colonization by other species (facilitation). Vigorous establishment of vegetation can reduce or eliminate sand movement (consolidation). The opposing processes of geomorphological and vegetation dynamics are operating simultaneously on coastal dunes and this creates considerable environmental heterogeneity in the system over time and space.

Applications that Arise from the Model

Natural Dune Dynamics and Plant Diversity

A new trend in coastal dune management is recognition of the importance of unstable areas and maintenance or restoration of dune activity whenever possible (Martinez *et al.*, 2004). Clearly the Pinery land cover change-detection data support the view that concurrent retrogression and colonization are the norm for coastal dunes (Dech *et al.*, 2005). Helesenfeld *et al.* (2004) included in their recommendations for dune preservation that "*dunes should not be artificially fixed or afforested: they should be promoted as dynamic self-sustained systems*". Martinez *et al.* (2004) suggest that richness and diversity are maximized when the full continuum of activity is represented within a system. Furthermore, coastal sand dunes have high susceptibility to invasion by non-native species (Castillo and Moreno-Casasola 1996), and artificial stabilization could allow for the establishment of aliens that typically lack burial tolerance adaptations. The clear zonation of woody and her-

Figure 1. Flow chart depicting the various top-down and bottom-up interactions that occur in association with burial activity in a coastal dune system based upon studies of woody plant burial at Pinery Provincial Park.



baceous species in relation to burial activity on dune lee slopes at the Pinery (Dech and Maun, 2005) further supports the notion that plant biodiversity is maximized by patch heterogeneity, and the fact that large trees are habitats for many other organisms suggests that this pattern may extend beyond plants to other groups of organisms such as insects and birds. However, natural burial levels can be exacerbated by anthropogenic activities such as trampling (Poulson and McClung, 1999) and lead to the loss of stable forested dunes (Martinez *et al.*, 2004), justifying artificial stabilization.

The Use of Woody Plants as Stabilization Agents

Typically, dune building grasses (e.g., *Ammophila* spp.) are planted for stabilization purposes on coastal dunes (Lewis, 1982); however, burial-tolerant woody species also have the potential to be used for these purposes. All tree species showed luxuriant growth after artificial planting at the experimental site on the windward face of the second dune ridge at the Pinery. Furthermore, woody species of shrubs (e.g., balsam poplar (*Populus balsamifera*) and heart-shaped willow) were shown to be sand dependent (Dech, 2004) and are capable of producing layers of roots and rapid vertical stem elongation to promote dune building in a similar manner to foredune grasses. Tree species also act as nucleation sites, facilitating the colonization of other species through modifying the microclimate and contributing nutrients to the soil (Yarranton and Morrison, 1974; Shumway, 2000).

On Lake Michigan coastal dunes, the European tree species *Pinus nigra* has been introduced as a stabilizing plant. However, in any introduction of an alien species their invasive potential must be carefully examined. Indeed, *P. nigra* has begun to spread into unplanted areas, and when established it alters soil moisture content and development, light intensity, as well as the composition and diversity of the understorey (Leege and Murphy, 2000). The results of experimental burial studies at the Pinery indicate that native tree and shrub species (e.g., balsam poplar and heart-shaped willow)) are able to thrive with burial and are better candidates for dune stabilization than non-native alternatives.

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