

Studies of vegetation burial: a focus for biogeography and biogeomorphology?

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Abstract: This paper examines the literature on research into the effects of burial by deposition of blown sand, volcanic deposits (tephra, lavas and lahars) or fluvial sediment on vegetation and the subsequent capacity of the vegetation for survival and regeneration. Research on this topic involves the understanding and skills of the biogeographer, the ecologist and the geomorphologist and represents a potentially very interesting area for integration between these areas of physical geography.

Burial is closely linked to concepts of plant succession and pedogenesis. A general model of burial stress is presented that shows how types of stress are linked to the burial environment and the characteristics of the burial event, in particular the magnitude and frequency. The importance of elasticity of response of species to burial is vital, as demonstrated by the evolution of certain species, such as those of the genus *Ammophila* in sand dunes that appear to respond positively to the burial process.

Research into burial by dust deposition, by volcanic tephra and lavas, by sand in coastal and lake dune environments, in desert environments and by alluvium and 'run-on' following hydrological events are reviewed in turn. The significance of burial to palaeoenvironmental and palaeoecological research is then demonstrated by reference to machair sand dune stratification in the Outer Hebrides and vegetation damage and burial following proximal volcanic impacts in New Zealand. Finally, methods of experimental research into burial in both the field and in the greenhouse are summarized and the conclusion stresses the need for more holistic

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approaches to the study of burial that link the biogeographical aspects of plant ecophysiology and both individual species and community ecology to the various geomorphic processes of deposition and sedimentation.

Key words: deposition, ecophysiology, geomorphology, palaeoecology, pedogenesis, plant ecology, plant succession, sand dunes, volcanic tephra.

I Introduction

Burial of vegetation is a recurring theme in physical geography. Primary mechanisms are both wind (aeolian deposition) and water (fluvial deposition). Perhaps the most widespread and obvious example is the frequent burial of vegetation within sand dune ecosystems (Ranwell, 1972; Packham and Willis, 1997) but considerable attention has also been paid to the effects of vegetation burial by volcanic tephra or lava after major eruptions (Oner and Oflas, 1977; Hendrix, 1981; Timmins, 1983; Tsuyuzaki, 1989, 1991; Nakashizuka *et al.*, 1993 and Mazzoleni and Ricciardi, 1993). In particular, the Mount St Helens eruption in Washington, USA, in May 1980 stimulated research in this area (del Moral and Wood, 1988, 1993; del Moral and Bliss, 1993; del Moral *et al.*, 1995; Zobel and Antos, 1997 and Titus and del Moral, 1998), although most of this research relates to the development of primary succession on new surfaces, rather than to the effects of burial.

Burial is also a common feature of plant species in arid and semi-arid dune environments (Viles, 1990; Bullard, 1997), but the amount of research in this specific area is minimal. Burial of vegetation is also a frequent occurrence after hydrological and geomorphological events of varying magnitude and frequency, such as land- and rockslides, earth movements and deposition of alluvial sediments following fluvial storm events (Antos and Zobel, 1985a, 1987). During flash floods, ephemeral streams in arid and semi-arid dryland areas commonly deposit and rework sediments on top of existing plant cover. Volcanic deposits are also often reworked fluvially, giving rise to the phenomena known as 'lahars'. Finally, plants may also be subject to stress as a result of burial by logs, litter and animal excavations (Antos and Zobel, 1985a). General differences between environments where plants are known to be subject to burial are summarized in Table 1, although clearly responses vary, depending on the magnitude

Table 1 A comparison of characteristics of various depositional environments important to plant survival of burial

Characteristic	Tephra	Sand dunes	Dust	Alluvium
Chemical toxicity	Sometimes	Unlikely	Unlikely	Unlikely
Nutrient deficiency	Likely	Likely	Unlikely	Unlikely
Frequency	Low	Highest	Low	Occasional
Predictability	Low	High	Low	Moderate
Relative potential for plant adaptation	Low	High	Low	Moderate
Estimated abundance of refugia within deposit	Low	High	High	High
Correlation with season and weather	None	Moderate	High	High

Source: from Antos and Zobel, 1987; reproduced with the kind permission of the authors and the University of California Press

of a given event, antecedent conditions and the particular species involved.

Examination of the literature shows very clearly that most research on vegetation and geomorphology has been concerned with vegetation cover and its protecting role in controlling or preventing erosion (e.g., Gregory and Gurnell, 1988; Thornes, 1990; Thomas and Tsoar, 1990; Rogers and Schumm, 1991; Wolfe and Nickling, 1993; Lancaster and Baas, 1998). In contrast, and taking a more biogeographical standpoint, the ecological and ecophysiological effects of burial on established plant cover have not been widely studied, despite the frequency of occurrence of such events. Plant response to burial involves consideration of factors such as the origins, nature and depth of deposit, frequency of redeposition, phenological stage and the presence or absence of propagules within the deposited material. Antecedent conditions are also important, not least the extent to which the plant community was under stress previously, perhaps in relation to earlier burial events, existing environmental conditions, its biogeographical position possibly near the limits of its range and the intensity of biotic pressures.

Plants subjected to frequent burial have evolved various strategies to cope. If burial is not too deep, regrowth through the deposited material is frequently possible and possession of geophyte characteristics (Raunkiaer, 1934) may prove valuable. Perennial species have the advantage of already being established and certain species, notably varieties of *Ammophila* (marram grass) on coastal dunes, have evolved tolerance and are able to grow through and keep pace with gradual deposition. When burial becomes too deep, annual or therophyte strategies assume importance and the presence/absence of an 'innoculum' of seeds and other propagules or vegetative fragments in the deposited material will prove vital in the initial stages of primary succession on the new surface (Owen *et al.*, 2001). Burial of large growth forms (trees and shrubs) largely occurs only after volcanic eruptions.

II Burial and plant succession

Burial is closely linked to concepts of plant succession (Burrows, 1990; McCook, 1994; Begon *et al.*, 1996). A burial event is retrogressive in successional terms but subsequent development depends on whether existing plants can initiate secondary succession by growing through the deposit or whether the existing vegetation cover is completely killed, in which case primary succession will be initiated. Often both types of succession will occur locally within an area following burial, as demonstrated by the work on Mount St Helens by del Moral and Bliss (1993), del Moral *et al.* (1995), Zobel and Antos (1997), del Moral and Wood (1988, 1993) and Titus and del Moral (1998). This results in a mosaic of plant community types of varying ages and successional stages.

Plant succession and pedogenesis are also closely linked. Regrowth of species after burial has important implications for soil development. The physical and chemical nature of the deposited material may be very different to the original solid geology or sediments, thus changing soil physical and chemical properties. Once re-established, species contribute organic matter to the surface, which assists in re-stabilization and the conservation of moisture. This process is important in palaeoecology and the frequent occurrence of palaeosols, corresponding to former soil surfaces within sequences of dune deposits and tephra, provides valuable evidence of periods of former stability and disturbance (see Section IX).

III Burial as a major plant stress – a general model

Burial is a major stress event for plants and the response of a plant to stress is an important aid in appreciating its geographical distribution and its performance along an environmental gradient (Grime, 1979). Plants may be buried by several different processes and a number of sources of burial stress have been recognized. Burial magnitude and frequency (Wolman and Miller, 1960), and thus the nature of the stress, vary in relation to the origin and source of the deposit. Burial in coastal or arid dune environments is characterized by relatively frequent occurrences of comparatively low magnitude, although there may be occasional extreme exceptions. In contrast, burial by volcanic tephra, by alluvial deposits following floods and by dust following drought or dust storms, are generally rare and extreme events, often of high magnitude. The ongoing stress of the sand dune environment thus requires a quite different plant response to the adaptations suitable for the occasional extreme volcanic or dust storm event (Table 1).

Antos and Zobel (1987) present a brief review of literature relating to the burial of vegetation by tephra (volcanic aerial ejecta), dust, alluvium and dune sand, and propose a theoretical model of how plants survive these burial processes (Figure 1). They postulate that, following burial, a plant is either totally buried by the deposit (Figure 1, path A), or is characterized by the presence of some emergent shoots (Figure 1, path B). The shoots of deciduous herbaceous species will die back with time, so that the plant is once again buried (Figure 1, path B). If, however, the emergent shoots are those of a perennial species (Figure 1, path C), the plant already has a distinct advantage in tolerating the burial process. At this point, if the root system can still function in the soil, the buried plant will survive (Figure 1, path D). If the buried root system cannot function, however, survival may still be possible through the development of new root material (Figure 1, path E).

If an individual is totally buried, bud break must occur before aerial shoots can emerge from the deposit (Figure 1, path F). Following bud break, emerging shoots of woody or evergreen species need only retain their root system in the old soil or form a new system in the deposit in order to survive burial (Figure 1, path G). However, if the emergent shoot is deciduous, survival is only possible if the root system and perennating structures remain in the old soil and shoots penetrate the deposit annually (Figure 1, path H). Alternatively, the plant must move its underground structures, particularly roots and perennating organs, into the deposit (Figure 1, path I).

The effects of deposition on the larger growth forms of trees and shrubs is very different. Such species are less common in the coastal and arid dune environments and most studies of tree burial relate to tephra and ash deposition from volcanic eruptions (Vucetich and Pullar, 1963; Thorarinsson, 1979, 1981; Whittaker *et al.*, 1992; and Burnham, 1994). Effects of volcanic ash on trees and shrubs is described in Section V 2.

IV Early work on dust deposition in the Great Plains

Weaver and Albertson (1936), Robertson (1939) and Mueller (1941) were among the first to discuss burial and the effects of dust deposition following drought on the prairie vegetation of the American Great Plains during the mid-1930s. A layer of dust 1.2–3.8

cm in depth was sufficient to kill the majority of short prairie grasses. However, prairie weeds, including *Agropyron smithii* and *Bouteloua gracilis*, thrived on areas of recently deposited dust through the development of long vertical rhizomes and the formation of new crowns on the surface of the deposit (Weaver and Albertson, 1936; Robertson,

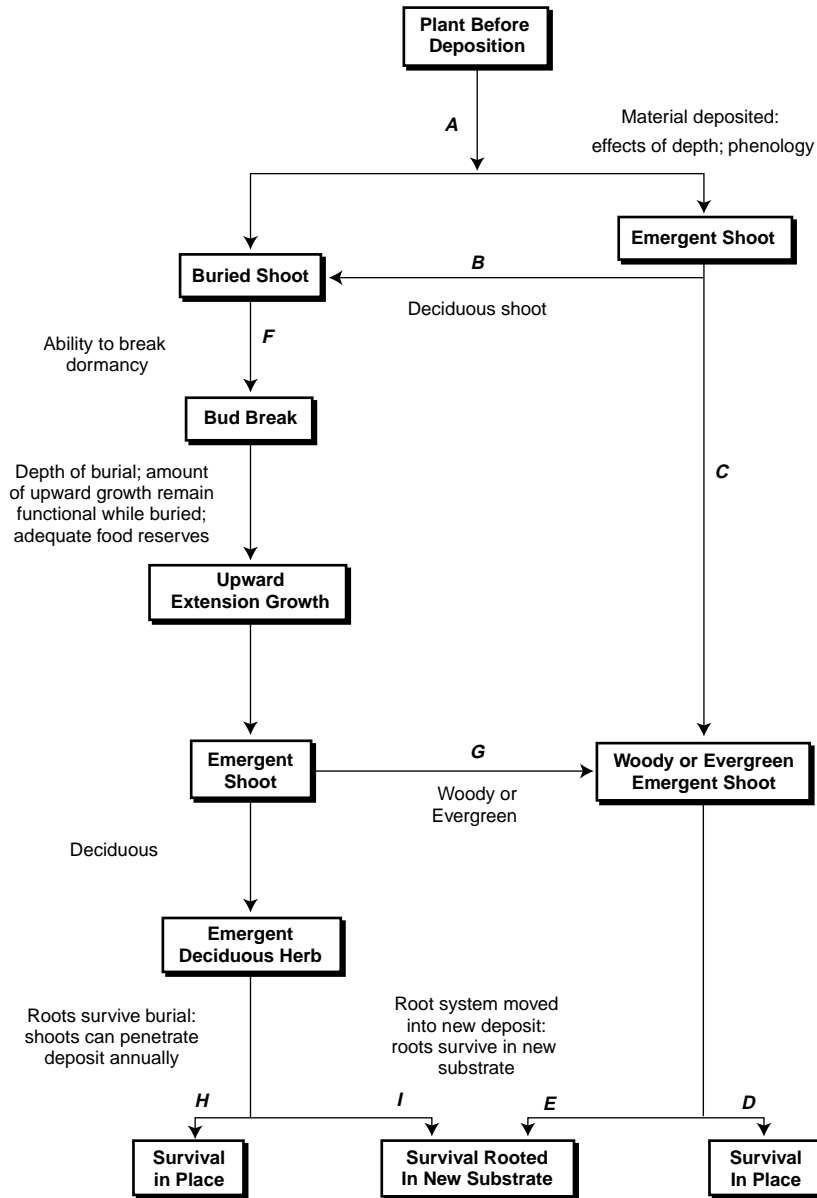


Figure 1 Responses to burial necessary for plant survival
 Source: redrawn from Antos and Zobel 1987; reproduced with the kind permission of the authors and the University of California Press

1939). Mueller (1941) confirmed the critical role played by rhizomatous growth after burial and illustrated that the growth rate of a rhizome and its ability to grow vertically through a deposit is of great importance to a grass following burial.

V Burial by volcanic deposits (tephra and lavas)

1 Burial effects on low-growing vegetation

The effects of burial by volcanic tephra have been the subject of a number of papers, for example, Egger (1948, 1959) and Griggs (1918, 1919). Mack (1981), Antos and Zobel (1985b, 1987) and Zobel and Antos (1997) focused their investigations on the botanical consequences of tephra deposition following the 18 May 1980 eruption of Mount St Helens, Washington State, USA. The results of their studies indicate that although, as illustrated in Figure 1, plants possess a number of solutions to the problem of burial, one of the most critical factors in an individual's survival and successful emergence is its ability to perform some degree of morphological transformation. Antos and Zobel (1985a) illustrated that graminaceous species buried by volcanic deposits were characterized by the development of a new crown from stems penetrating the tephra. Shrubs produced adventitious roots on the parts of their stems buried by tephra. Other individuals survived deposition through a transformation from short to long rhizome internodes, a re-orientation of rhizomes and/or the production of unusual vertical shoots. In a subsequent investigation, Antos and Zobel (1985b) recorded the upward movement of underground plant parts into Mount St Helens tephra deposits. Of the eight species studied, seven responded to burial by moving their perennating organs into the deposit. Species with extensive rhizomatous growth positioned their rhizomes vertically in the tephra, and produced aerial shoots from depths as great as the tephra base. Clearly, although a plant's phenological stage may be an important factor affecting the impact of tephra deposits (Antos and Zobel, 1987), those species with the greatest degree of morphological plasticity will be the most successful in burial situations (Mack, 1981). Local environmental variation has also been shown to be particularly important in determining patterns and depth of tephra deposition and subsequent variability in successful regrowth (Mack, 1981; Zobel and Antos, 1997).

2 Burial effects on trees and shrubs

Ash accumulation has varying effects on vegetation and damage from unpolluted ash usually depends on the thickness of the ash layer (Blong, 1996; Newnham *et al.*, 1999a). Burnham (1994) described the effects on vegetation following the eruptions of Mount St Helens (1980) and El Chichon (1982), when vegetation was affected over 20 km and 15 km radii, respectively. The most surprising observations were that proximal cocoa tree plantations, up to 12 km from the crater, withstood the initial violent eruptions but areas with less dense forest canopy were subsequently damaged by wet ash accumulation on leaves. Burnham reports that the leaves of the cocoa trees are coriaceous (leathery) and are therefore more resistant to ash loading and pollutants. Leaves of other trees appeared to have been snapped off and torn by the burden of ash, probably exacerbated by the additional weight of water from rainfall following the eruption.

Thus, chances of survival of ash-laden vegetation appear to be greatly reduced if rainfall follows or occurs along with ash deposition. Rainfall also exacerbates chemical impacts, for example by converting the sulphates, fluorides, chlorides, that are common constituents of tephra, to their respective acidic forms and this 'acid rain' may further increase acidity in the deposits themselves.

Whittaker *et al.* (1992) assessed the ecological effects of ash fall on the islands of Sertung and Panjang, situated 3–5 km from Krakatau volcano. Examination of sediment profiles on the islands revealed thick ash layers and buried soils, with evidence for considerable vegetation damage by ash accumulation during ash-fall events in the 1930s and 1950s. They also reported light ash-fall events that had localized effects, resulting in short-term loss of tree leaf cover, owing to chemical effects, rather than to the direct physical impacts of heavy ash fall.

Working on White Island, a near-continuously active volcano in the Bay of Plenty, North Island, New Zealand, Clarkson and Clarkson (1994) emphasized the zonation and variability of distribution of damage to trees and other vegetation. Toxic fumes, acid rain and wet ash were listed as prime causes of plant death away from the immediate vicinity but immediately adjacent to the source, blasting, burning and burial were far more significant. Where the deposition layers are shallow, trees and shrubs may survive. Turner (1928) and Wilmshurst and McGlone (1996) report that many species that were stripped of leaves and small branches by the 1886 Tarawera eruption resprouted prolifically in the years following the eruption. Morphological and eco-physiological differences between species were particularly important in this respect, as noted by Mack (1981) following the Mount St Helens event.

Covering of trees, shrubs and vegetation by lava flow represents an extreme form of the burial process, whereby the excessive heat and considerable thickness of the deposit make it virtually impossible for any vegetation to survive. However, because lava flows typically follow valley courses and other depressions in the landscape, they often result in a mosaic of burial with some areas that survive direct contact with lava providing propagules that can rapidly colonize the solidified lava surface. Often these 'refugia' contain species that are specially adapted to growth on fresh rock surfaces, good example being species of 'ironwood' (*Metrosideros* [Myrtaceae]) in volcanic regions of the Pacific, such as Hawaii and New Zealand (Clarkson *et al.*, 1989; Clarkson, 1990, 1998; Newnham and Lowe, 1991).

An exception to this mosaic landscape resulting from lava burial may occur when fires, ignited by the flowing lava, spread beyond the lava body to cause much more widespread destruction of vegetation. In such cases, the vegetation response will be a combination of primary succession on the freshly solidified lava surfaces and secondary succession of the burnt areas (Clarkson *et al.*, 1989; Clarkson, 1990, 1998).

Pyroclastic flows are another volcanic process resulting in an extreme form of burial marked by excessive heat. A lack of published research into this phenomenon probably reflects the near total incapacity of plants to survive or respond in any way other than through primary succession. Some examples of complete burial by late Holocene pyroclastic flows in New Zealand and the subsequent plant communities developed have been described from pollen and plant macrofossil records (Clarkson *et al.*, 1988; Lees and Neall, 1993).

VI Burial in coastal and lake dune environments

Burial by sand is a frequent environmental stress in the coastal and lake dune environment and a number of authors (for example, Oosting and Billings, 1942; Salisbury, 1952; Ranwell, 1958; Hewett, 1970; van der Valk, 1974; Moreno-Casasola, 1986; Houle, 1996) have recognized sand movement and the related burial stress as the most important environmental factor controlling plant distribution in coastal dunes.

1 Rates and depths of burial

Maun (1994: 59) has stated that the risk of burial by sand in the dune environment is high, owing to the 'spatial and temporal variation in the substrate'. Estimates of rates of sand deposition vary widely between dune systems and range from 8.7 cm yr⁻¹ at the Lake Huron sand dunes (Maun, 1985) to 90 cm yr⁻¹ on an active dune site at Newborough Warren, UK (Ranwell, 1958). Although the landward dunes are comprised of relatively easily moved fine-grained sand (Chapman, 1964), the processes of stabilization and fixation lead to an overall decrease in sand movement with the progression of the dune system landwards from the sea. Strandline and foredune species are, therefore, the most likely subjects of burial. During storms and high winds, however, rates of sand accretion may be significantly increased. For example, Seliskar (1990) recorded the deposition of a total of 28 cm of sand as a result of a single storm on the coast of the USA. Such violent climatic episodes are frequently important in extending the deposition of sand further back along the dune profile, even as far as the dune grassland.

2 Geomorphic processes of sand deposition

The actual processes of sand deposition have been extensively studied by geomorphologists in both coastal and desert dunes. After the pioneering work of Bagnold (1941), more recent research is summarized in Pethick (1984), May (1985), Sarre (1987), Anderson (1989), Pye and Tsoar (1990), Cooke *et al.* (1993), Sherman and Bauer (1993), Thomas (1997), Livingstone (1999) and Goudie *et al.* (1999). Most of these have studied the physics and physical properties of sand movement in the field and within wind tunnels assuming the absence of any vegetation cover. Nevertheless, some work has been published on the role of vegetation cover in modifying processes of dune formation and stability (Ash and Wasson, 1983; Tsoar and Møller, 1986; Wasson and Nanninga, 1986; Lancaster, 1994; Wiggs *et al.*, 1995; Musick, and Trujillo, 1996; Lancaster and Baas, 1998). However, most of these relate to desert dunes and, again, stress the protective role of vegetation in preventing or slowing processes of sand movement and deposition, rather than examining the effects of deposition on the plants themselves.

3 The effects of burial by sand on the strandline flora

Rates of sand accretion at the strandline are greatly influenced by the high mobility of the substrate (Lee and Ignaciuk, 1985) and may have important consequences with

regard to the establishment of annual species, as burial of seed below a certain critical depth may result in germination failure or failure of the seedling to emerge (Maun and Lapierre, 1986; Baskin and Baskin, 1989; Hesp, 1991; Maun, 1994; Houle, 1996; Greipsson and Davy, 1996). Lee and Ignaciuk (1985) studied the effect of burial by sand on the germination of three annual strandline species, namely *Atriplex laciniata*, *Cakile maritima* and *Salsola kali*, whilst Maun and Lapierre (1986) examined the effects of artificial seed burial on the germination of *Elymus canadensis*, *Ammophila breviligulata*, *Cakile edentula* and *Corispermum hyssopifolium*. The results of both investigations suggested that the total germination of strandline species decreases with increasing depth of seed burial (Lee and Ignaciuk, 1985; Maun and Lapierre, 1986). Studies conducted by Maun and Lapierre (1986) and Greipsson and Davy (1996) found that the rate of emergence and total emergence of seedlings of strandline species tended to decrease with increased sowing depth. Other investigations (e.g., Johnson, 1978, cited in Barbour *et al.*, 1985) have indicated an important relationship between seed mass and emergence depth, and it is generally accepted that species with larger seed size are able to emerge from deeper burial treatments than small-seeded species. Species possessing large seeds have an increased ability to successfully send up seedlings from deeply buried seeds (Barbour *et al.*, 1985; Lee and Ignaciuk, 1985; Maun and Lapierre, 1986).

4 Burial responses of foredune species

Literature relating to the effects of burial on foredune plants is largely restricted to the burial responses of the Poaceae and of members of the genus *Ammophila*, in particular. Studies have shown that a number of foredune species do not merely tolerate burial, but are characterized by the capacity to respond positively to sand accumulation. Maze and Whalley (1992a,b), for example, illustrated that burial of *Spinifex sericeus*, a common Australian foredune grass, stimulated a positive growth response and demonstrated that inundation by sand is a requirement for germination in this species. Zhang and Maun (1990b) studied the effects of burial by sand on the germination, seedling emergence, growth and survival of *Agropyron psammophilum*, a species endemic to the foredunes of the Great Lakes. Field and glasshouse investigations indicated that burial of *A. psammophilum* seedlings up to a depth of 6 cm stimulated an increase in height, leaf and tiller production, and overall dry weight. Similar findings were recorded by Zhang and Maun (1990a, 1991) for the effects of sand burial on the foredune species *Panicum virgatum*. Partial burial of seedlings of the sandgrass *Triplasis purpurea* results in increased survival, growth and eventual reproduction compared with unburied seedlings (Cheplick and Grandstaff, 1997).

Tropical sand dune species respond to burial by sand in similar ways to temperate species. Martinez and Moreno-Casasola (1996) investigated the burial responses of six tropical species from the Gulf of Mexico and showed that all species, through increased leaf area and total biomass, responded positively to sand accretion. The ability of these foredune species to respond positively to burial (e.g., Zhang and Maun, 1990a,b, 1991; Maze and Whalley, 1992a,b; Martinez and Moreno-Casasola, 1996; Cheplick and Grandstaff, 1997) may represent an adaptation to the dune environment.

Investigations by van der Valk (1974) on six representative forbs from the foredunes of the Cape Hatteras National Seashore yielded similar results to those of Lee and

Ignaciuk (1985), and Maun and Lapierre (1986), with the larger and heavier seeds of certain species proving capable of successful germination and production of seedlings from increasingly greater depths of burial. *Strophostyles helvola*, for example, had the largest and heaviest seed of the six species studied. Seeds of this species were able to germinate and reach the surface through sand deposits as great as 14 cm (van der Valk, 1974). Subsequent investigations at Lake Erie further examined the effects of burial by sand on the seeds and seedlings of *S. helvola*. Yanful and Maun (1996a,b) found that individual plants from the seaward dunes produced a significantly greater number of heavier seeds than those on the strandline. Seedlings from heavier seeds were able to emerge from greater depths of burial, and took fewer days to re-emerge from different burial depths, than individuals from small seeds. The largest *S. helvola* plants were produced from the heaviest seeds (65–75 mg).

However, whereas the foredune species discussed above merely tolerate burial through an ability to exhibit a positive growth response, other species, notably *Ammophila arenaria* and *Ammophila breviligulata*, are known to actively require burial by sand for maximum growth and successful completion of their life cycle. *Ammophila arenaria* is an abundant grass of coastal dune systems occurring along all European coasts south of latitude 63°N (Huiskes, 1979). Often the only species present in areas of mobile sand (Huiskes, 1979), its distribution in the dune environment is largely related to the fact that adult *A. arenaria* individuals are exceptionally tolerant of sand mobility and are capable of withstanding burial by up to one metre of sand per annum (Ranwell, 1972). In North America, *A. arenaria* is largely replaced by populations of *A. breviligulata*. Regarded as the ecological and sociological equivalent of *A. arenaria* (Laing, 1958), *A. breviligulata* is characteristic of the sandy beaches, foredunes and stable dunes of the Great Lakes and sea coasts of North America (Maun and Baye, 1989).

Leafy shoots of *A. arenaria* are capable of growing up through a moderate thickness of sand by simple elongation of the individual leaves (Gemmell *et al.*, 1953). However, once an individual plant is overwhelmed by increasing depositions of sand, the axillary buds develop to create vertical shoots with long internodes termed 'vertical rhizomes' (Gemmell *et al.*, 1953). With continuing growth, the vertical rhizomes will eventually reach the sand surface, the apex of each becoming a new leafy shoot. The initial post-burial emergence of *A. breviligulata* also relies on the formation of long stem internodes (Maun and Lapierre, 1984) and follows a similar pattern to that described by Gemmell *et al.* (1953) for *A. arenaria*.

Studies have shown that *A. breviligulata* is capable of a range of positive burial responses and typically demonstrates an increased vigour with increased burial depth. Disraeli (1984), for example, indicated that below- and above-ground biomass, leaf area, number of tillers per plant, number of buds per tiller, number of new plants from horizontal and vertical rhizomes, total chlorophyll concentration, plant height and plant cover of *A. breviligulata* were all positively affected by burial. Investigations by Yuan *et al.* (1993) focused on the effects of sand accretion on the photosynthesis of *A. breviligulata*. Working on the hypothesis that enhanced growth and vigour in buried adult *A. breviligulata* plants is largely due to increased carbon assimilation, Yuan *et al.* (1993) undertook a series of field studies. Their results supported the hypothesis that sand accretion leads to an increase in net CO₂ uptake, leading to increased photosynthetic rates. Buried *A. breviligulata* seedlings also exhibited an increased rate of CO₂ uptake. Yuan *et al.* (1993) concluded that the reported increase in biomass following

burial (e.g., Disraeli, 1984), is partly due to increased carbon assimilation levels. Seliskar (1994) recorded a significantly higher concentration of ethylene in the stems of seedlings covered with sand than in those of unburied controls, suggesting a source for the stimulation of stem elongation described in previous studies (e.g., Maun and Lapierre, 1986).

Ammophila arenaria and *A. breviligulata* are clearly both excellent examples of frequently buried, highly adapted foredune species, apparently requiring regular fresh depositions of sand to maintain their vigour. The relationship between decline in vigour in *Ammophila* (decreased shoot weight per plant, lesser number of plants per unit area, decreased plant height, less prolific flowering) (Eldred and Maun, 1982) and the stabilization of the dune sand surface, has been discussed by a number of authors (for example, Tansley, 1949; Salisbury, 1952; Laing, 1958; Olson, 1958; Marshall, 1965; Hope-Simpson and Jeffries, 1966; Huiskes, 1979 and Krajnyk, 1979). Past studies have attributed this decline in vigour to an increase in soil acidity (Salisbury, 1952), increasing inter-specific competition (Tansley, 1949; Salisbury, 1952; Marshall, 1965) and accumulation of dead and decaying organic matter (Wallen, 1980). Further proposed explanations for the differences in vigour of *A. arenaria* and *A. breviligulata* on sand accreting and nonaccreting sites are summarized by Marshall (1965) and Eldred and Maun (1982). Expanding on the work of Marshall (1965), Eldred and Maun (1982) used multivariate statistical methods in an attempt to identify the plant and environmental variables responsible for a decline in vigour in *A. breviligulata*. Numerical analysis of their experimental results indicated that of all the environmental variables measured (sand deposition and flux, soil temperature and competition), sand accretion had the greatest influence on the growth of *Ammophila*. More recent studies, however, have implicated nematodes and soil-borne fungi in the decline of *Ammophila* (van der Putten *et al.*, 1988, 1989; de Rooij-van der Goes, 1995; de Rooij-van der Goes *et al.*, 1995a,b; Little and Maun, 1996).

5 Burial responses of other species

Other frequently studied species in burial investigations include the grasses *Elytrigia juncea* and *Calamovilfa longifolia*. Whereas *E. juncea* is a common species of the sandy coasts of Britain and Western Europe (Hubbard, 1984), *C. longifolia* is primarily found occupying the sand hills, sandy prairies and sand dunes of the Great Lakes of North America (Maun, 1985). Adult and seedling individuals of *C. longifolia* respond to burial in a similar manner to *A. breviligulata*, increasing carbon assimilation, leaf thickness and number of bundle sheath cells (Yuan *et al.*, 1993). The results of investigations by Maun and Riach (1981) into seedling emergence in *C. longifolia* strongly agree with those of Maun and Lapierre (1986) for a range of strandline species: emergence of *C. longifolia* seedlings is related to seed burial depth.

Elytrigia juncea is capable of elongating its shoots through layers of sand as deep as 23 cm and has the capacity to withstand repeated depositions of sand; two facts accounting for its common occurrence as a pioneer colonist on British foreshores (Gimingham, 1964). Harris and Davy (1987) illustrated that, although growth after seven days burial was supported by re-distributing dry matter between plant parts, so that existing photosynthetic tissues were maintained at the expense of roots, shoots and

developing leaves, *E. juncea* seedlings were unable to survive two weeks of burial by sand. Investigations by Brown (1997) on three dune plant species, namely *Sarcobatus vermiculatus*, *Chrysothamnus nauseosus* and *Distichlis spicata*, also indicated that plants may respond to burial through a shift in biomass from below-ground to above-ground components. Working on the assumption that photosynthetic competence is not impaired by short-term burial, Harris and Davy (1988) subsequently undertook an investigation into carbon and nutrient allocation in *E. juncea* seedlings after burial. Results of their experiments revealed that photosynthetic capacity during burial may be maintained by a reversal of the normal source-sink relationships for carbohydrate between photosynthetic and nonphotosynthetic organs. Translocation of carbohydrate to stem, roots and expanding leaves was virtually suppressed during burial, whereas burial by sand increased the proportional allocation of total nitrogen, phosphorus and potassium to fully developed leaves (Harris and Davy, 1988). Investigated adult burial responses of four of the dune grasses discussed above are summarized in Table 2.

Chen and Maun (1999) used greenhouse experiments to examine the effects of sand burial on seed germination and emergence of *Cirsium pitcheri*, a threatened species of

Table 2 Summary of the recorded adult burial responses of four commonly studied dune grasses

Species	Burial responses	Reference
<i>Ammophila arenaria</i>	Increased internode length, tiller production and adventitious rooting	Sykes and Wilson, 1990a
<i>Ammophila breviligulata</i>	Increased vertical growth of tillers and rhizomes Increased net photosynthesis Increased leaf thickness Increased above- and below-ground biomass Increased leaf area Increased tiller production Increased total chlorophyll concentration Increased shoot emergence time Decreased shoot density	Maun, 1985 Yuan <i>et al.</i> , 1993 Yuan <i>et al.</i> , 1993 Disraeli, 1984 Disraeli, 1984 Disraeli, 1984 Disraeli, 1984 Maun and Lapierre, 1984 Maun and Lapierre, 1984
<i>Calamovilfa longifolia</i>	Increased vertical growth of tillers and rhizomes Increased net photosynthesis Increased leaf thickness Increased number of bundle sheath cells Decreased shoot density Increased shoot emergence time Increased number of nodes, internode length and adventitious rooting	Maun, 1985 Yuan <i>et al.</i> , 1993 Yuan <i>et al.</i> , 1993 Yuan <i>et al.</i> , 1993 Maun, 1996 Maun, 1996 Maun, 1996
<i>Elytrigia juncea</i>	Increased internode length, tiller production and adventitious rooting	Sykes and Wilson, 1990a

the Lake Huron sand dunes. Seeds were buried at varying depths and the results showed that seedling emergence occurred at a maximum depth of 6 cm, with most seedlings only emerging from 2 cm depth. Percentage seed germination and emergence of seedlings were also shown to be uncorrelated with seed size.

6 Burial of plants from the landward dunes

One of the earliest accounts of the effects of sand deposition on dune vegetation is that given by Farrow (1919), who artificially buried an area of grass-heath to a depth of 5 cm with sterile sand. After a period of eight weeks, *Agrostis capillaris*, *Galium verum*, *Rumex acetosella*, *Thymus serpyllum* and *Lotus corniculatus* were among the species to have colonized the new sand surface. Although the exact processes of re-colonization were observed to vary between the different plant species, emergence through the sand surface generally involved an elongation of the main stem to reach the surface, or the development of lateral stems from the buried crown, followed by the production of adventitious roots within the sand (Farrow, 1919).

In a study of 30 New Zealand sand dune species, many perennials survived partial burial, although most were killed by full sand cover (Sykes and Wilson, 1990a,b). In contrast, the majority of annual grasses were unable to survive even when partly buried. Results of the investigation indicated that the dune species studied have a range of morphological responses to burial by sand. Most herbs with a creeping habit e.g., *Centella uniflora* and *Hydrocotyle novaezelandiae* responded well to burial, re-growing from small pieces of stolon and generally following a vertical line of growth up to the sand surface (Sykes and Wilson, 1990a,b). Similar morphological responses in plants buried by volcanic ash (tephra) were chronicled by Antos and Zobel (1985a, 1985b).

Although bryophyte species constitute an important part of a dune system's flora, excepting a series of experiments undertaken by Birse *et al.* (1957), very few investigations into their responses to burial have been conducted until recently. Field studies by Birse *et al.* (1957) suggested that the maximum depth of sand through which dune mosses can grow in the natural environment is 5.5 cm. Others have suggested that some mosses actually require partial burial in sand to maintain their vigour (Marshall, 1965; Eldred and Maun, 1982; Disraeli, 1984; van der Putten *et al.*, 1988; Little and Maun, 1996; Maun *et al.*, 1996). In bryophytes, a range of physiological attributes appeared to respond to burial, including biomass, net photosynthetic rate, photosynthetic efficiency and number of leaves. However, Martinez and Maun (1999) reported results of experimental burial of 11 moss species found growing along the gradient of habitats from foredunes to inland forests on the Lake Huron sand dunes. Various burial treatments were applied, both in the field and in the greenhouse. Species were classified into three types in terms of plant cover response: inhibited, neutral and stimulated, but most species showed an ability to survive burial depths of up to 7 cm. Species occurring in areas of high sand mobility and deposition were shown to be the most tolerant and emerged from depths up to 35 times their height. Species of landward dunes showed the least tolerance of burial.

VII Burial in arid and semi-arid environments

Burial in arid and semi-arid environments is frequent and various studies have been made of plant adaptations in these environments. However, most research has concentrated on plant evolutionary response to water stress (Goodall and Perry, 1979; Bullard, 1997; Wainwright *et al.*, 1999). Other important characteristics of the vegetation are its 'patchiness', commonly a response to spatial variability in moisture and temporal variability in what is termed 'ephemeral' or 'accidental' vegetation, which often comprises annuals that grow and reproduce very rapidly, usually after a single infrequent rainfall event. Thomas (1988) and Bullard (1997) emphasize, however, that stability of the growth medium is equally as important in primary succession as moisture availability.

Yeaton (1988, 1990), working in the Namib Sand Sea, demonstrated a relationship between the distribution of species on dunes with differing life-cycle characteristics and the quantity of surface sand movement that occurred. Species establishing predominantly from seed occurred in lower and more stable parts of dunes (e.g., *Stipagrostis ciliata* and *Cladoraphia spinosa*), while vegetative reproduction through rhizomes was favoured near dune crests and in more mobile dune sand. Yeaton (1988) also showed a clear relationship between monthly rates of sand movement and plant cover (Figure 2), indicating that, even in deserts, species have problems in evolving tolerance to high sand mobility. Nevertheless, as with coastal dunes, certain species have evolved in direct response to sand accumulation and will die if accumulation ceases. *Aristida pungens*, for example, grows actively through fresh blown sand and can create small dunes up to 2 m high (Bendali *et al.*, 1990). Given the limited nature of these studies,

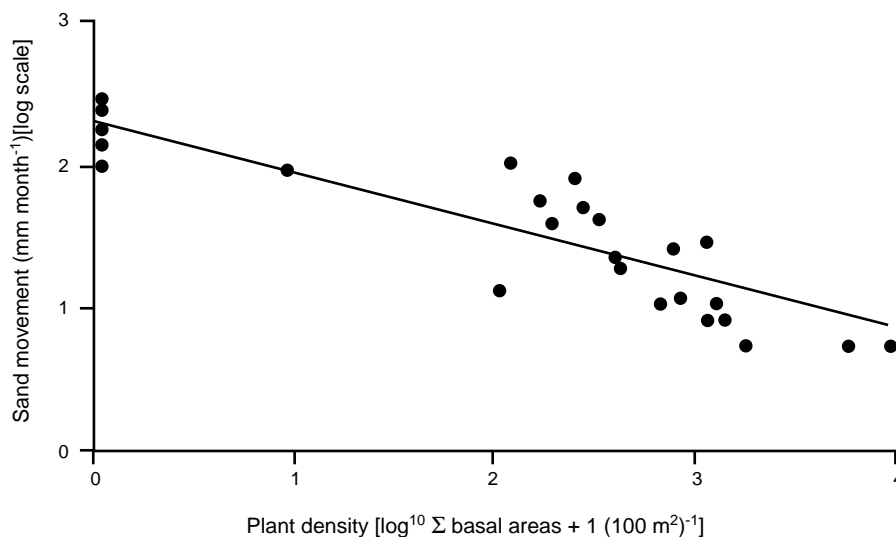


Figure 2 The relationship between monthly rates of sand movement (mm) and plant biomass (basal cover per 100 m²) in the Namib Desert
Source: redrawn from Yeaton, 1988 and reproduced with kind permission of *Journal of Ecology*

there is ample scope for further research into plant response to burial in the desert environment.

VIII Burial by alluvium in hydrological events

Although burial by 'run-on' and deposition of eroded material from streams and rivers following hydrological events is commonplace in most fluvial environments, comparatively little research appears to have been completed on vegetation response. Nanson and Beach (1977), Hupp (1982, 1983, 1988), Hicken (1984), Hupp and Osterkamp (1985), Hughes (1988), Kalliola and Puhakka (1988) and Dunham (1989) have examined vegetation patterns in channels and on floodplains or bottomlands. The role of vegetation in acting as a binding agent in alluvial deposits and sediments is often vital and much depends on the magnitude and frequency of burial and the ability of species to survive inundation. Plant propagules may also be selectively sorted and concentrated by fluvial action. Riparian vegetation has also been examined (e.g., Gregory *et al.*, 1991; Van Coller *et al.*, 1997) with specific vegetation types linked to differing fluvial geomorphic features but again without burial being examined specifically.

Combined volcanic and fluvial activity burial results in lahars or volcanic mudflows, that occur frequently in the vicinity of active volcanoes in montane and tropical environments. However, the response of vegetation to lahar burial and subsequent post-burial response has received scant attention.

IX Palaeoenvironmental dimensions to vegetation burial

Once burial has occurred, existing vegetation and soil horizons, particularly surface organic matter accumulations, become trapped by the deposit. In the various burial environments, numerous examples exist of former soil and vegetation surfaces that have been preserved. Often repeated horizons or surfaces are detectable and these can assist with interpretation of past environmental variability, the nature and intensity of catastrophic events, particularly volcanic eruptions and the timing and extent of human impact.

1 Machair sand dune stratification in the Outer Hebrides of Scotland

The climate of the Outer Hebrides is dominated by the strong prevailing wind that originates from the south and southwest. Gales are recorded on 50 days or more a year (Manley, 1979) and the average wind speed at Stornaway has been calculated as 7.4 m s^{-1} (Birse and Robertson, 1970; Angus, 1991). Burial by wind-blown sand is thus a common problem for the vegetation of the dunes and machairs, which extend along the west coast of the archipelago (Ritchie, 1967, 1979, 1991; Mather and Ritchie, 1977). Sand movement also occurs widely as a result of anthropogenic impacts. Foremost amongst these are the effects of agricultural activity, chiefly ploughing and lazy-bedding (Pankhurst and Mullin, 1991; Angus, 1996; Owen *et al.*, 1996, 2000; Owen, 1998).

Gilbertson *et al.* (1995) have partly attributed the vegetational uniformity of the Hebridean machair sand dune plains to these burial processes that occur most

frequently during the winter months but also following storms and gales throughout the year. Gilbertson *et al.* (1995) hypothesized that perennial machair species are adapted to burial by sand and, provided that burial is not too deep, will recover within a few months of inundation. However, if the depth of burial becomes too great, re-growth fails and the existing vegetation becomes buried under the sand, resulting in a process they described as 'machair stratification' (Figure 3; Plate 1).

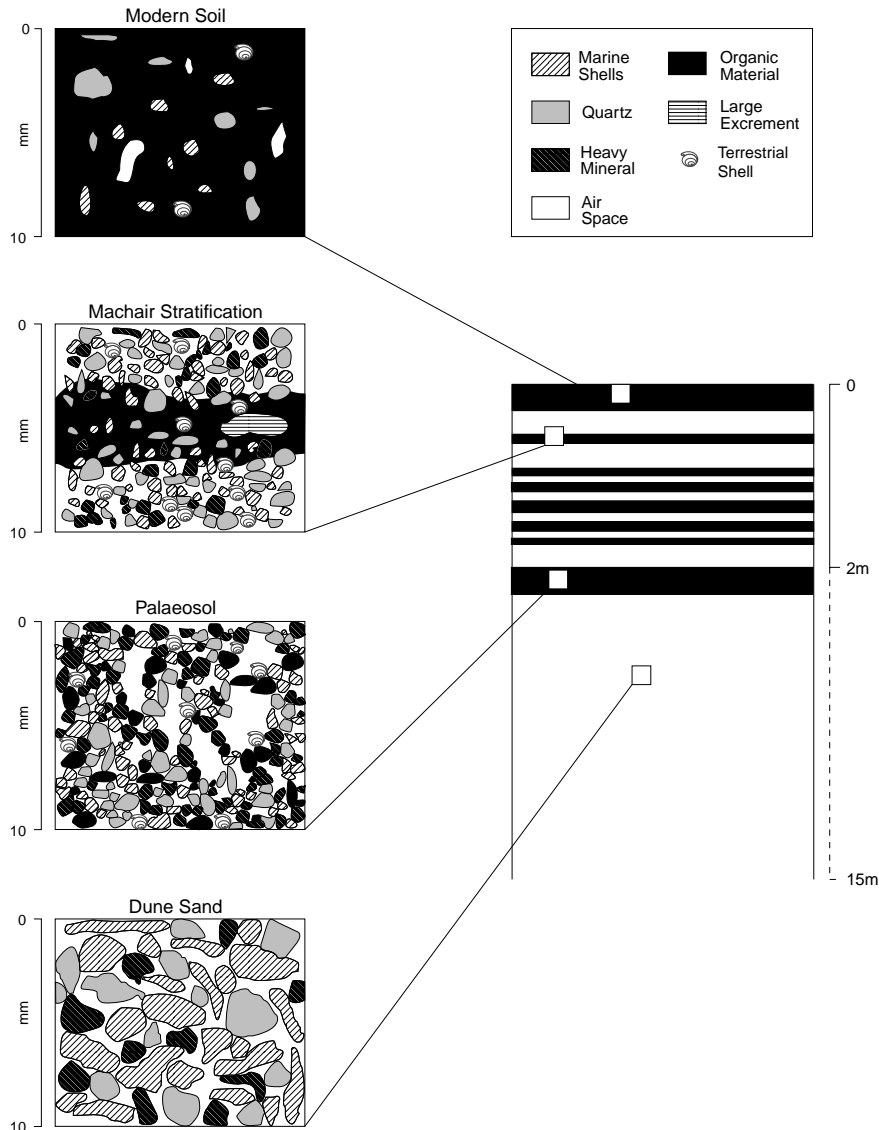


Figure 3 Schematic diagram representing the major micromorphological features associated with machair soils

Source: adapted from Gilbertson *et al.*, 1995; reproduced with the kind permission of Blackwell Publishers



Plate 1 'Machair stratification' in the sand dunes of South Uist in the Outer Hebrides, Scotland. The main palaeosol underlying the stratified layers is clearly seen, as are the numerous organic horizons within the stratification itself. See text for explanation (photo: M. Kent)

Gilbertson *et al.* (1995, 1996) describe the phenomenon of machair stratification as an apparently very young geomorphological feature that is invariably associated with the vegetation of the low machair grassland and that typically does not occur below one substantial palaeosol (Plate 1). Deposits exhibiting machair stratification typically range from 0.5 to 1.5 m in thickness and Gilbertson *et al.* (1996: 73) describe these deposits as displaying:

thin couplets of (1) laminae of white/grey to brown comminuted shell-sand (sometimes graded) which are 1 mm to 3 mm thick with a sharp lower boundary; and (2) laminae of grey to black organic shell-sand, variously 1 mm to 4 mm thick, with a bioturbated and diffuse lower boundary. (Figure 3; Plate 1)

The detailed micromorphological features of machair stratification are further discussed by Gilbertson *et al.* (1995).

It is hypothesized that the origins of machair stratification are intimately associated with the quantities of wind-blown shell-sand characteristic of the machair environment (Gilbertson *et al.*, 1996). Sand exposed as a result of rabbit activity, plough and spade cultivation along with sand from blow-outs and quarries may spread in a thin sheet across areas of the machair during storms and times of high wind activity (Owen *et al.*, 2000). This phenomenon produces the first part of the machair stratification couplet and is described as (1) in the above definition (Figure 3). Subsequent plant growth through this sheet of sand during the spring and summer months eventually produces a layer of organic material, producing the second part of the couplet and described as (2) in the preceding definition (Figure 3).

Gilbertson *et al.* (1996) thus conclude that machair stratification is closely related to particular types of land use that have been practised over the historical period. This palaeoenvironmental explanation ultimately leads to the hypothesis that the Hebridean machair dune grasslands are a direct consequence of a particular combination of burial resulting from both human activity and their natural situation (Owen *et al.*, 2000).

2 Vegetation damage and volcanic impacts in New Zealand

Situated amidst one of the most diverse active volcanic regions anywhere on Earth, the northern New Zealand region has provided numerous examples of vegetation response to burial by tephra. In broad terms, these studies can be divided into examples of primary vegetation succession following essentially complete burial at sites proximal to the volcanic centre (e.g., Turner, 1928; Nicholls, 1963; Vucetich and Pullar, 1963; Burke, 1974; Clarkson and Clarkson, 1983, 1994; McGlone *et al.*, 1988; Clarkson, 1990; Clarkson *et al.*, 1995; Horrocks and Ogden, 1998; Newnham *et al.*, 1999b – see also Section V 2 above) and examples of secondary succession following partial burial at sites distal to the volcanic centre (e.g., McGlone, 1981; Wilmshurst and McGlone, 1996; Wilmshurst *et al.*, 1997; Giles, 1999; Giles *et al.*, 1999). In both categories, investigations involve detailed analysis of plant macrofossils or pollen preserved in organic sediments interbedded with the tephra layers, often allied with reference to present-day spatial differences in forest structure and floristic composition.

Vucetich and Pullar (1963) examined plant macrofossils buried by tephra layers at a range of sites to determine approximate critical depths of tephra deposits that would cause significant damage to the forested regions of central North Island. They concluded that a tephra depth of 38 cm or more typically resulted in complete destruction of forest trees, 30–38 cm in almost complete destruction, and 23–30 cm in partial destruction. These depths relate to primary airfall deposits with no overthickening resulting from redeposition of sediment. It seems likely that for nonforested vegetation communities, severe damage would be inflicted following less substantial tephra fall. However, it should be emphasized that these critical thicknesses can only be useful as broad approximations as the nature of the vegetation and in particular its susceptibility to damage, local site factors, tephra chemistry, time of season and meteorological factors are likely to be as important in determining vegetation response to burial. Nicholls (1963) cites the example of bracken (*Pteridium esculentum*) reportedly emerging through 50-cm-thick volcanic deposits one year after the AD 1886 Mount Tarawera eruption. Several trees and shrubs, such as *Aristotelia serrata*, *Coriaria arborea*, *Griselinia littoralis* and *Weinmannia racemosa*, have the capacity to resprout from stout basal shoots and these, along with bracken, grasses and other seral species figure prominently in pollen assemblages in sediments immediately above tephra layers.

A number of recent investigations into distal volcanic impacts have confirmed that even comparatively minor tephra fall, resulting in just a few centimetres of accumulated deposit, can cause some disturbance to vegetation communities, often at considerable distance from the volcanic centre (Newnham *et al.*, 1999a). Perhaps the best known example from New Zealand is the c. 1850 BP Taupo eruption. Forests within a roughly circular area 70–90 km from the vent were completely destroyed by pyroclastic flows but revegetation of the forest complex similar to pre-eruption forests

was complete within *c.* 200 years of the eruption (Wilmshurst and McGlone, 1996). However, tephra fall from this eruption also generated much more widespread disturbance at sites up to 170 km away (McGlone, 1981; Newnham *et al.*, 1989, 1995; Wilmshurst and McGlone, 1996). At these distal sites, burial of vegetation ranged from complete to partial, with significant damage associated with tephra deposits of <10 cm. Nevertheless, patterns of damage and vegetation response were extremely variable and not always related to tephra thickness. In areas that escaped complete burial or suffocation of root systems, the damage to vegetation was probably inflicted by a variety of mechanisms. Tephra fall would have broken small branches, defoliated and damaged crowns of canopy and emergent trees whilst burying exposed smaller plants (Wilmshurst and McGlone, 1996). Chemical effects from the highly acidic tephra would have exacerbated the physical damage. Senescent or already weakened trees would have been more susceptible, but more youthful or robust individuals would have survived and replaced foliage in the following year. Numerous pollen records indicate that besides inflicting damage, tephra fall provided opportunities for the more youthful and vigorous survivors to exploit canopy gaps and thus facilitate forest regeneration. In some instances, there is evidence for tephra deposition acting as a catalyst for accelerating the pace of longer-term environmental change. This is especially evident during the transition from the last glacial to the present interglacial, a period of reforestation associated with general climatic amelioration (Newnham *et al.*, 1989; Giles, 1999). Often post-eruption changes in vegetation composition are related to changes in substrate, where volcanic deposits have given rise to very different soils from those present earlier. In some cases soils have actually become more fertile (Burke, 1974; Clarkson *et al.*, 1988; McGlone *et al.*, 1988; Newnham and Lowe, 1991; Lees and Neall, 1993). Vegetation burial by lahar in the Taranaki region of New Zealand during the last interglacial is reported by Newnham and Alloway (2001) (Plate 2).

In summary, besides indicating the frequency and magnitude of burial events for a region, these and other palaeoecological investigations have provided some insights into rates of change and recovery of vegetation following burial. These records also demonstrate the importance of recurrent burial in the vegetation dynamics of volcanic regions and have indicated that certain species are adapted to and can withstand the burial process. These species in particular are subsequently important in both primary and secondary succession and may facilitate the return of pre-eruption vegetation cover in surprisingly short timescales. In some cases, burial may serve to increase rates of turnover in mature forest communities or even to accelerate the pace of underlying long-term change. At a broader phytosociological level, the history of burial from past eruptive activity and associated soil developments can explain at least some of the more complex patterns of vegetation distribution that are typically found in volcanic regions (McGlone, 1985).

The primary significance of the palaeoecological record is that it provides the time dimension to burial processes. Nevertheless, certain aspects of change in palaeoecological sequences can only be interpreted by understanding the mechanisms by which certain species are able to survive and even prosper following the burial process.



Plate 2 Cliff section of Airdale Reef, Taranaki, New Zealand, showing a >4-m-thick laharic deposit (uppermost layer) that has overwhelmed vegetation represented by a layer of wood, roots and leaves preserved at the top of the underlying peat (Newnham and Alloway, 2001) (photo: B.V. Alloway)

X Experimental research into the ecophysiological effects of burial

The way forward, in terms of research into vegetation burial, has been shown by Maun and Lapierre (1984), Zhang and Maun (1990a,b, 1991), Maun (1996), Maun *et al.* (1996), Yanful and Maun (1996a,b), Owen (1998), Martinez and Maun (1999) and Owen *et al.* (2000). Field experiments are desirable but are problematic and extremely difficult to control. They are also subject to partial or complete disruption following events of even moderate magnitude. Disturbance of the surface and introduction of any structures to contain blown material alters patterns of wind blow and subsequent deposition. Nevertheless, valuable results can be achieved. Controlled experiments in greenhouses

are generally more successful and allow species to be buried to differing depths and with differing frequencies over time. Monitoring of subsequent regrowth is made easier.

Most studies have been carried out on single species regarded as significant components of the plant communities of which they are a part. However, Owen (1998) working on the machair sand dune systems of the Outer Hebrides of Scotland, took $0.5 \times 0.5 \text{ m}^2$ turves of dune grassland as 'microcosms' and having stabilized them in the greenhouse, subjected the whole community of each turf to burial at varying depths and time frequencies. The performance of all species was monitored and five different species response strategies were determined. Turves from the same communities were also placed in an infrared gas analyser to determine photosynthetic efficiency following long- and short-term burial by sand. Clearly, the scope for further research on both individual and community responses to burial in the many different environments described in this paper, using these various techniques is very considerable.

XI Conclusion

The literature on vegetation burial demonstrates that in the various different environments where burial occurs, species are characterized by different degrees of adaptation and response to burial. Typically, those habitats that experience the greatest amount and frequency of deposition contain species that have evolved adaptations to survive burial and even benefit from it. For example, some foredune species, notably members of the genus *Ammophila* are so tolerant of inundation by sand that they actively require regular depositions to maintain optimum growth. Similarly, desert species, such as *Aristida pungens* have evolved in the same way. The role of evolutionary processes in the development of elastic responses in species is crucial in the burial environment (Berrie, 1984). A range of other species responses can be identified and this information is clearly important with regard to a species' position along the burial stress gradients of deposition depth and frequency.

However, with the exception of the investigations of Farrow (1919) and Owen (1998), studies of the effects of burial are largely restricted to species-specific responses and tolerances, and there is a paucity of information relating to the effects of burial at the community level. A more holistic approach to plant burial research is required that links the biogeographical aspects of plant ecophysiology and both individual species and community ecology to the various processes of deposition and sedimentation studied by the geomorphologist.

Viles (1988) in the introduction to her edited volume entitled *Biogeomorphology* states:

For many years geomorphologists in general have given only passing attention to biological factors. Several recent geomorphology texts give the impression that landform development occurs within a largely abiotic environment . . . Ecologists and biogeographers have also given little consideration to the interactions between their subject and geomorphology. (Viles, 1988: 1-2)

This paper has been concerned with a relatively understudied research area that provides a link between ecology, biogeography and geomorphology, namely the effects of burial on vegetation cover. Since Viles's classic volume of 1988, physical geographers and ecologists have gradually paid more attention to the interactions between plants,

animals and geomorphological processes, good examples being the volume on vegetation and erosion edited by Thornes (1990) and more recently research summarized by Evans (1998) on the relationships between erosion and grazing animals and the paper by Gurnell (1998) on the hydrogeomorphological effects of beaver dam building. Perhaps burial studies can provide a new focus for the combined research efforts of biogeographers, ecologists and geomorphologists.

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