8 Burial of Plants as a Selective Force in Sand Dunes

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8.1 Introduction

Burial of plants is a recurrent event in coastal dunes because of the activity of waves and wind. Waves dump large quantities of sand on the beach that is later moved inland by the action of wind velocities exceeding about 16 km/h. Plants growing on the foredunes not only have to contend with burial by sand but also with a wide variety of other environmental stresses such as desiccation, nutrient shortage, and salt spray along sea coasts. Perhaps the most important stress is burial in sand because burial alters all aspects of the plant and the soil micro-environment, such as soil temperature, soil moisture, bulk density, nutrient status, soil pH and oxygen levels. This physical alteration of the micro-environment may increase soil microorganisms, change the ratio between aerobic and anaerobic microbes, decrease mycorrhizal fungi, increase the rate of respiration and curtail photosynthesis. Burial stress occurs with such regular frequency that it has strong selective consequences to fitness and organisms must make physiological adjustments in succeeding generations in order to survive. I define stress according to Grime (1979) "the external constraints that limit the rate of dry matter production of all or part of vegetation". Could burial in sand be defined as a stress? It depends on the amount of burial. Small amounts of burial specific to a species do not cause any stress. Actually, it is beneficial and plants exhibit a stimulation response. However, above a certain threshold level of burial, specific to each species, it becomes a stress.

At the community level, if burial occurs on a regular basis in a habitat, there is selection against species with a conservative growth habit. Burial acts as a filter that eliminates species when burial exceeds their threshold of survival. Eventually the community consists of plant species that have become functionally adapted to grow and prosper under conditions that deny survival opportunities to other species. These adaptations or physiological adjustments are the most successful means of coping with the encountered environmental constraints and may range from changes to allocation patterns of

metabolic resources, and/or modification of structural components. As shown in other chapters, plants adapted to live in sand dunes play a major role in dune formation and dune morphology because of their different growth forms and their significant abilities to grow through the sand deposits and utilise the meagre resources of sandy habitats.

In this chapter, I would like to emphasise three major objectives. The first major objective is to demonstrate relationships between vegetation and burial as an environmental force. It is important to know how individual species of foredunes are distributed in relation to the gradient in sand deposition. The second major objective is to show the responses of seeds, seedlings, and adult plants to burial episodes because each stage in the life cycle of a plant has a slightly different mechanism to cope with this stress. The third major objective is to examine the process of stimulation of growth under continued burial conditions and degeneration when burial ceases. It would be useful to critically evaluate the hypotheses generated over the past century and present experimental evidence in favour or against these hypotheses.

8.2 Storm Damage of Foredunes – A Case History

The major problem faced by foredune plants along coasts is disruption of habitat by wind and wave action. I present a case history of a storm that occurred in1986–1987 along the Lake Huron shoreline. The lake levels started to rise in 1984 and by 1986 had risen by about 1.25 m above the long-term average. Wave storms in fall of 1986 and early spring of 1987 eroded the middle beach, upper beach and approximately half of the first dune ridge (Fig. 8.1). All populations of *Ammophila breviligulata, Calamovilfa longifolia* and other annual and biennial species of the beach and foredune were completely destroyed and a bare area was created. In addition, major changes occurred in the physiography and re-arrangement of the foredune terrain. However, within about 1 month, some of the sand began to return and was deposited on the beach along with the flotsom and jetsom from the lake. The deposited material consisted of seeds of annuals, biennials, perennials and rhizome fragments of grasses especially *A. breviligulata*, cuttings of herbaceous plants such as *Potentilla anserina* and *Tussilago farfara*, and twigs and branches of different trees and shrubs. Seeds of almost all species germinated and fragments and cuttings of grasses, shrubs and trees started to grow, however, a large majority of the species were short lived. The main reasons for their mortality were desiccation, erosion of sand, burial in sand, sand blasting and insect attack. Since there was little or no vegetation on the beach to arrest the movement of sand, a large proportion of sand was deposited on the crest of the first dune ridge through openings in the dune ridge caused by pedestrian traffic. Perumal (1994) installed 96 steel stakes at different places on the first dune ridge and measured the amount of sand depo-

Fig. 8.1. The erosion of first dune ridge during the wave storms of fall 1986 and early spring 1987

sition at each stake at regular intervals for two years. He showed that sand accretion ranged from 0 to 74 cm. By the end of 2 years the original complement of sand dune species consisting of *Cakile edentula, Corispermum hyssopifolium, Euphorbia polygonifolia, Artemisia caudata, A. breviligulata* and *Calamovilfa longifolia* had re-established on the upper beach and started to arrest sand movement and re-build the foredune. These species reclaimed the habitat because of two traits, (1) ability to disperse back to the habitat (return) and (2) then show high rates of re-establishment.

8.2.1 Return

A species must have a mechanism of dispersing back to the habitat. I will elaborate two main mechanisms. First, the most important trait used by propagules of plant species is *dispersal in water*. According to Ridley (1930), to be successful in water dispersal, the propagules (1) should be able to float in water without being waterlogged, (2) should not imbibe water while afloat and (3) should not lose viability while being transported in water. The worldwide distribution of some species of several genera such as *Cakile, Ammophila, Ipomoea, Calystegia, Sesuvium, Honckenya, Crambe* and several

others can be attributed to the ability of seeds, and fragments of plants to meet all three criteria. *Wind dispersal* also contributed to the establishment of some plant species particularly annuals. Second, a large number of most successful species on coastal foredunes are grasses and vines that expand into the open areas of the beach by producing *creeping rhizomes or stolons* (Table 8.1). The storm waves that destroyed their habitat also fragmented these rhizomes or stolons and transported them back to the same shoreline or to another shoreline where they quickly regenerated and established new populations (Maun 1984, 1985). Many species of different genera and families listed in Table 8.1 along coasts of the world exhibit this mode of vegetative regeneration. This trait provides an efficient solution to the demand exerted by frequent destructive storms along shorelines and may be an example of parallelism or convergence. *Parallelism* may be defined as independent acquisition of similar phenotypic traits in species with a common heritage in response to similar selective pressures imposed by the environment. When species do not have a common heritage, evolutionary parallelism is called *convergence*. According to Mayr (1977), "if there is only one efficient solution for a certain functional demand, very different gene complexes will come up with the same solution, no matter how different the pathway by which it is achieved".

Table 8.1. Partial list of species of taxa that produce rhizomes, stolons or suckers along different shorelines of the world. These rhizomes or stolons are fractured by storm waves in autumn and early spring months and transported back to the same shoreline or to new shorelines where they establish new populations. This is a convergent trait exhibited by many families of plants

Name of species and family	Occurrence
Ammophila breviligulata, *A. arenaria* (Gramineae)	North America and Europe
Calamophila baltica (Gramineae)	Europe
Leymus arenarius, *L. mollis* (Gramineae)	North America and Europe
Elymus farctus, (Gramineae)	Europe
Panicum racemosum (Gramineae)	South America (Brazil)
Phragmitis communis (Gramineae)	North America and Europe
Ischaemum anthrefroides (Gramineae)	Japan
Spinifex hirsutus, *S. sericeus* (Gramineae)	Australia
Spinifex littoreus (Gramineae)	India, Malay Peninsula
Distichlis stricta (Gramineae)	North America and Europe
Ehrharta villosa (Gramineae)	South Africa
Thinopyrum distichum (Gramineae)	South Africa
Carex arenaria, C. kobomugi, C. eriocepahala (Cyperaceae)	Europe, Japan, America
Ipomoea pes-caprae, *Ipomoea stolonifera* (Convolvulaceae)	Tropics
Calystegia soldanella (Convolvulaceae)	Europe
Sesuvium portulacastrum (Portulacaceae)	Tropics
Honkenya peploides (Caryophyllaceae)	Europe and North America

Vegetative regeneration along coasts is adaptive for three main reasons:

1. It takes less time for a species to establish, become adult and reach reproductive stage because of large carbohydrate reserves in these fragments. For example, normally *Crambe maritima* plants establishing from seeds take about 5 to 8 years before they come to flower but plants establishing from fragments flower within one year (Scott and Randall 1976).
2. The rate of establishment of plants is much higher from fragments compared with seeds. In a comparison between survivorship of *A. breviligulata* from rhizome fragments and seedlings, more than 85 % of plants established from rhizome fragments compared to only 4 % from seedlings (Maun 1984).
3. It provides the fastest way of re-occupying the habitat. Populations of *A. breviligulata, Ipomoea pes-caprae, Spinifex hirsutus* expand towards the shoreline by forming an advancing front consisting entirely of rhizomes or stolons. According to Woodhouse (1982), planted stands of *A. breviligulata* were capable of 50-fold increase in area per year. Similarly, many other beach species expand very fast into the open bare areas along the coast.

However, all foredune perennials also allocate resources into sexual reproduction. There are three main advantages of seed production. First, even though the establishment from seeds is a stochastic event in dunes (Maun 1985; Lichter 1998), it incorporates genetic variability into the population and eliminates the major disadvantage of vegetative regeneration in that the offspring is genetically identical to that of its parents. Second, the seeds of most species possess enforced or innate dormancy that allows them to prolong their life. Third, seeds are able to disperse to more distant shorelines than rhizome or stolon fragments.

8.2.2 Re-Establishment

The problems for re-establishment of plant species are similar to those of other habitat types but foredune species have to contend with additional stresses imposed by (1) burial by sand, (2) sand blasting, (3) salt spray and (4) very low nutrient levels. Periodic observations over the years showed that within about ten years all traces of storm damage were completely obliterated and the plant community recovered approximately to its former levels (Fig. 8.2). The most important observation was that in spite of the invasion by a large number of species after the storm only the original complement of species prior to the storm reestablished and reclaimed the habitat. The species that contributed to reclamation of the habitat were the perennial rhizomatous grasses, *A. breviligulata* and *Calamovilfa longifolia*. Their success was primarily due to their ability to re-establish and grow vertically in response to burial by sand. The species on other shorelines of the world may be different

Fig. 8.2. The recovery of plant community to approximately its former levels. Note the gradual foredune slope of the first dune ridge formed by *Ammophila breviligulata* and *Calamovilfa longifolia*. Photograph taken after 8 years of recovery in June 1995

but the process of re-colonization and dune formation by lateral and upward extension of plants in response to burial is the same.

8.3 A Conceptual Model of Plant Response to Burial

As mentioned above, all foredune species returned after the storm but many aliens also dispersed to the habitat. Maun (1998) showed that plants exhibited three types of responses to burial (Fig. 8.3).

1. A *"negative inhibitory response"* in which the plant is unable to withstand burial and dies soon after the episode. For example, large trees of *Quercus velutina* and *Pinus resinosa* are readily killed by burial in sand. As shown earlier, propagules of many plant species are cast on the shorelines by waves. They may produce seedlings or ramets but the conditions on the beach and foredunes are not suitable for their survival and they succumb to burial and other unfavourable conditions.

2. A *"neutral and then negative response"* in which the plant shows little or no visible response initially because burial depth is within its limits of tolerance. However, as the level of sand accretion increases the response

Fig. 8.3. Three possible response curves of plant species: *a* a negative inhibitory response, *b* a neutral and then negative response and *c* a positive stimulatory response, to being buried in sand on coastal dunes. (Adapted from Maun 1998)
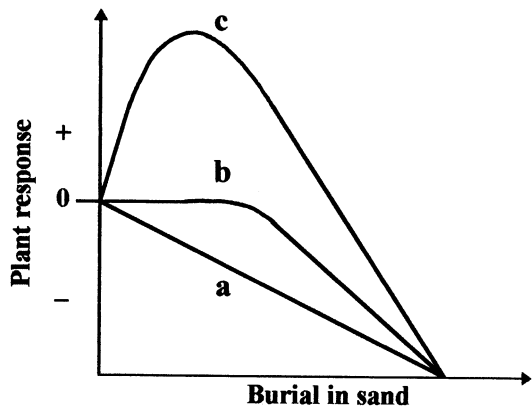
becomes negative and the plant eventually dies (Maun 1998). Some tree species such as *Juniperus virginiana* may survive burial for a few years but are eventually killed depending on the amount and rate of sand accretion.

3. A *"positive stimulatory response"* in which the species exhibit enhancement of growth following a certain threshold level of burial. This is by far the most common response shown by all sand dune species (Maun and Baye 1989). Different life forms vary, by many orders of magnitude, in the relative amounts of burial at which they exhibit a stimulatory response but their response curves are similar. For example, the amount of burial may only be a few mm in lichens and mosses but a meter or more in some grass and tree species (Maun 1998). However, plant species vary in their maximum tolerance limits above which they start to show a negative response and are eventually killed.

8.4 Post-Burial Responses of Plants

Each stage in the life history of a plant has its own mechanism to tolerate the stress caused by burial. We will examine the response of seeds, seedlings, adult plants and communities to burial episodes.

8.4.1 Seeds and Seed Bank

Following dispersal, the seeds of plants accumulated in depressions in the sand surface where they were covered with leaves of deciduous trees and herbaceous plants (Maun 1981). During the autumn and winter months, these

micro-sites are buried to various depths by sand depending on their location and wind velocities. The seeds respond to burial in three ways. First, the seeds will germinate and the seedlings will emerge if they are situated at an optimal depth specific for the species. Second, the seeds will germinate but the seedlings are unable to emerge because the seed is buried too deep and it does not have enough stored energy to take the growing point above the sand surface. These seedlings eventually decay in the soil and are lost. Third, the seeds may not germinate because they undergo enforced or innate dormancy and become part of the seed bank. This was by far the most common response shown by deeply buried seeds of seven dune species (Zhang and Maun 1994). The seeds were forced to become dormant as a result of burial and as the depth of burial increased, the degree of enforced dormancy increased.

The emergence of a seedling is dependent on the energy contained in the seeds and there is clear evidence of a positive relationship between seed mass and depth of emergence (Maun 1998). The larger the seed, the greater was the maximum depth from which its seedlings emerged (Maun and Lapierre 1986). This relationship held true for seed mass both within and between species. However, since the variability in burial depths in foredune habitats is very high and even though a certain proportions of seeds may be buried too deep, there is always a certain proportion of seeds buried at optimum depths (Maun 1981).

Most species on sand dunes possess a transient *seed bank* and do not have a significant carryover of seeds from one year to the next (Rowland and Maun 2001; Planisek and Pippen 1984; Barbour 1972; Mack 1976; Watkinson 1978). Overall, the number of seeds in the seed banks of sand dunes is very low as shown by Baptista and Shumway (1998). They determined seed bank composition of four coastal dunes along Cape Cod National Seashore by collecting sand samples and germinating seeds in a greenhouse. Seedlings emerged from only 20 % of the sand samples indicating that the seeds were highly clumped. A total of 254 seedlings emerged from all sand samples of which 85 % belonged to *Artemisia caudata*, 5 % to *A. breviligulata* and 3 % to *Solidago sempervirens*. Several other species, *Chenopodium rubrum, Hudsonia* spp.*, Artemisia stelleriana, Cakile edentula* and *Polygonella articulata* contributed less than 2 % to the seedling population. Moreover, as shown earlier, many species of foredunes have the potential to form a seed bank (Zhang and Maun 1994). Another source of seeds is a temporary seed bank on the above ground plant parts. Several species of foredunes retain seeds in cones or inflorescences as an above ground seed bank and release them gradually at appropriate environmental cues thus ensuring the dispersal of some seeds into safe sites (Zhang and Maun 1994).

8.4.2 Seedlings

The survival of seedlings is usually extremely low in sand dunes because of various environmental stresses such as desiccation, erosion of sand, insect attack and excessive burial in sand. However, there is evidence that partial burial stimulates the growth of seedlings. For example, partially buried seedlings of *A. breviligulata* and *Calamovilfa longifolia* showed higher net CO_2 uptake (Yuan et al. 1993), *Uniola paniculata* seedlings responded to burial by an increase in tillering (Wagner 1964), and *Cakile edentula* exhibited greater production of flowers and seeds per plant compared to control (Maun 1994). Similarly, seedlings of all six tropical species, *Chamaecrista chamaecristoides, Palafoxia lindenii, Schizachyrium scoparium, Trachypogon plumosus* (formerly *gouini*)*, Canavalia rosea* and *Ipomoea pes-caprae* responded to burial by an increase in biomass and leaf area (Martínez and Moreno-Casasola 1996). All species except *T. plumosus* allocated greater biomass to aboveground plant parts.

Burial beyond a certain threshold level proved fatal to the seedlings. Young plants of *Cakile edentula, C. maritima, Corispermum hyssopifolium, Salsola*

Fig. 8.4. A plant of *Cakile edentula* var. *edentula* being buried on a beach along the sea coast of Prince Edward Island, Canada, on the Gulf of St. Lawrence. Note the formation of a shadow dune on the lee of the plant. Complete burial of annual or biennial plants usually kills them

kali, Honckenya peploides and many others often grow in clumps at the location of last year's plants or as single plants on the midbeach where they may be partially buried and form shadow dunes (Fig. 8.4). With few exceptions complete burial almost always killed the seedlings unless they were re-exposed within a few days. According to Harris and Davy (1987), the seedlings of *Elymus farctus* survived if they were re-exposed after about 1 week, but died if left buried for 2 weeks. The energy for this short term survival came from stored reserves in the roots and stems (Harris and Davy 1988). Brown (1997) showed that upon burial the normal source-sink relationship was reversed and the stored material was mobilized and transferred to existing photosynthetic tissues. A morphological examination of buried seedlings showed etiolation of leaves and stems within about 10 days of burial. Under field conditions seedling survival may also be affected by the depth from which it emerged. Seedlings of *Panicum virgatum* emerging from deeply buried seeds survived significantly lower post-emergence burial depths than those emerging from shallow depths (Zhang and Maun 1991).

8.4.3 Adult Plants

Below a certain threshold level of burial specific for each dune species, plants show an increase in vigour by exhibiting higher net CO_2 uptake (Yuan et al. 1993), higher density, percent cover, and biomass per plant and per unit area (Maun 1998). For example, dominant foredune grasses of the Great Lakes, *A. breviligulata, Calamovilfa longifolia, Agropyron psammophilum*, and *Panicum virgatum*, showed an increase in density at burial depths ranging between 5 and 20 cm but started to decline at higher levels of burial (Maun and Lapierre 1984; Perumal 1994; Maun 1996). Seliskar (1994) also showed a similar relationship between the number of panicles and burial depth. However, even though the density decreased there was an increase in biomass per shoot after their emergence above the sand surface. Similar conclusions were reported by Eldred and Maun (1982) and Disraeli (1984) in natural stands of *A. breviligulata* and by Sykes and Wilson (1990) who artificially subjected 30 New Zealand sand dune species to different burial treatments.

8.4.4 Plant Communities

In natural foredune communities the distribution of plants is related to variability in burial depths in the habitat. Moreno-Casasola (1986) showed that there was a close relationship between natural sand movement, topography, and spatial distribution of plant communities. In habitats with high levels of sand mobility *Croton punctatus, Palafoxia lindenii* and *Chamaecrista chamaecristoides* survived and reproduced successfully. Similarly, in a study

on primary succession on mobile tropical dunes, Martínez et al. (2001) showed that the spatial distribution, coverage, diversity and relative frequency of early colonizers, *Chamaecrista chamaecristoides* and *Palafoxia lindenii*, were positively correlated with the amount of burial in sand. In contrast, the later colonizing species, *Schizachrium scoparium* and *Trachypogon plumosus*, were less tolerant of sand deposition and were abundant only in areas where sand movement had decreased substantially. Although sand mobility was probably the most important factor, other factors such as soil moisture, soil temperature, biotic interactions and plant life histories also played a role in spatial and temporal variability (Martínez et al. 2001). In an artificial burial experiment Maun and Perumal (1999) showed that the number of plant species in the community decreased with an increase in burial. As the burial depth increased beyond the level of tolerance of a species, the plants started to deteriorate and eventually died. Indeed, sand dune species may be classified as non-tolerant, tolerant and sand dependent. Annual species were eliminated first followed by biennials and then perennials (Maun and Perumal 1999). Eventually, however, a stage was reached when the amount of sand accretion exceeded the tolerance limits of even the sand-dependent species and a bare area was created. The survival of plants is also dependent on the rate at which a plant is buried in sand. In an experiment on *Cirsium pitcheri* plants buried gradually recovered within a few days probably because their leaves were still above the sand surface and had continued to function normally (Maun et al. 1996). In contrast, one time burial of plants significantly delayed the emergence and recovery of plants.

8.5 Burial – The Primary Cause of Zonation

The differential tolerance of sand dune species to burial may be one of the principal causes of zonation of plant species on coastal foredunes (Maun and Perumal 1999). Martin (1959) showed that as one moved inland from the shoreline along the Atlantic coast of North Carolina, the total deposition of sand decreased and the species occurrence was related to the amount of sand burial. For example, *A. breviligulata* and *Carex kobomugi,* were very vigorous in areas with average sand deposition of about 17 to 28 cm/year in the first 40 m from the beginning of the primary foredune. When the sand deposition in the next 20 m (41–60 m) decreased to about 3–5 cm, the two species became sparse. Farther inland deflation exceeded sand deposition and both species degenerated and exhibited a significant decline in vigour. Burial also retards sand dune succession (Poulson 1999). He showed that abiotic forces such as burial by sand, high winds and substrate instability along Lake Michigan continuously modified the local environment and did not allow species of the next stage in succession to gain a foothold. Similarly Olff et al. (1993) showed

that earliest dune stage deviated from the general successional pattern because of sand deposition. This constant disturbance of the habitat did not allow the species to converge to permanent plant communities. Similar observations were made by Houle (1997) in a sub-arctic foredune along Hudson Bay, where productivity was low and plant-plant interactions were non-existent because of high disturbance caused by wind and wave action.

8.6 Degeneration Response

Burial of plants has both a positive and a negative aspect. It has a stimulating positive effect on plant growth up to a certain level of burial in sand. However, in plant communities with little or no sand deposition there is a decline in density, plant height, net CO_2 uptake, flowering, tillering and biomass per unit area. Several possible causes of degeneration such as deficiency of nutrients (Willis 1965), increase in competition (Marshall 1965; Huiskes and Harper 1979), desiccation of growing point (Olson 1958), accumulation of organic matter (Waterman 1919), decortication of roots (Marshall 1965), and harmful soil organisms (Van der Putten et al. 1988), have been proposed over the years. However, strong counter arguments, as shown below, have been advanced against each hypothesis. For example, *nutrient deficiency* can not be a factor because even burial by leached sand or acid washed sand (no nutrients) increased growth (Hope-Simpson and Jefferies 1966; Maze and Whalley 1992). Decline due to *increase in competition* is not relevant because debilitated stands of *Ammophila* do not contain any other species (Hope-Simpson and Jefferies 1966; Baye 1990; Poulson 1999). Actually, *A. breviligulata* retards natural sand dune succession (Poulson 1999) and heterospecific removal of two species showed no effect on either species (Houle 1998). *Desiccation of growing point* is a good possibility because even in the absence of sand burial, *A. breviligulata* continues to elongate its internodes into the dry surface sand where it desiccates. However, the hypothesis has not been tested. *Accumulation of organic matter* cannot be responsible for the decline because experimental addition of organic matter did not inhibit growth of plants (Zaremba 1982). Actually, it stimulated growth. Hope-Simpson and Jefferies (1966) found no evidence for the *decortication of roots* because wiry decorticated roots frequently terminated in a fully functional fleshy distal end. *Nematodes and harmful soil organisms* do destroy functional roots (De Rooij-van der Goes 1996), however, the injurious effects of pathogenic fungi (Newsham et al. 1995) and nematodes (Little and Maun 1996) were mitigated by mycorrhizal fungi.

What then are the possible reasons for the degeneration of plants? In spite of the many studies conducted to answer this question, the reasons are obscure and any suggestions must remain tentative. However, there are strong

indications that this decline is caused by an interaction of several factors. For example, five factors, (1) complete exploitation of the soil volume by roots, (2) decline in the formation of new roots thereby causing a decrease in colonization by mycorrhizal fungi, (3) desiccation of the growing point as it continues to grow upward even in the absence of sand deposition (4) physiological deterioration in plant functions, and (5) soil microorganism activity, may interact to cause a decline in plant growth.

8.7 Stimulation Response

What are the possible causes of stimulation? There is strong evidence that single factors are inadequate to explain the enhancement of plant vigour. I would therefore propose a *"Multifactor hypothesis"* composed of four major biotic and physical variables, (1) increased soil volume, (2) increased soil nutrients, (3) increased activity of mycorrhizal fungi, and (4) reactive growth by the plant to burial (Fig. 8.5). Burial increases soil volume and creates more new space for the growth and expansion of the plant and its roots. The apical meristems of the plant grow through the burial deposits probably because of the etiolation response and emerge above the new sand surface. The new sand deposit increases the amount of soil nutrients that cannot be used by the plant until new roots develop in the sand deposit that may take 2–4 weeks. However, mycorrhizal fungi, ubiquitous in sand dune systems (Perumal 1994), expand into the new deposit almost immediately and exploit the soil resources to the benefit of the plant. For more details on the occurrence of mycorrhizal fungi in sand dunes refer to Koske et al. (Chap. 11, this Vol.). The mycorrhizal fungi
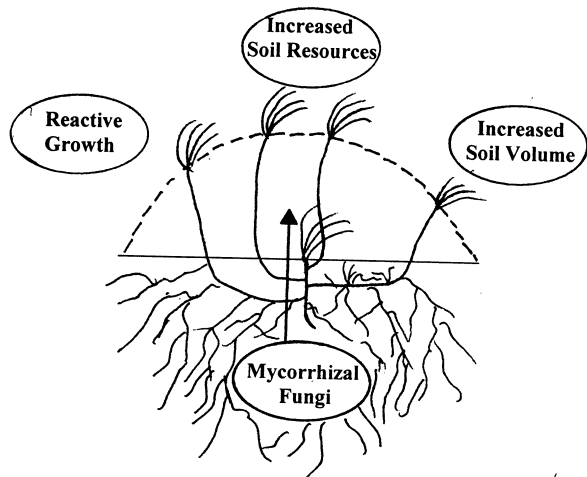

Fig. 8.5. A "Multifactor hypothesis" to explain the stimulation response of sand dune species following burial in sand

not only enlarge the nutrient absorbing surface of the roots, but also compete with harmful soil organisms for space on the roots. In addition, the plant reacts to the burial stress by mobilizing all its resources that allows it to overcome the burial episode. The response may be mediated by hormone production whereby the plant directs all its energy towards making physiological adjustments, changing its morphology, and finally emerging from the burial deposit.

8.8 Summary

Coastal sand dune systems are highly dynamic because of the activity of wind, waves and tides. The most important stress encountered by plant species growing here is probably the burial by sand. Burial acts as a very strong selective force that alters the composition of plant communities by selective elimination of species with a conservative growth habit. Burial curtails the photosynthetic capacity of the plant, increases the respiration rate and alters the microclimate around the plant. However, all foredune plant species have developed adaptations that allow them to withstand certain threshold levels of sand burial. Other traits such as dispersal in water, vegetative growth by rhizomes and stolons and lateral and vertical growth also allow them to occupy this habitat permanently. Deep burial of seeds induces enforced dormancy of seeds. The response of seedlings and adult plants to burial is similar and emergence of plants is related to the amount of stored energy reserves in their roots and rhizomes. They not only survive certain amounts of burial but their growth is also stimulated by it. There is mounting evidence that the principal causes of this stimulation are an increase in soil volume around the base of the plant that contains nutrients, probably in small amounts, which are exploited by the mycorrhizal fungi already associated with roots of dune plants. A plant also exhibits a reactive growth response to burial. Conversely, as soon as the sand dune stabilizes and sand accretion ceases, there is a marked decline in vigour and density of foredune populations. Several possible hypotheses and counter arguments have been advanced in the past century but no consensus has been reached. In all likelihood, the phenomenon of decline in sites with no sand deposition is caused by an interaction of several environmental factors.

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