Chapter 3

Desert Ecogeomorphology

John Wainwright

Introduction

Previous reviews have suggested that the rôle of vegetation has often been given scant regard in the understanding of dryland geomorphology (Francis, 1994; Bullard, 1997). Bullard (1997) emphasized the landmark collections of papers in Viles (1988), Thornes (1990a) and Millington and Pye (1994) as reflecting a turning point in geomorphological perspectives, that is further emphasized by the 118 papers recorded in the ISI database since 1990 (but none before) up to mid-2007 which deal explicitly with the topic in some way. While it is untrue to suggest that work on the subject was not carried out before the 1980s – for example, Bryan (1928), Cooke and Reeves (1976), Hadley (1961), Huntington (1914), Melton (1965), Rempel (1936) and White (1969) – what has changed is the framework in which such research is carried out in dryland environments. This change is two-fold. First, geomorphologists have more explicitly recognized the need to incorporate a consideration of vegetation and, more broadly, ecosystems into their research designs. Secondly, ecologists have equally perceived the need for a more explicit evaluation of geomorphic and related hydrologic processes in order to be able to understand vegetation and ecosystem patterning. There have been parallel developments in ecology, hydrology and geomorphology alike that suggest that there is a need for producing understanding across different spatial and temporal scales. Likewise, patterns and process change depending on the scale of observation. This trans-scale understanding is particularly critical in relation to considerations of system dynamics and the move away from narrow equilibrium perceptions (e.g. De Angelis and Waterhouse, 1987; Perry, 2002; Sullivan and Rohde, 2002; Bracken and Wainwright, 2006). Furthermore, understanding the development of spatial patterns in both vegetation and landforms requires a move away from small-scale and highly reductionist foci on local processes. To provide these understandings, both inter- and trans-disciplinarity work within an integrated framework are critical. This framework requires openness in both methodology (e.g. Balsiger, 2004) and discourse and dialogue, especially when applied to human aspects of ecosystems and environments (e.g. Wear, 1999; Tress et al., 2007; MacMynowski, 2007).

Research Frameworks

While systems approaches have been common in geomorphology since the 1960s (e.g. Stoddart, 1967; Chorley and Kennedy, 1971), the shift from a rather abstract "biosphere" system to an (explicit) ecosystemic approach has been somewhat slower to develop. In part, this sloth may relate to the relative detachment of biogeography from process-based and quantitative developments in physical geography from the 1960s (Gregory, 2000). The work of Thornes (1985, 1988, 1990b) in developing the population-modelling approach of May (1975) and applying it to understanding vegetation-erosion dynamics stands out as an early exception. This work notwithstanding, few of the

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J. Wainwright (✉)
Department of Geography, Sheffield Centre for International Drylands Research, University of Sheffield, Sheffield
S10 2TN, UK
e-mail: j.wainwright@sheffield.ac.uk

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papers in the collection edited by Thornes (1990a) go beyond broadly empirical contributions. Despite Stoddart's (1967) early recognition of the importance of the ecosystems concept to the discipline, it was not until the 1980s that a more widespread acceptance developed (Simmons, 1980; but note that only three papers before 1992 in the *Journal of Biogeography* considered ecosystems important enough to mention them in the abstract). The more rapid advances since the 1990s have in part been due to a cross-fertilization of expertise, with the number of (especially landscape) ecologists finding homes in geography departments and carrying out collaborative research increasing significantly.

At the same time, there have been developments leading to the definition of the new field of ecohydrology. Early definitions of ecohydrology (see reviews in Baird, 1999; Kundzewicz, 2002) tended to focus on wetland systems, but from the later 1990s, the utility of linking ecology and hydrology was recognized more broadly. One of the problems with the establishment of ecohydrology has been the difficulty of definition (e.g. the debate in Kundzewicz, 2002; Zalewski, 2002; Nuttle, 2002; Bonell, 2002), which may reflect its immaturity as a scientific approach. Definitions vary from the utilitarian "science which seeks to describe the hydrologic mechanisms that underlie ecological patterns and processes" (Rodriguez-Iturbe, 2000: 3) via the evolutionary engineering approach of Eagleson (2002) to "a more general or "universal" understanding about how environmental systems work . . . combining Newtonian principles of simplification, ideal systems, and predictive understanding (often, but not solely embraced by hydrologists) with Darwinian principles of complexity, contingency, and interdependence (often, but not solely embraced by ecologists)" (Newman et al., 2006: 2). More extreme proponents suggest taking on Gaian principles by considering catchments as "superorganisms" (Zalewski, 2002: 827). Often this work is also framed within an applied (or even [green] engineering) framework, especially in the literature using terms such as hydro-ecology (i.e. the impact of flows on stream ecosystems: e.g. Acreman, 2001) and hydromorphology (which occurs from the late 1980s, predominantly in the applied water management or ecological literatures). This framing may produce problems in the move from more descriptive approaches to ones that are clearly founded in the need to *understand* complex systems and their behaviour. What is clear is that ecohydrology is yet to emerge as an approach that is more than the sum of its parts, but nevertheless, progress will not be made without more explicit linkages at conceptual, methodological and interpretive stages of research.

Conversely, there has been little effort to develop corresponding ideas that might be called "ecogeomorphology". While the collection of papers edited by Viles (1988) is introduced in relation to ecological principles it is clearly largely focused on the more empirical interaction between plants, animals and landforms "to assess what is known about the *biological* component of geomorphology" (*ibid*., p. 3, emphasis added), and ecosystems get nary mention in the main text. For this reason, Viles' term "biogeomorphology" does seem appropriate. The fact that more than just hydrological processes drive landform development in drylands points to the notion that a broader approach than just ecohydrology is necessary. The uneven development of the necessary integrated approaches towards an overarching ecogeomorphology, of which ecohydrology would be part, reflects the more general lack of involvement in interdisciplinary developments such as Earth-System Science (Wainwright, 2009).

Conceptual Framework

Within this chapter, an approach will be taken that integrates both ecohydrological and ecogeomorphological perspectives. It does so in the knowledge that a fully integrated approach is a long way from being developed. In the first part, it concentrates on mechanisms of vegetation adaptations to the extremes of desert environments. The principal purpose here is essentially to answer the question *why* are plants found in deserts? Despite the recent increase in investigations discussed above, there is still a poor level of understanding as to the frequency with which specially adapted plants are found in drylands. The chapter then moves on to the understanding of processes and process interactions with a range of Earth-surface (sub-)systems, in order to evaluate *how* plants are important to the evolution of dryland landforms. At a third level, the chapter evaluates the patterns that emerge both in terms of spatial and temporal distributions of vegetation and in terms of the interrelated distributions of landforms. The aim here is to demonstrate *what* patterns develop and *when*, and in what ways they are important to understanding landscape evolution.

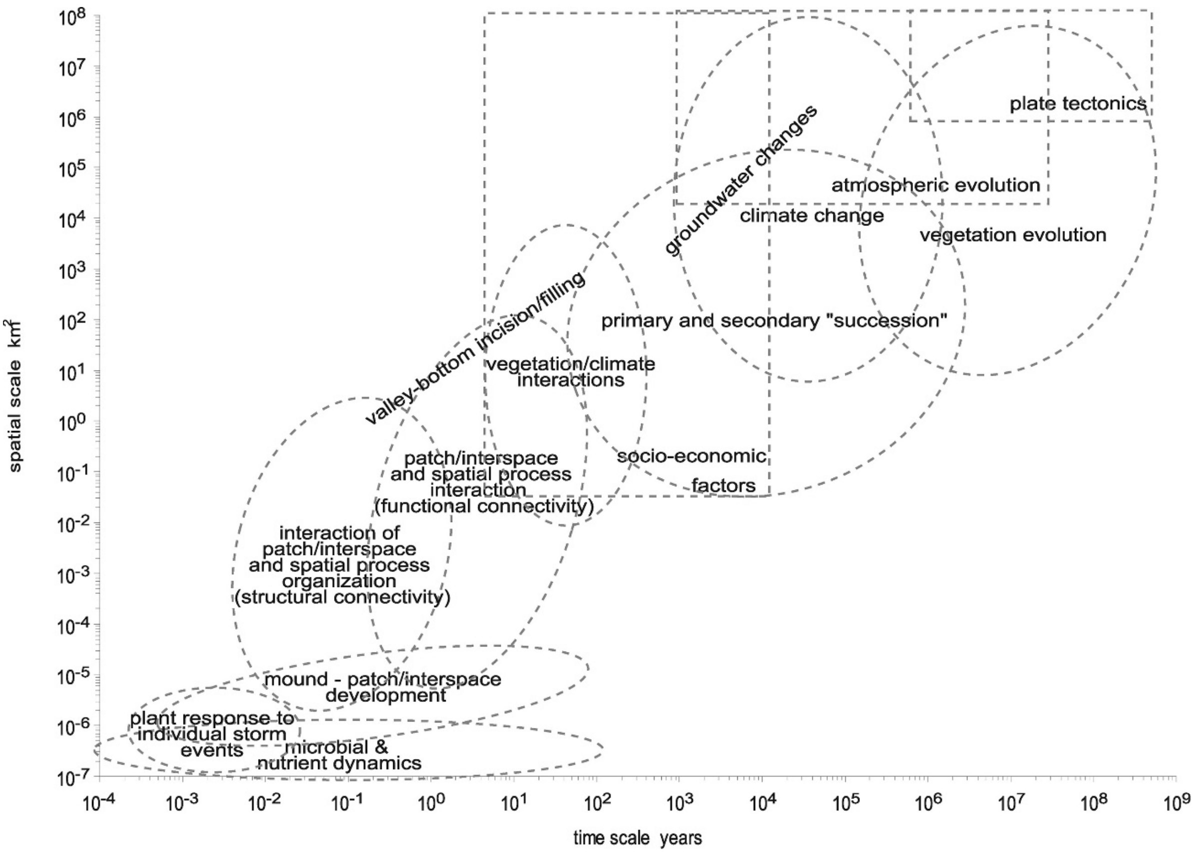


Fig. 3.1 Spatial and temporal scales of interaction of desert vegetation and geomorphic and related processes

Across all these questions, the issue of scale is fundamental. The set of processes driving different aspects of vegetation dynamics operates across many orders of magnitude of both spatial and temporal scale (Fig. 3.1). At the smallest spatial scale, microbial communities have developed and may persist beneath individual stones on the desert surface; much has been made of these lifeforms as potential analogues in the search for life on other planets. At progressively larger scales, it is necessary to understand how individual plants and groups of plants grow within harsh desert environments, and how interactions between them and their environment lead to the development of spatial patterns from hillslope to landscape scales. The evolution of different plant types, with notable stages in the development of land plants and the more recent development and dispersal of grass species, occurs at the largest spatial scale.

Timescales of adaptation are generally positively correlated with spatial scales, albeit with a great deal of fuzziness and overlap. Processes of evolution and climate change are strongly controlled by plate tectonics and the Earth's orbital variation. Climate variability on a range of progressively shorter timescales may affect the patterning on a range of spatial scales, generally with significant connectivity across different scales. For example, extreme storm events may last for a period of tens of minutes or a few hours in many dryland areas, but may significantly disrupt riparian vegetation with spatial effects potentially over hundreds of kilometres and temporal effects lasting for decades. Similarly, disturbance of biological crusts may take decades to recover, with significant feedbacks on dust emissions, atmospheric variability and nutrient cycles. The development of such complex behaviour and responses is an inherent and highly significant component of desert vegetation and thus desert environments as a whole. Explaining the complexity of desert geomorphology within an ecohydrological/ecogeomorphological framework as considered above is thus the aim of this chapter.

Types and Evolution of Desert Plants

Plant Functions and Stresses in Extreme Environments

Given the extremes of both temperature and moisture in desert environments (Noy-Meir, 1973; Cooke et al., 1993; D'Odorico and Porporato, 2006; Thomas, 1997; Wainwright, 2006a; Wainwright et al., 1999a), plants need to develop appropriate coping strategies. Plants interact with their environment in order to extract energy, carbon, water and mineral resources (Fitter and Hay, 1987). Photosynthesis converts solar energy to chemical energy. The radiation-use efficiency (proportion of radiation energy with wavelengths of 400–700 nm that can be stored as chemical energy) of photosynthesis is about 8–10% under ambient CO_2 conditions (Larcher, 1995). To allow CO_2 from the atmosphere to enter the plant so that it can be used in photosynthesis, stomata on the surface of the leaf must open. As water is an important component of the capture of CO_2 by dissolution and subsequent photosynthetic processes, the mesophyll cells immediately below a stoma are typically saturated. This saturation creates a vapour-pressure deficit between the plant and the atmosphere, especially in deserts, where the air is rarely saturated. Water molecules thus diffuse out of the mesophyll cells and into the atmosphere through the open stoma in the process of transpiration (Fitter and Hay, 1987). Transpiration is thus a significant potential problem in drylands because the rate of transpiration is proportional to the vapour-pressure deficit, which is generally high. The loss of water through transpiration also sets up a potential gradient through the plant, and it is this gradient that allows water to be drawn up through the roots, and with it nutrients from the soil. However, given that desert soils are generally dry – in other words at high soil-moisture suctions – the water-potential gradient in the plant must drop sufficiently to allow it to be less than the water potential in the soil. The danger to the plant in so doing is that it can lead to unsustainable water loss, and the development of high internal pressures. In order to avoid the former, roots send chemical signals to the stomata to remain closed when soil-moisture conditions are unfavourable (Tyree, 1999), although this mechanism may not be sufficiently rapid in more extreme conditions, so that some plants can respond to changes in relative humidity surrounding the leaf, or to leaf biochemical processes directly. Transpiration thus causes problems for desert plants in inducing water stress, but it is a necessary evil in that the same process drives the movement of water through the plant, which in turn leads to the transport of photosynthesized sucrose around the plant and thus to growth.

Water stress is thus almost an omnipresent problem for desert plants. According to Fitter and Hay (1987) the consequences of water stress are multiple. As the cell water potential reduces, plant turgor – and thus efficiency of water transport within the plant – decreases until ultimately leaves wilt – and thus become inefficient for transpiration and thus photosynthesis. Extreme and persistent drought can lead to permanent cell damage. Increasing water stress also affects the plant biochemistry and metabolic processes, again making their growth increasingly inefficient.

In hot deserts, plants are also subjected to frequent temperature stress. As well as the heating effect of the ambient temperature, leaves absorb energy during photosynthesis, with pigments such as chlorophyll and xanthophyll absorbing the visible light and leaf water absorbing mid-infrared light. This incoming energy must be balanced by outgoing energy (as long-wave radiation), or the plant will progressively heat up. The resulting temperature stress leads to the breakdown of metabolic processes of photosynthesis, respiration and enzyme activity at temperatures above 45–55°C, even for durations as short as 30 min (Fitter and Hay, 1987). While transpiration is an effective regulator of leaf temperature by changing the microclimate, it is inactive during periods of stomatal closure when plants are water stressed. Radiation is not an effective means of cooling as it is controlled by the ambient temperature, so desert plants must cool themselves either by convection or by metabolic adaptation. Temperature stress can also occur in relation to periods of cold, with freezing conditions occurring often at night during winter months (e.g. Wainwright, 2005), and the limits of a number of desert plants are often discussed in terms of their tolerance of these periods (e.g. Nobel, 1980; Pockman and Sperry 1997; Loik and Redar, 2003).

Plant Responses to Extreme Environments

To survive in deserts, plants must find strategies for adjusting to the consequences of water and/or temperature stress. These strategies can be considered broadly as relating to *avoidance* of the stress or *adaptation* to the stress. Stress avoidance generally entails either spatial or temporal adaptations. Many desert plants have a high concentration of their biomass in the roots, so that it is minimally affected by stress at the surface and can allow the plant to respond rapidly to changes in resource availability. Between 60 and 90% of biomass is concentrated in the roots of desert plants (Fitter and Hay, 1987). The pattern of these roots varies with species, with grasses typically concentrated nearer the surface to take rapid advantage of infrequent rainfall, while shrubs have deeper roots to allow them to take up moisture stored on an interannual basis. Some species such as mesquite and types of acacia have very deep tap roots, with some examples noted as extending several tens of metres below the surface (Gibbens et al., 2005; Fig. 3.2). Plants growing on coastal dunes often increase root-biomass production during periods of burial by sand as an adaptation mechanism (e.g. Maun, 1994; Zhang, 1996; Bach, 1998) and there is some evidence of dryland plants reacting in the same way (e.g. Brown, 1997; Shi et al., 2004; Zhao et al., 2007).

Other direct spatial adaptations relate to the location within the landscape. The riparian zones of channels provide less variable supplies of water than elsewhere, and biomass is often concentrated here. Species such as honey mesquite (*Prosopis glandulosa*), which occur as shrubs elsewhere in the landscape, will commonly exhibit tree phenotypes in these locations. Species such as desert willow (*Chilopsis linearis*) are confined to growth in the riparian zone. Local hollows or depositional environments may also allow plants to avoid water stress by concentrating moisture (and usually other resources). For example, Wainwright et al. (2002) demonstrated that depositional splays or "beads" along small channels in New Mexico were foci for enhanced grass and shrub growth (see also Bull, 1997). Hollows may also occur in joints in rock faces, and the concentration of root biomass often allows desert plants to extract the moisture from relatively deep within them. Rock faces also provide opportunities for shading to avoid heat stress, but there are issues here for C_4 plants (see below), which are adapted to tolerate high temperatures (Table 3.1) but cannot tolerate more than 25% shading. Temporal adaptations may also occur on a range of different scales. Dormancy of seeds is a commonly adopted mechanism, but as Fitter and Hay (1987) point out, this approach can be unreliable in drylands unless the plants also have some means of establishing whether appropriate conditions will be maintained. Some seeds require prolonged hydration while others produce both dormant and non-dormant seeds as a way of overcoming this problem. Venable (2007) has demonstrated that Sonoran winter annuals with the highest degree of dormancy have the highest long-term reproductive success. Short-lived rains in most deserts produce a rapid response of annuals. Senescence is also a useful avoidance mechanism, where a plant drops leaf, and in progressively more extreme conditions shoot, biomass. Some plants may take this approach to the extreme that they appear to have died totally, but they have simply reduced transpirational needs to the absolute minimum, and grow back again from the ample root system once conditions become favourable. To maximize efficiency, dryland plants have developed a range of mechanisms for resorbing nutrients in leaves, and may resorb about 50% of nitrogen and phosphorus before excision (Killingbeck and Whitford, 2001). Some evergreen species are drought-deciduous in a similar way.

Adaptation to stress can occur in a number of ways. Changes to leaf morphology can help this adaptation by a number of mechanisms. Many dryland plants have very small leaves as a means of maximizing convection by reducing boundary-layer resistance and thus minimizing temperature stress. This effect is further emphasized in plants with sparse canopies with non-overlapping leaves. Similarly, thick leaves – as in many succulents – may be an adaptation to temperature stress because the high specific heat of the high leaf-water content minimizes temperature fluctuations (Fitter and Hay, 1987). There may be a further advantage in this approach as it allows the plant to produce more photosynthetic mesophyll for a corresponding transpiring leaf area, and thus be more photosynthetically efficient in limited moisture conditions. Some species increase the cuticular thickness to prevent transcuticular diffusion of moisture, and this can be seen (and felt) in their surface morphology with thick layers of cutin and wax. Others produce hairs on the leaf to increase the boundary-layer thickness and thus increase resistance to loss of moisture. The clustered pattern of leaf hairs in some species acts to restrict gas exchange through stomata. Leaf hairs have been shown to increase plant albedo (Ehleringer, 1980), for example in brittlebush (*Encelia farinosa*) and bursage (*Ambrosia dumosa*), thus reducing temperature stress. In some cases, plants

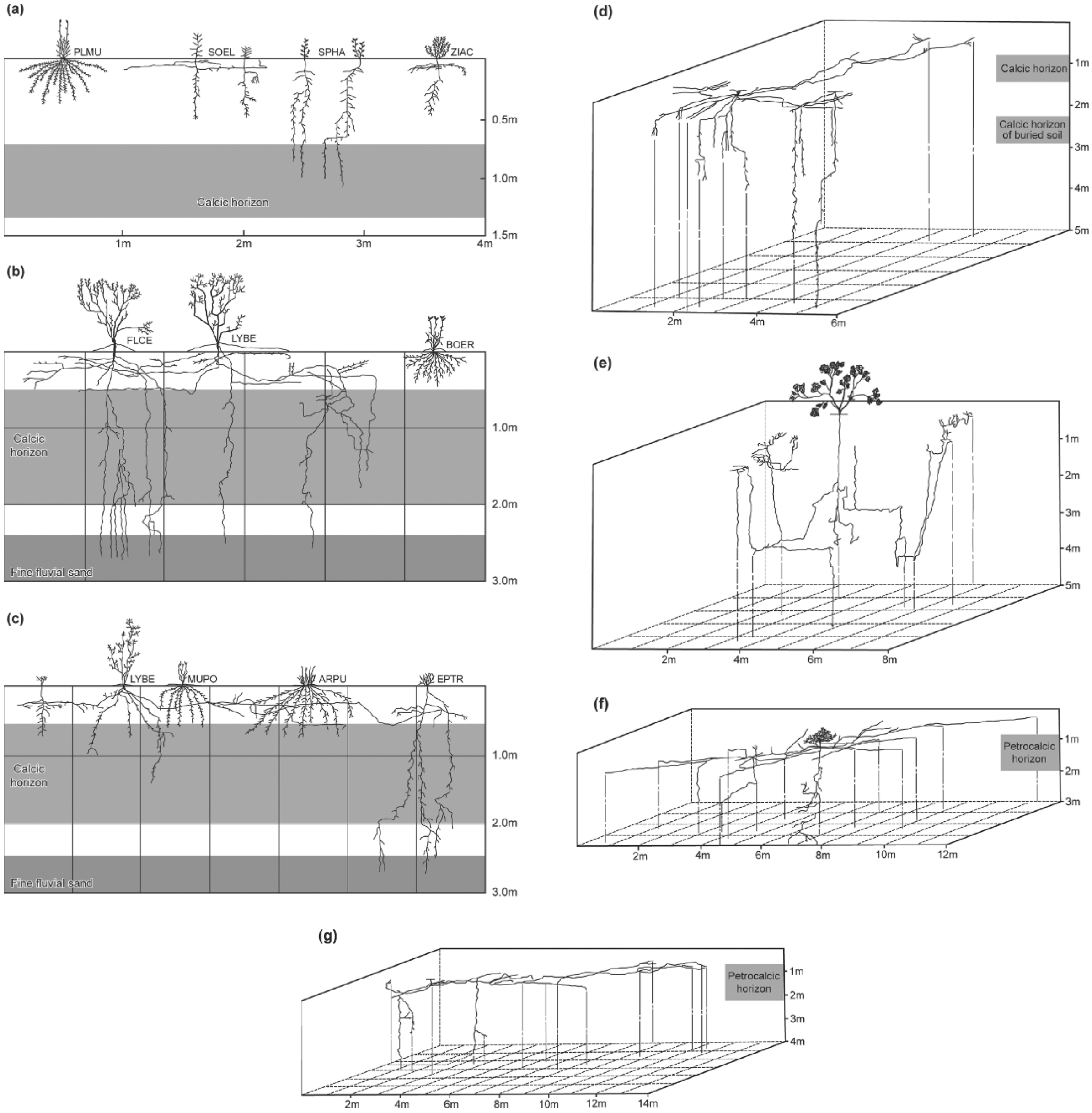


Fig. 3.2 Examples of root distributions for a range of grass, forb and shrub species in the Chihuahuan Desert, New Mexico, USA: (**a**) tobosa grass (PLMU: *Pleuraphis mutica*), and the forbs silverleaf nightshade (SOEL: *Solanum elaeagnifolium*), wrinkled globemallow (SPHA: *Sphaeralcea hastulata*) and desert zinnia (ZIAC: *Zinnia acerosa*) in a fine-loamy, Typic Calciargid; (**b**) tarbush (FLCE: *Flourensia cernua*) and Berlandier's wolfberry (LYBE, *Lycium berlandieri*) shrubs, and black grama grass (BOER, *Bouteloua eriopoda*) growing in a fine-loamy Typic Calciorthid; (**c**) Berlandier's wolfberry shrub (LYBE: *Lycium berlandieri*), bush muhly (MUPO: *Muhlenbergia porteri*) and red threeawn (ARPU: *Aristida purpurea*) bunch grasses, and a longleaf ephedra shrub (EPTR: *Ephedra trifurca*) growing in a fine-loamy, Typic Calciorthid; (**d**) two creosotebush (*Larrea tridentata*) shrubs growing in a fine-loamy, Typic Calciargid (above-ground part of plant not shown); (**e**) large crucifixion thorn (*Koberlinia spinosa*) shrub growing in a fine-silty Ustic Haplocalcid; (**f**) small mesquite (*Prosopis glandulosa*) shrub growing in a coarse-loamy, Argic Petrocalcid; and *g*. four-wing saltbush (*Atriplex canescens*) shrub growing in a coarse, loamy, Argic Petrocalcid. Where the roots end in arrows, they descend deeper but were not followed further (Gibbens and Lenz, 2001)

Table 3.1 Plant characteristics according to different photosynthetic pathways (based on Fitter and Hay, 1987; Larcher, 1999; Long, 1999; Whitford, 2002)

Characteristic	C_3	C_4	CAM
Initial CO_2-fixing enzyme	RuBP carboxylase	PEP carboxylase	RuBP (in light) PEP (in dark)
First product of photosynthesis	C_3 acids (PGA)	C_4 acids (oxaloacetate, malate, aspartate)	PGA (in light) Malate (in dark)
Operating internal CO_2 concentration (ppm)	220–260	100–150	
Photosynthetic rate (mg CO_2 dm^{-2} $leaf^{-1}$ h^{-1})	25	60	3
Water-loss rate (g H_2O g^{-1} C fixed)	650–800	250–350	$\sim$50
Nitrogen-use efficiency (g C fixed g^{-1} N)	53–81	66–130	?
Maximum light-use efficiency (μmol CO_2 mol^{-1})	$53.8 - 1.3\,T + 0.099\,C$[†]	50–70	Similar to C_3[‡]
Optimal temperature (°C)	$\sim$25	$\sim$45	$\sim$35
Light saturation	1/4 full sunlight	>full sunlight	Fixes CO_2 at night
Redistribution of assimilation products	Slow	Rapid	Variable
Dry matter production	Medium	High	Low
Carbon-isotope ratio in photosynthates ($\delta^{13}C$, ‰)	-20 to -40	-10 to -20	-10 to -35

[†] Based on model of Ehleringer et al. (1997): *T* is daytime growing-season temperature (°C) and *C* is atmospheric CO_2 concentration (ppmV).

[‡] Drennan and Nobel (2000).

adapt the growth of different types of leaves at different periods. For example, brittlebush has hairy leaves in the dry part of the year to minimize stresses and less hairy leaves during the rainy season to maximize transpiration and thus potential growth (Ehleringer et al., 1976; Sandquist and Ehleringer, 1998). Creosotebush produces larger leaves in the summer than in response to spring rainfall (Barker et al., 2006), probably relating to the more likely continued availability of moisture through the summer monsoon. Some species such as crucifixion thorn (*Canotia holacantha*) and Mormon tea (*Ephedra spp.*) have evolved to have their photosynthetic tissue in the stems. As well as changes to leaf morphology, leaf angle in the canopy can be an important adaptation. High leaf angles minimize radiation interception and thus the potential for temperature (and thus moisture) stress. In some cases, dynamic changes occur to the leaf shape, particularly the rolling of the leaf to shade stomata in the hotter parts of the day. Leaf angle may also be adjusted dynamically. Paraheliotropic sun tracking involves maintaining the leaves parallel to the sun through the day in order to minimize incident radiation (Ehleringer and Forseth, 1989). Paradoxically, some desert plants exhibit diaheliotropic sun tracking (maintenance of the leaf at right angles to the sun), which has been interpreted as a means of maximizing growth during the short time periods when sufficient moisture is available. Smith et al. (1998) suggest that the ability of plants to track the sun has evolved in parallel with changes in the leaf morphology, so that dryland plants will exhibit a number of the adaptive traits described here (see also Sayed, 1996). Some plants – for example the saltbush (*Atriplex hymenelytra*) – secrete salt onto the leaf surface to increase albedo and thus reflectance of radiation. This mechanism is likely to be more present in halophytes and in particular C_4 plants. Certain plants have modified leaf cells to allow them to absorb moisture from dew or fog, which is a particularly important mechanism in the coastal deserts of southern America and southern Africa, where much of the precipitation occurs in this form. A direct adaptation to moisture stress is to store moisture directly in plant tissues. In some species, this approach is carried out within seeds or tubers, while in others it occurs within the plant as in succulents, cacti and some thick-trunked trees. Succulence is also thought to be a means of adaptation to the high salt conditions found in many drylands (Greenway and Munns, 1980; Gul et al., 2001). Other adaptations to elevated salinity levels are leaf glands that secrete salts and selective uptake of different ions by plant roots (e.g. Arndt et al., 2004).

Photosynthetic Pathways

A more fundamental adaptation of some plants to desert conditions may relate to the photosynthetic pathway used. Until the mid-1960s, it was thought that all plants used the Calvin-Benson cycle to produce carbon from the photosynthetic process (Fig. 3.3a). The output of the Calvin-Benson cycle are molecules with three carbon atoms, hence plants that employ this process alone are called C_3 plants. The C_3 approach to photosynthesis is most effective in relatively high atmospheric CO_2 concentrations and lower temperatures and can tolerate shaded conditions (Table 3.1). However, they are relatively inefficient in their use of water and nutrients, both of which are typically problematic in dryland environments.

An alternative approach to photosynthesis is to divide its operation spatially within the leaf. Plants employing this approach convert incoming CO_2 into aspartate or malate within the mesophyll cell (Fig. 3.3b). These molecules have four carbon atoms, so plants using this pathway are termed C_4 plants. The aspartate or malate is then passed into bundle sheath cells, where the Calvin cycle produces sucrose that can be used by the plant. At least three mechanisms have evolved in different species to accomplish this process (Sage, 2004). Plants with C_4 photosynthesis perform better under conditions of lower CO_2 and higher temperature, and are relatively efficient users of water and nutrients (Table 3.1). Recent confounding results where some C_4 plants perform better under elevated current atmospheric CO_2 may be explained by the elevated CO_2 causing moisture stress to be less significant (Körner, 2006), so the simple explanation that C_3 persistence relates to a climate feedback (Gill et al., 2002; Polley et al., 2002, 2003; Morgan et al., 2004) must be employed with care (see also Hanson et al., 1993; Archer et al., 1995). C_4 plants tolerate shade conditions less well, however. They have also been found to require sodium as a micronutrient (Brownell and Crossland, 1972; Grof et al., 1989), which may be one reason why they are more salt-adapted or tolerate conditions of higher salinity typical of many dryland environments (Fitter and Hay, 1987).

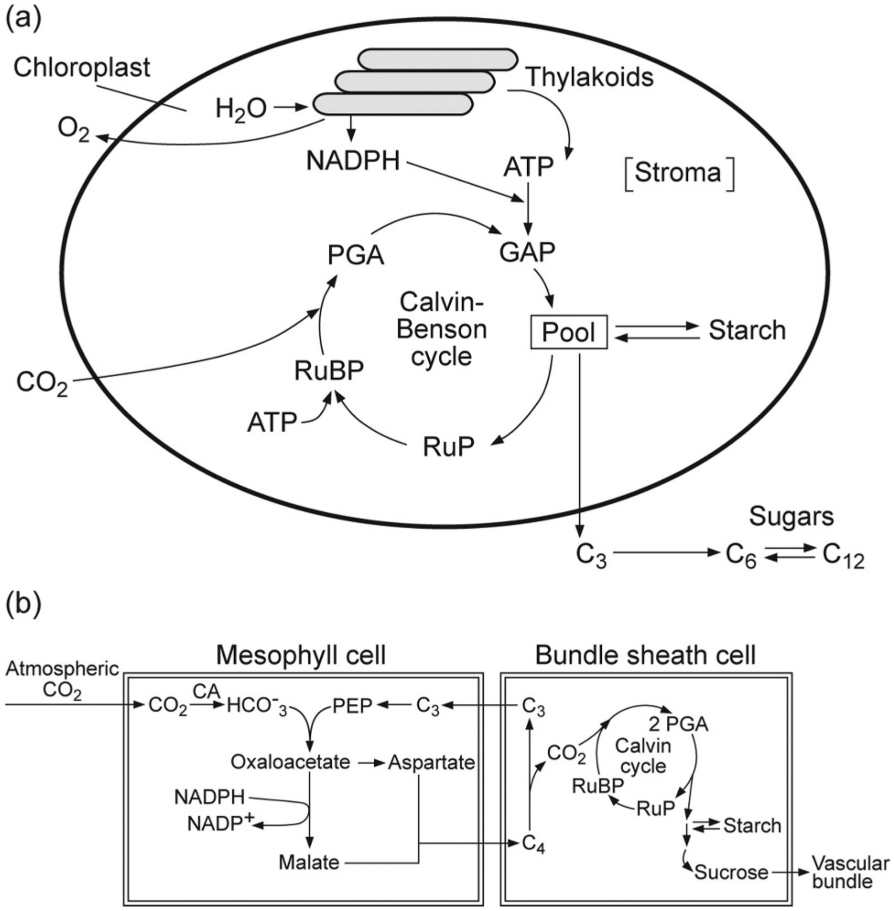


Fig. 3.3 Photosynthetic pathways in plants: (**a**) the Calvin-Benson cycle used by C_3 plants; and (**b**) the two-part approach used by C_4 plants (after Larcher, 1995)

A third photosynthetic pathway is that of crassulacean acid metabolism, or CAM, so-called because it was first observed in plants of the Crassulaceae family. CAM uses a temporal separation of the stages in photosynthesis. With their stomata closed at nighttime to minimize water loss, the process is similar to the C_4 photosynthetic pathway, producing CO_2, which is stored within the leaves of the plant. During the day, this CO_2 is converted to sucrose by means of the Calvin cycle, with a feedback in the process producing the phosphoenolpyruvate required in the nighttime C_4 process. Although the CAM pathway is much more water-efficient than the other two pathways, the complexity of the process means that the photosynthetic rate is comparatively much lower. They have similar temperature and atmospheric CO_2 preferences to C_3 plants (Table 3.1), and indeed many CAM plants revert to C_3 photosynthesis when they are not moisture-stressed.

One further consequence of the different photosynthetic pathways is that they produce different isotopic fractionation. The rubisco enzyme that controls C_3 photosynthesis strongly favours the lighter ^{12}C rather than the ^{13}C isotope, so that it is possible to use $\delta^{13}C$ values to estimate presence of different types of vegetation. C_3 plants have significantly lower values of $\delta^{13}C$ than C_4 plants, with CAM plants having intermediate values (Table 3.1). Thus, analysis of carbon isotopes in soils and fossil materials can be used to evaluate the relative balance of plants with different photosynthetic pathways in the landscape. This approach has been used to document the first appearance of C_4 plants in the Oligocene, and their rapid expansion in many drylands in the later Miocene (8–5 Ma) (Sage, 2004; Osborne and Beerling, 2006; Tipple and Pagani, 2007).

Although plants using CAM are the stereotypical desert plants of cacti and other succulents, the division is not so straightforward, and examples of C_3 and C_4 plants are commonly found in drylands (and some CAM plants are adapted to wetland conditions). Typical examples of C_3 plants include shrub and tree species such as creosotebush (*Larrea tridentata* or *L. divaricata*), mesquite (*Prosopis glandulosa*) in the North American deserts; holm and kermès oak (*Quercus ilex* and *Q. coccifera*), Aleppo pine (*Pinus halepensis*), retama (*Retama spaerocarpa*) and oleander (*Nerium oleander*) in the Mediterranean; acacia (*Acacia spp.*), bushwillow (*Combretum spp.*) and guiera (*Guiera senegalensis*) in Africa; tamarisk (*Tamarix spp.*) in Asia (and subsequently introduced into North America where it has expanded widely); and mulga (*A. aneura*) and poplar box (*Eucalyptus populnea*) in Australia (Fig. 3.4). C_4 plants on the other hand are dominated by grasses such as *Aristida*, *Bouteloua*, *Andropogon* and *Panicum*, as well as herbaceous and shrubby plants (eudicots) such as saltbush (*Atriplex*), hogweed (*Boerhavia*), amaranths, samphires (*Halosarcia*), *Bienertia*, *Blepharis*, *Aerva* and *Zygophyllum*. Sage (2004) defines at least four centres – Mexican, South American, African and Central Asian – where C_4 plants evolved separately, with the possibility of a fifth centre in Australia.

Investigation of the presence of C_4 plants in the geological record has demonstrated that they are a relatively recent adaptation. Although undisputed fossil evidence only extends back to about 12.5 Ma in a sample from California, isotopic evidence (see above) and "molecular clock" techniques suggest that they first emerged between 32 and 25 Ma, probably related to declining global atmospheric CO_2 values (Osborne and Beerling, 2006). It was initially thought that their rapid expansion in the late Miocene (8–5 Ma) was also explained by declining atmospheric CO_2 values, but more recent reviews have demonstrated that this hypothesis is unlikely, not least because CO_2 values slightly increased during this period. Osborne and Beerling (2006) emphasize the importance of disturbance régimes such as herbivory and fire, as well as seasonal drought such as the development of monsoonal systems, with the relative importance of these factors being different in different locations where C_4 plants came to dominate. The development of savannah landscapes in semi-arid areas is intimately related to the development of these climatic and disturbance régimes. It should be noted, therefore, that the relatively recent appearance of C_4 plants means that some caution is necessary in the investigation of some modern desert environments in order to understand the functioning and sedimentology of past (pre-Miocene or in places pre-Oligocene) desert environments. The uniformitarian assessments in so doing will be flawed as the conditions are not equivalent. Similarly, conditions further back in time may vary due to the presence of different plant structures, and pre-Ordovician deserts would have had no land plants (and possibly not until much later, as the earliest land plants have affinities with wet-adapted species: Wellman et al., 2003; although Belnap, 2003, points

Fig. 3.4 (continued)

Fig. 3.4 Examples of dryland plants: (**a**) C_3 trees and shrubs (i. is creosotebush [*Larrea tridentata*]; ii. is detail of the leaves and seeds of a creosotebush; iii. is holm oak [*Quercus ilex*] with a mixed shrub understorey including kermès oak [*Q. coccifera*] in Catalunya; iv. are phreatophytes growing in Tunisia; and v. shows the use of leaf-curling as a stress-avoidance mechanisms in the Sahel); (**b**) C_4 grasses (i. is black grama [*Bouteloua eriopoda*] grassland at Sevilleta, New Mexico in the Chihuahuan Desert; and ii. is a bunchgrass growing on the Kelso Dunes, Mojave Desert); and (**c**) cacti and succulents using the CAM photosynthetic pathway (i. is Mojave yucca or Spanish dagger [*Yucca schidigera*]; ii. is soaptree yucca [*Yucca elata*]; and iii. is prickly pear [*Opuntia spp.*])

to the evidence for microphytes as early as 1,200 Ma, which would probably have had some stabilizing effects – see below).

Plant Interactions

Of course, an ecosystem perspective requires a consideration not only of single plants, but also of interactions between plants. Interactions may include processes of *competition* and of *facilitation*. Competition relates to the ability of different plants (which may be of the same species) to access water, nutrient or light resources, and corresponding strategies that have been developed to adapt to spatial and temporal variability in resources. The conventional view follows Walter (1971), whose two-layer hypothesis suggests shallow-rooting (e.g. <50 cm) grasses and annuals are able to compete more effectively for water following short-lived storm events, whereas shrubs and trees with deeper roots are able to access deeper reserves and thus more reliable water sources in the longer term (see also Reynolds et al., 1999; TM Scanlon et al., 2005). This binary split may not be present in all circumstances, however. Rodriguez et al. (2007) demonstrated that roots of both creosotebush (*Larrea divaricata*) and *Stipa tenuis* grass could occupy the top 50 cm of the soil profile, and suggested the two-layer hypothesis may relate to drylands where rainfall is not seasonally variable. Spatial competition for resources may mean that shrub roots also radiate over larger areas than the canopy (Brisson and Reynolds, 1994), and some authors have suggested that vertical distributions of roots of plants of the same species will often appear very different if the plants are adjacent (Fitter and Hay, 1987). Novoplansky and Goldberg (2001) suggest that processes of competition are complex and poorly understood in general, not least because studies have often focussed on too short a time scale to evaluate their presence or absence.

The "islands of fertility" hypothesis (Garcia-Moya and McKell, 1970; Charley and West, 1975) has been used to explain patchy distributions of desert shrubs (Schlesinger et al., 1990). In this hypothesis, shrub canopies focus water and nutrient resources at their base, which results in a positive feedback for more shrub growth. Away from the shrub canopy, erosion creates conditions where less water infiltrates and nutrients are stripped, thus making the inter-plant locations more extreme and less likely to be colonized. C_4 grasses and annuals are less likely to compete under the canopy of the shrubs due to their relative intolerance to shading. More controversially, some authors have argued for the existence of allelopathy, or the production of chemicals that inhibit or prevent the growth of other plants in the neighbourhood, and in extreme cases kill them. Various phenolic and turpene substances produced by plants have been suggested as playing this rôle. Fitter and Hay (1987) have discussed the difficulties in demonstrating the existence of allelopathy, and in particular that experimental approaches have used plant extracts that are not directly produced by the plant in question. They cite studies of Californian chapparal as being probably the best-documented example (Muller, 1965; 1966), with turpenes produced by shrubs inhibiting the growth of grasses, and thus being a potential explanation for bare areas around the shrubs. Hyder et al. (2002) have suggested that phenolics in all parts of creosotebush plants may be a way of inhibiting herbivory, which has been suggested as being one way in which these C_3 plants can outcompete C_4 plants in the same location (Knipe and Herbel, 1966).

Facilitation between plants may also occur in the "islands of fertility" because of the availability of nutrients and differentiation in root zones. Indeed, taller shrubs have been suggested as having an important "nurse-maid" rôle in the propagation of younger plants, by providing protection from harsh conditions – either from solar radiation or from predators. A similar mechanism for propagation in tiger bush has been proposed (e.g. Lefever and Lejeune, 1997; Lejeune et al., 1999). Haase (2001; Haase et al., 1997) has argued that in Mediterranean environments, plants growing near to *Artemisia*, especially *Anthyllis*, enjoy a nurse-maid effect because *Artemisia* is strongly aromatic in order to discourage grazers. Maestre et al. (2003) have demonstrated that Aleppo pine (*Pinus halepensis*) in Mediterranean settings tends to produce microclimates that favour the germination of a perennial grass understorey, but not that of shrubs – which might subsequently compete with the pine for resources. Recent work has also demonstrated that certain mycorrhizal fungi may have a symbiotic rôle in the propagation and survival of arid region plants. Such fungi are present in both grasses (Barrow et al., 2007) and shrubs (Barrow et al., 1997; Barrow and Aaltonen, 2001). One suggested benefit for the plant is the ability of the fungi to transfer water into the root cells when soil conditions are so dry that the plant would be unable to exert sufficient suction to extract moisture.

The discussion above has tended to focus on individual plants or groups of individuals. In reality, most vegetation communities in drylands contain a mixture of different species, often with different growth forms. In ecosystem terms, these different plants inhabit different niches and provide different functions and habitats within the landscape. There is a tendency to use terms such as “shrubland” or “grassland”, which suggest homogeneity within the landscape. Usually, most shrublands will contain grasses and annuals, and conversely most grasslands will contain scattered shrubs. Only in relatively extreme conditions will monospecific stands be found – e.g. the *Thymnus*-dominated matorral in parts of southern Spain. As well as variability in niches and habitats, most desert vegetation is found in distinctive spatial patterns. The types and mechanisms of formation of these patterns will be discussed in more detail below following a consideration of the impacts of vegetation on geomorphic and related processes within the landscape.

Process Interactions

Climate and Microclimate

Charney (1975) suggested that the presence of vegetation in drylands is strongly coupled to precipitation via feedback with surface albedo. Bare surfaces have a relatively high albedo, producing higher reflection of energy which reinforces the sinking circulation of dry air masses over the continental areas. These dry air masses produce little or no precipitation, and thus surfaces typically support less vegetation. Conversely, vegetation has a higher albedo, producing higher surface heating and thus stronger land-ocean temperature gradients, which in turn enhance monsoonal circulation in the tropics. Enhanced monsoons and rising air masses produce more precipitation, and thus typically more vegetation. Charney thus argued that precipitation-albedo feedbacks operating via the removal of vegetation by grazing would control the pattern of vegetated and unvegetated areas in the Sahel. Numerical modelling of coupled vegetation-atmosphere conditions, with varying degrees of complexity, has tended to support Charney’s hypothesis (Xue and Shukla, 1993; Claussen, 1997; Zeng et al., 1999; Zhou et al., 2007). However, there has been some debate as to whether there are strong correlations between satellite-derived albedo measurements and rainfall over the Sahel, or whether observed albedo changes are as high as those suggested theoretically by Charney (Jackson and Idso, 1975; Wendler and Eaton, 1983). Some authors have used similar hypotheses to posit significant past climate changes as a function of human action. Reale and Dirmeyer (2000; Reale and Shukla, 2000) argued for significant aridification of the northern African climate following Roman deforestation. However, their study implies that there was more extensive forest in the region before this period than was actually the case (see review in Wainwright and Thornes, 2003), and thus probably over-emphasizes the impact.

A further process in the feedback between vegetation and climate that may explain this disparity is that of soil moisture. Entekhabi et al. (1992) suggest that soil moisture as affected by vegetation cover (see below) is likely to have strong feedbacks on regional climate in three ways. First, the inverse relationship between soil-moisture content and albedo changes the radiative régime. Secondly, wetter soils typically have higher values of thermal diffusivity, thermal conductivity and heat capacity, and so more energy is transferred into the soils. Thirdly, soil moisture provides a direct supply of moisture to the atmosphere by evaporation, or an indirect supply via transpiration. Thus there should be a feedback between vegetation cover and precipitation. Entekhabi et al. argue that the longer “memory” of soil-moisture changes would mean that the link between albedo and precipitation would not be as distinct as proposed by critics of the Charney hypothesis. They used a simple atmosphere-hydrology model to demonstrate that patterns of persistent drought could result following large perturbations to the system because of these feedbacks. Scheffer et al. (2005) and Dekker et al. (2007) have taken these studies further by suggesting very local scale feedbacks with vegetation and infiltration, and again supported them with model simulations. Given the speed with which evaporation from bare surfaces in drylands occurs, it is more likely that the deep channelling and reuse of water from depth by transpiration is the source of the longer memory posited by Entekhabi et al. (1992). This effect has been demonstrated experimentally using weighing lysimeters in the Mojave (BR Scanlon et al., 2005a). While such a simple point-feedback with infiltration may be considered to be reasonable, there are a number of reasons as discussed in the following sections why it may not be as straightforward as it first seems.

As well as regional scale feedbacks, vegetation is also important in creating microclimates. Humidity will be elevated around transpiring leaves, but the extent to which this moisture remains local rather than contributing to some of the feedbacks noted above is controlled largely by the dynamics of wind flow and their interaction with the canopy structure, as discussed below. Temperatures under the canopy are lower than elsewhere, and Whitford (2002) notes a moderation of 10–12°C of peak temperatures under surface litter, which is concentrated under the canopy by a variety of processes. Ambient temperatures may be reached between 15–45 cm below the surface, making the area under the canopy a very attractive habitat for animals. Breshears et al. (1998) considered temperature and soil-moisture differences between piñon-juniper canopy and intercanopy areas dominated by blue grama (*Bouteloua gracilis*). They found that canopy temperatures were more moderate, providing protection at the surface both from cold in winter and heat in summer. Evaporation rates were also significantly reduced with the strongest differences seen for the driest initial conditions. Breshears et al. concluded that these microclimatic effects were a strong feedback on germination processes, and particularly enhanced the ability of C_3 plants to germinate in the canopy areas. Similar feedbacks have been observed beneath *Retama* canopies in southern Spain (Moro et al., 1997), for cacti beneath shrubs in the Sonoran Desert (Franco and Nobel, 1989), for savanna in Kenya (Belsky et al., 1989) and in tiger bush (Lefever and Lejeune, 1997) suggesting that it is a widespread feature of dryland systems.

Canopy

Canopy-related processes can thus be considered to be fundamental in the ways that vegetation interacts with climate and thus geomorphic processes in deserts. There is still a tendency to consider aeolian and pluvial/fluvial processes separately, often resulting in different conceptual frameworks. However, this separation belies a number of similarities.

Both wind and water flows can be considered using the same fluid-dynamics framework. The interaction between vegetation and fluid flows produces in general terms a deceleration of the fluid. The extent of this deceleration is called the effect of vegetation roughness on the fluid flow. Vegetation is one of several surface components that make up the total roughness of a surface-flow interaction. The vertical velocity profile of a fluid flow is described by the Prandtl-von Kármán equation, which is also often called the "law of the wall":

$$u\,(z) = \frac{u_*}{\kappa} \ln\left(\frac{z}{z_0}\right) \tag{3.1}$$

where $u(z)$ is the mean fluid velocity [m s^{-1}] at height z [m] above the surface, u_* [m s^{-1}] is shear velocity, κ is the von Kármán coefficient [dimensionless, usually with a value of 0.35–0.45 and thus often incorrectly called a constant], and z_0 [m] is the roughness height. Where the roughness elements are dense, they can absorb the entire momentum of the flow and move the entire wind profile upwards:

$$u\,(z) = \frac{u_*}{\kappa} \ln\left(\frac{z-d}{z_0}\right) \tag{3.2}$$

where d [m] is the displacement height. In theory, the definition of the effects of vegetation on the values of z_0 and d should therefore completely describe the interaction of vegetation and wind or water flow. For wind flows, it is common to estimate the parameters directly by the empirical fitting of vertical wind profiles. Factors affecting the values of the parameters include canopy density (or conversely, porosity), height and volume, and flexibility of stems and branches (Table 3.2).

In practice, there are a number of complications. The work of Wolfe and Nickling (1993), Judd et al. (1996) and Leenders et al. (2007) suggests that for wind flows, these equations are applicable at large scales. At the resolution of a single plant, they break down because of the more complex interactions between the porous vegetation canopy and the wind flow. These interactions can be divided into six zones (Fig. 3.5). In the approach zone, the flow decelerates

Table 3.2 Vegetation controls on wind profiles. Effects of simple and complicated vegetated surfaces on the displacement height (z_0) of the logarithmic wind profile (Equation 3.1) with comparative data for representative, unvegetated desert surfaces

Site description	Mean z_0 (m)	Range of z_0 (m)	Mean vegetation height (m)	Mean vegetation width (m)	Mean spacing between plants (m)	Source
annuals, nebkha, rough interspace	0.0279	0.0166–0.046	0.2–0.45	0.3–0.5	0.5–5	MacKinnon et al. (2004)
creosotebush, annuals, rough interspace	0.0194	0.0089–0.042	0.1–1.7	0.1–2.3	0.5–9.7	MacKinnon et al. (2004)
creosotebush, annuals, rough interspace	0.0054	0.0026–0.0113	0.09–1.3	0.1–2.3	0.75–12	MacKinnon et al. (2004)
succulents, annuals, nebkha	0.0310	0.0194–0.0496	0.4–0.7	0.5–0.71	2.5–2.8	MacKinnon et al. (2004)
creosotebush and borage	0.0266	0.0157–0.0449	0.2–1.3	0.1–1.4	0.2–6.6	MacKinnon et al. (2004)
grass and nebkha	0.0559	0.0335–0.0933	0.5–0.71	0.77–0.77	1.9–1.9	MacKinnon et al. (2004)
creosotebush, bursage, pavement	0.0148	0.0091–0.024	0.01–1.4	0.01–1.9	0.05–9.3	MacKinnon et al. (2004)
shrub, nebkha, salt push–up structures	0.00014	0.000053–0.00039	0.02–0.8	0.1–1.1	0.5–30	MacKinnon et al. (2004)
shrub, nebkha, annuals	0.0178	0.0116–0.0273	0.2–0.55	0.1–0.96	0.5–5	MacKinnon et al. (2004)
creosotebush, other shrubs and nebkha	0.071	0.0468–0.1078	0.6–1.7	0.8–2.6	3–7.5	MacKinnon et al. (2004)
shrubs and nebkha	0.0071	0.00194–0.0115	0.26–0.83	1.5–1.7	5–6.1	MacKinnon et al. (2004)
sparse vegetation	0.0037				(0.04% cover)	Wolfe (1993)
sparse vegetation	0.054				(8% cover)	Wolfe (1993)
sparse vegetation	0.068				(10.3% cover)	Wolfe (1993)
sparse vegetation	0.072				(13.5% cover)	Wolfe (1993)
sparse vegetation	0.083				(26% cover)	Wolfe (1993)
grassland	0.00088					Gillette et al. (1980)
alluvial fan surface	0.00175	0.00076–0.0031				Blumberg and Greeley (1993)
playa		0.000077–0.000166				Blumberg and Greeley (1993)
desert pavement	0.00133					Gillette et al. (1980)
alluvial fan	0.00088					Gillette et al. (1980)
crusted playa	0.00059					Gillette et al. (1980)
playa	0.00083					Gillette et al. (1980)
sand dune	0.00007					Gillette et al. (1980)
bare agricultural field	0.00031					Gillette et al. (1980)

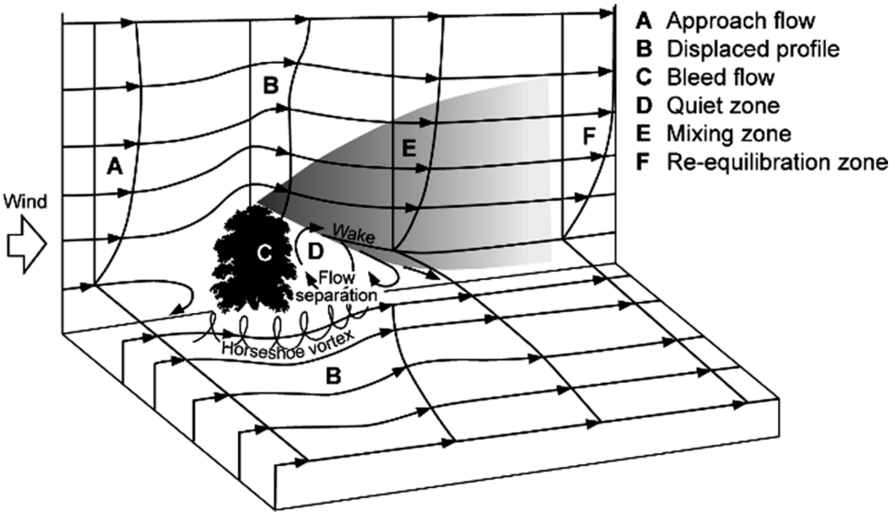


Fig. 3.5 Wind flow around a single vegetation element (based on Wolfe and Nickling, 1993, Judd et al., 1996, and Leenders et al., 2007)

and diverges around the plant. Flow above and to the sides of the plant will accelerate because of streamline compression, while the part of the flow that continues through the plant will decelerate as a function of the canopy density. Downwind, there is a low-velocity zone behind the plant and a mixing zone above, before the flow profile reestablishes itself. Understanding these local variations are thus important in drylands, where vegetation patterns and canopies are sparse.

Leenders et al. (2007) used sonic anemometers positioned around a number of shrub and tree species in Burkina Faso to evaluate the variations. They found that the shrubs had a significant effect in reducing flow velocities near ground level, while single-trunked trees caused acceleration (Fig. 3.6). Deceleration was displaced upwards to heights of $>2\,\text{m}$, relating to the location of the main canopy. Gillette et al. (2006) measured variations in roughness height, z_0, and displacement height, d, around mesquite bushes on nebkhas in New Mexico. They found that d was non-zero for distances between up to five and ten times the vegetation/nebkha height. Beyond this, $d = 0\,\text{m}$ and $z_0 < 0.06\,\text{m}$, so that the vegetation had minimal impact on the wind flow. Within the vegetation canopy, $d > 0.4\,\text{m}$ and $z_0 > 0.06\,\text{m}$, while in the transitional zone they found three different types of intermediate behaviour, depending on whether measurements were taken upwind or downwind, with interference from other plants important in certain wind directions. The roughness parameters thus vary spatially over short scales, and will vary temporally as a function of wind direction.

Morris (1955) defined three categories of flow that allow a distinction to be drawn as to whether vegetation-windflow interaction should be considered at the level of single plants rather than as compound elements. Isolated-roughness flow tends to occur with sparse vegetation cover ($<16\%$) and where the spaces between elements is more than 3.5 times their height (Lee and Soliman, 1977). Wake-interference flow occurs in intermediate conditions so that only the tails of the mixing zones are affected. Skimming flow, where the entire wind profile is displaced upwards, occurs in covers of more than 40%, and where the spacing between roughness elements is less than 2.25 times their height (Fig. 3.7). The greatest protection against wind erosion (see Chapter 17) occurs where skimming flow is developed. Other feedbacks in relation to point-scale changes in aeolian entrainment and the development of fetch effects through areas of interconnected, unvegetated space are dealt with in Chapter 17.

There is a further feedback with climate, in that as vegetation roughness decreases, faster, more turbulent flows occur closer to the surface, which will act to increase evapotranspiration and thus the upward moisture flux. This feedback may be one reason why the vegetation-albedo feedback may not be as strong as first anticipated.

For water flows, the main complication is the fact that except for rare occasions within channels and riparian zones, the vegetation will not be completely inundated by the flow. Water flowing across the surface will interact in the same way with single plants as the wind-flow interaction described above, except for the compression of streamlines above the plant in non-inundated situations. The law of the

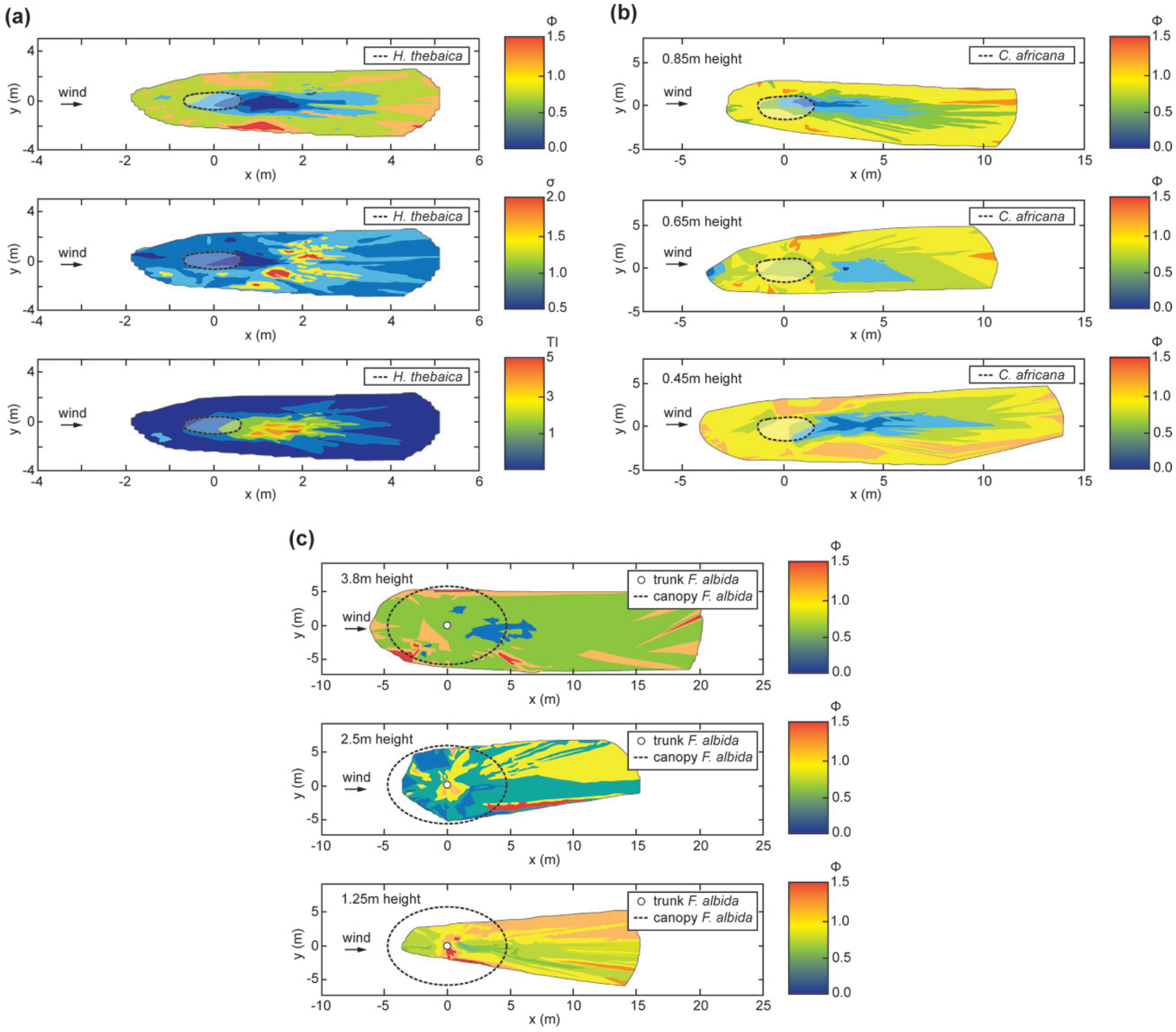


Fig. 3.6 Interactions between wind speeds and vegetation elements for: (**a**) a 0.6-m tall *Hyphaene thebaica* shrub; (**b**) a 1.9-m tall *Commiphora africana* shrub; and (**c**) a 11.5-m tall *Faidherbia albida* tree in Burkina Faso (Leenders et al., 2007)

wall parameters tend not to be fitted in studies of resistance to water flow, not least because of the practical difficulties in measuring velocity profiles that are only a few millimetres deep in unconcentrated overland flows (e.g. Abrahams and Parsons, 1990, 1991; Parsons et al., 1994) to some tens of millimetres in concentrated rill flows (e.g. Parsons and Wainwright, 2006); or due to the equipment damage that may occur in highly turbid, deeper gully and ephemeral channel flows. As an alternative, research has tended to focus on the estimation of flow resistance using the dimensionless Darcy-Weisbach friction factor *ff*:

$$ff = \frac{8\,g\,h\,S}{v^2} \tag{3.3}$$

where g is acceleration due to gravity [$\mathrm{m\,s^{-2}}$], h is flow depth [m], S is surface slope [-] and v is mean flow velocity [$\mathrm{m\,s^{-1}}$] – or dimensionally inaccurate but equivalent equations using Manning's n or Chézy's C parameters as the roughness terms. Abrahams et al. (1988, 1994) demonstrated that *ff* might be a complex function of dimensionless flow discharge (Reynolds number) in shrublands in Arizona due to its interaction with a variety of microtopographic features including vegetation and the mounds on which the

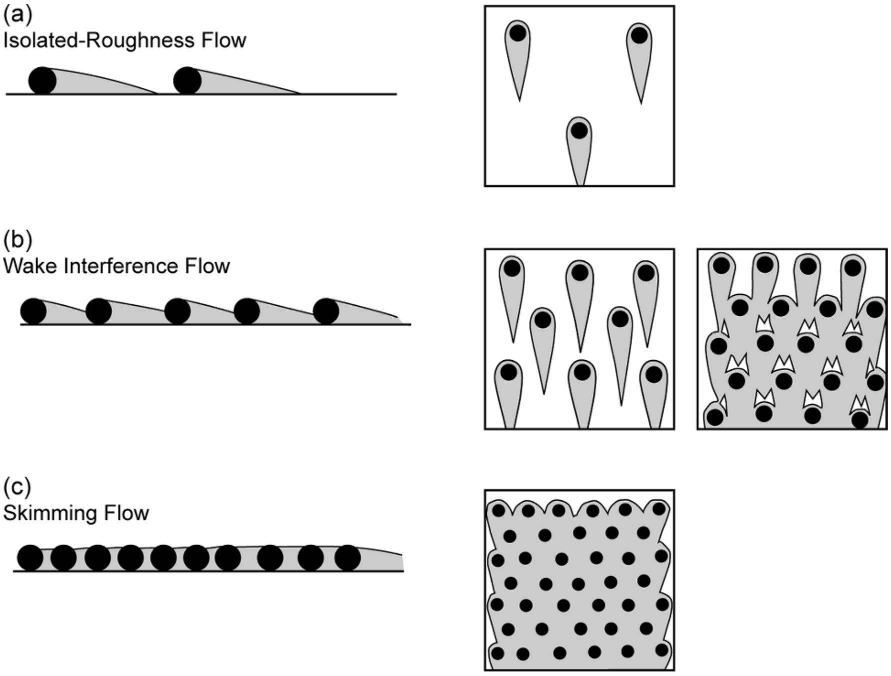


Fig. 3.7 Effects of multiple roughness (vegetation) elements on wind profiles (Wolfe and Nickling, 1993)

vegetation stands. Significantly higher roughness values were found for desert grasslands in the same setting (Weltz et al., 1992; Parsons et al., 1994). This effect is opposite to the one found for resistance to wind flow. In part, this result occurs because the grass is more fully inundated so that it has a greater proportional effect, but also because of other feedbacks imparted by the vegetation. Grasses often cause the formation of tread-and-riser topographies because the higher resistance causes flow deceleration and significant local sediment deposition. These topographies increase the apparent resistance by increasing the flow path length and decreasing the local slope (Parsons et al., 1997). Similar topographies have been described in matorral in Spain (Boer and Puigdefábregas, 2005). Shrubs tend to promote the formation of mounds (see below), which divert flow around them but tend to channel it into deeper, more hydraulically efficient threads. Surfaces dominated by biological crusts (see below) tend to have very low roughness (Belnap et al., 2005), except in cases where the soil surface freezes.

The effects of vegetation on roughness and thus resistance to flow are not independent of other local factors, as noted above. Some authors have attempted to separate the different effects, using the roughness partitioning approach originally due to Schlichtling (1936), which states that different roughness elements have an additive effect to total roughness. For example, in the approach of Weltz et al. (1992):

$$ff_e = ff_{rs} + ff_{rr} + ff_{gc} + ff_{pb} \tag{3.4}$$

where the subscript e denotes the effective total value, and the other subscripts relate to grain roughness, microtopography, surface cover and standing vegetation. This approach is incorporated in the WEPP soil-erosion model. Abrahams et al. (1992) have also developed a similar analysis for overland flows, and it has been widely used in wind-erosion studies (e.g. Marshall, 1971; Gillette and Stockton, 1989; Lancaster and Baas, 1998; Crawley and Nickling, 2003). In the Weltz et al. approach, vegetation would have a direct effect on resistance through the ff_{pb} term, and indirect effects through ff_{rs} by the effects on grain size (e.g. relating to differential erosion processes as discussed by Parsons et al., 1992), ff_{rr} by changing the local topography (e.g. the tread-and-riser or mound forms described above) and ff_{gc} by changing stone cover (e.g. the inverse relationship described by Scoging et al., 1992 resulting in pavement formation as discussed by Wainwright et al., 1995, 1999b) and concentrations of surface litter. An implication of the Schlichtling approach is that it suggests shear stress should also be linearly separable in the same way. A complication that this relationship produces is that it implies that shear velocity, u_*, is not independent of roughness height, z_0, in equations (3.1) and (3.2). Other implications of the approach are discussed by Crawley and Nickling (2003).

The canopy also interacts with the environment by processes of interception. In the case of wind flow, interception is of dust and other particles (e.g. pollen and more recently, anthropic pollutants) that are deposited on the canopy. Dust may contain important nutrients that can be transported to the soil by leafdrip or stemflow or fixed by symbiotic fungi, and thus become available to plants. Dust deposition usually provides a net input of nitrogen to the desert ecosystem in this way (Schlesinger et al., 2000; Baez et al., 2007), and the deposited dust is a significant soil-forming material in a number of environments (e.g. McFadden et al., 1987; Yaalon, 1997). Dust may travel for significant distances while gradually settling through the atmosphere (Chapter 20). Vegetation is likely to be a significant location for dust deposition, because the flow resistance slows the wind flow and thus increases the rate of settling, especially in the slower-flowing areas immediately upwind and in the lee of individual plants. In general, the greater the resistance, the more deposition will occur, and this may be enhanced by the waxy nature of the leaves, and conditions where the leaves have been wetted by prior rainfall, dew or fog, or in conditions where salts are deposited on the surface – either by the plant itself, or due to its location (Grantz et al., 2003). Dust deposition on the plant surface can also cause negative effects, for example by reducing photosynthesis, by causing abrasion and damaging plant tissue, and by increasing the albedo of the surface. Recent studies have also demonstrated the potential effects of nitrogen toxicity in areas of elevated deposition, for example downwind of industrial areas (Clark and Tilman, 2008) and the strong co-limitation of productivity by nitrogen and water availability (Hooper and Johnson, 1999).

Interception of water occurs during rainfall events as water lands on leaves and branches during storm events. Martinez-Meza and Whitford (1996) estimated that interception by creosotebush was 44% of rainfall on average, compared to 42–47% for tarbush and 36–38% for mesquite, albeit with significant seasonal variability. The remaining rain passes through the canopy as throughfall and hits the ground directly. Some intercepted water remains on the canopy and is subsequently lost by evaporation. Experiments by Abrahams et al. (2003) suggest that canopy storage is small in desert shrubs, and even mature creosotebush (1.29–1.9-m tall with diameters of 1.37–2.50 m) may only store <5 mm of rain in this way. A similar amount was found for juniper (*Juniperus ashei*) in Texas (Owens et al., 2005). The remaining water reaches the ground by one of two pathways. First, water accumulating on leaves produces drops that are big enough to exceed the storage capacity of the leaf and/or associated surface tension, and falls to the ground (or is reintercepted in more dense canopies). Depending on the shape and structure of the leaves, these drops may be larger than the raindrops formed even in intense storms, and their effect on impact will be a function of their velocity as controlled by fall height. Brandt (1989) demonstrated that tall canopies can produce drops approaching terminal velocity, which are thus more erosive than the smaller raindrops. In drylands, this situation may occur in savannah where there are isolated trees with little understorey. For shrubs, Wainwright et al. (1999c) demonstrated that despite the sparse canopies of creosotebush, there was a 30% reduction in total kinetic energy beneath the plant, although this figure is dominated by throughfall drops that do not interact with the canopy. The kinetic energy of leafdrip was estimated as only 6% of the incoming rainfall energy. Leafdrip had a smaller drop size than the rainfall, which is probably a function of the small leaf size in creosotebush.

The second pathway is by stemflow. It has typically been assumed that water flowing along stems and infiltrating into the crowns of shrubs is a significant water supply. Martinez-Meza and Whitford (1996) estimated values of 10% of rainfall in creosotebush and tarbush and 5% in mesquite entered the ground in this way. However, Abrahams et al. (2003) subsequently demonstrated that the value for creosotebush was probably only 6.7% on average, because some of the water runs off across the surface, especially given the high rates of throughfall also reaching the ground. Runoff generated from stemflow was only moderated or eliminated where there was a significant understorey (usually of muhly grass [*Muhlenbergia porteri*]). Owens et al. (2006) found only 5% of rainfall on juniper in Texas was converted into stemflow. Stemflow may be more important in some other environments. For example values as high as 42% have been observed in acacia and eucalyptus shrubs in Australia (Pressland, 1973; Nulsen et al., 1986).

As well as interception of rainfall, interception of dew and fog by desert plants can also have a significant impact on the water budget. In hyperarid areas such as the Atacama, the presence of fog is directly related to that of lichens, in areas otherwise devoid of vegetation (Warren-Rhodes et al., 2007). Lange et al. (2006) found that maximum rates of photosynthesis in epilithic lichens in the Namib Desert coincided with peaks in fog formation in spring. Epiphytic lichens also occur in the Namib, taking in moisture at night and having short bursts of photosynthetic activity shortly after sunrise (Lange et al., 2007). There seems to be little information about whether these lichens modify the microclimate sufficiently to benefit the host plant. Days with fog in the Namib can produce 0.5–2.3 mm day^{-1}, which can be an important source where 60–200 days per year are foggy (Shanyengana et al., 2002). Kidron (2005) demonstrated that interception of both fog and dew in the Negev was inversely related to the angle of the receiving surface. Dew was measured as producing 0.12–0.28 mm day^{-1} on average in the Negev (Kidron, 2000). Malek et al. (1999) measured dew deposition of 13 mm a^{-1} in semi-arid shrubland in the Great Basin. The recent review of Agam and Berliner (2006) suggests that adsorption of soil-water vapour may be a more important process than fog or dew interception in these extreme environments. Ramírez et al. (2007) have also suggested the existence of this process in Mediterranean Spain in an area with a mean annual rainfall of 291 mm.

As noted several times already, one indirect consequence of the presence of the vegetation canopy is the development of mounds. In areas with actively blowing sand, the vegetation canopy decelerates the wind to cause deposition in streamlined forms known as nebkha (pl. nebkhat), which may be up to 25-m long and 5-m high (Fig. 3.8). Although a variety of

Fig. 3.8 Nebkha dunes in: (**a**) Tunisia (looking upwind – the nebkha in the foreground is approximately 1-m tall (cf. Fig. 3.9); (**b**) the Chihuahuan Desert around mesquite plants (the nebkha in the centre is about 1.5-m tall and 3.5-m in diameter – note also the evidence of fluvial activity in this landscape in the form of the rill running to the left of this nebkha and towards the bottom left of the image); and (**c**) miniature nebkhas formed behind grass clumps in the Mojave (lens cap is 55 mm in diameter)

names has appeared in the literature, such as coppice dune, phytogenic mound, kthib, rebdou or rehboub, convergence on the widely used “nebkha” seems preferred (see Cooke et al., 1993: 356 for yet further alternatives). Tengberg and Chen (1998) studied fields of nebkhat around *Ziziphus lotus* in Tunisia and *Acacia sp.* and *Balanites aegyptiaca* in Burkino Faso and found that dune height correlated well with dune length up to a threshold length then, for further increases in length, the relationship broke down (Fig. 3.9). This pattern was interpreted as being the result of three phases of development. In the growth phase, the dune height can keep growing until it reaches the threshold height defined by the point at which the wind profile is sufficiently fast to reentrain sediment. At this point, the dune enters a stabilization phase, where it may grow in length by trapping progressively more sediment, but cannot increase in height. The third, degradation phase occurs when sediment supply drops sufficiently for the wind to restart entrainment, and may occur because of changes in the surrounding supply area or due to interactions between the nebkhat themselves. Nebkha dunes have been recorded in a wide range of other desert settings in the US (Gibbens et al., 1983; Langford, 2000), Africa (Nickling and Wolfe, 1994; Dougill and Thomas, 2002), the Middle East (El Bana et al. 2003; Pease and Tchakerian, 2002; Saqqa and Altallah, 2004), China (Wang et al., 2006) and Australia (Hesp, 1979, 1989 cited in Cooke et al., 1993; Ash and Wasson, 1983). Parsons et al. (2003) noted that nebkhat provide a further strong feedback controlling runoff and fluvial erosion processes in mesquite nebkhat in the US southwest.

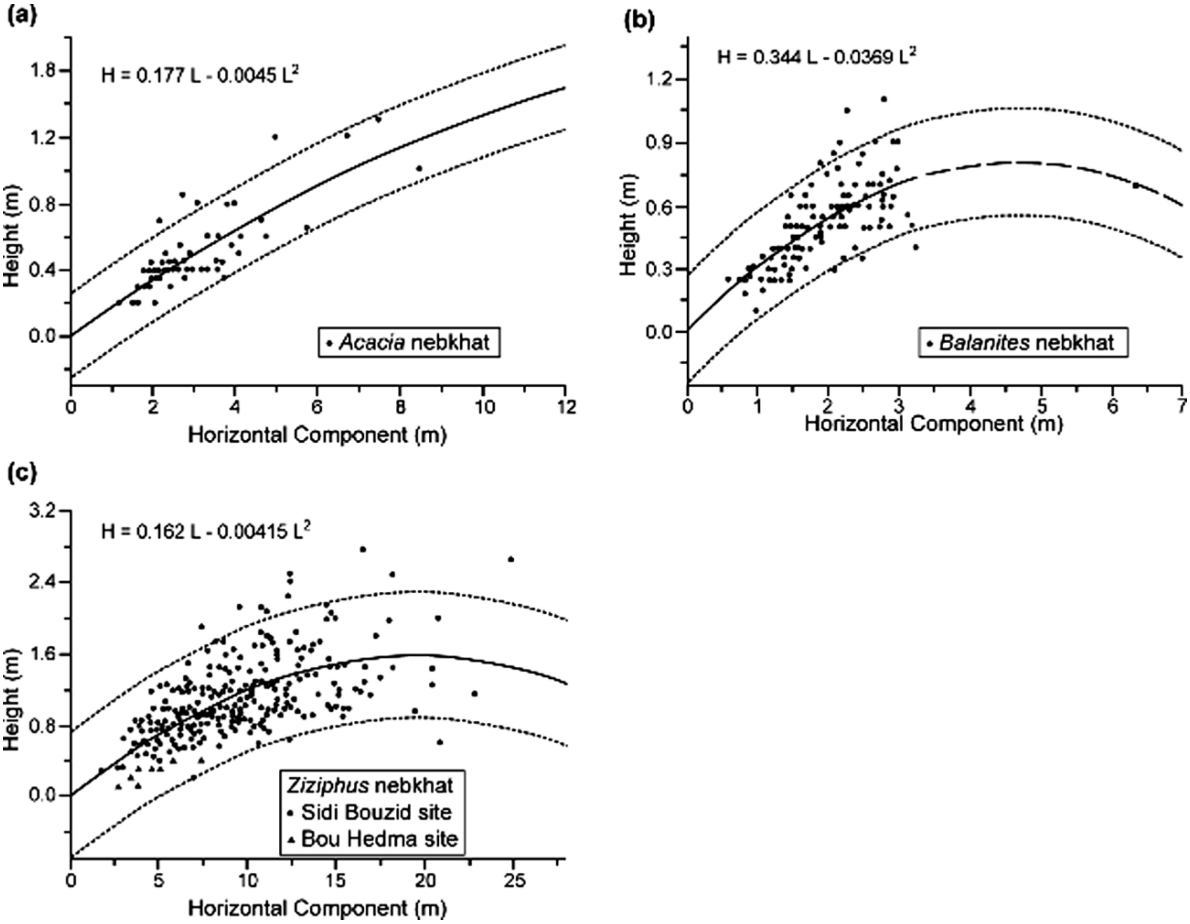


Fig. 3.9 Length-height relationships measured by Tengberg and Chen (1998) for nebkha dunes formed around *Acacia* and *Balanites* shrubs in Tunisia and Burkina Faso

As well as a response to aeolian deposition of sediment (e.g. Cooke et al., 1993), there are a number of hypotheses as to how mounds form in relation to the presence of vegetation. Rostagno and del Valle (1988) suggested that the mounds are upstanding remnants following erosion of the intershrub areas by overland-flow erosion. In the Negev, Shachack and Lovett (1998) found no significant difference in atmospheric dust deposition between shrub mounds and adjacent crust areas. Thus dust is part of the sediment source, but the mounds are due to subsequent redistribution of this material. Parsons et al. (1992) demonstrated a similar mechanism of erosion and deposition based on differential splash (Carson and Kirkby, 1972: 189), while Wainwright et al. (1995) supported this mechanism further, as well as its interaction with erosion related to unconcentrated overland flow. Pelletier et al. (2007) have more recently criticized this explanation for the formation of desert pavements and associated shrub mounds in the US southwest, preferring the aeolian deposition hypothesis for the formation of pavements. However, their hypothesis is unable to explain the presence of mounds or the development of pavements where dust deposition is shown to be negligible (Wainwright et al., 1999b), and lacks an independent demonstration of the process in operation. Biot (1990) also suggested that mounds could form in areas where plant roots and rates of termite digging are high, while Neave and Abrahams (2001) also emphasize the rôle of other animals. It is therefore likely that the interaction of several processes is likely to be important in the formation of mounds beneath vegetation.

Vegetation mounds have become central to the understanding of the functioning of dryland environments over the last three decades as part of the concept of "islands of fertility"; the vegetation canopy is critical in modifying processes to mitigate stresses on plant and animal life in dryland environments. A further interaction with the canopy and the development of islands of fertility is by the production of leaf and other litter. Whitford (2002) notes that litter-decomposition rates tend to be high in drylands due to the high temperatures and ultraviolet radiation present. Intermittent, often intense, rainfall can also contribute by the mechanical breakdown of litter fragments. Annual rates of litter mass loss may vary from 31% to 93%.

The canopy is also critical in a further process in most drylands – that of wildfire. As noted previously, it is thought that the evolution of C_4 grasses was favoured by drying climates during the Miocene. Many drylands – especially the savannah and grassland landscapes – would not exist in their present form without the presence of fire. In the US southwest, McPherson (1999) has suggested that woody plants tend not to occur in areas with annual fires, while they may occur in a scattered way if burning has not occurred for a period of 5–10 years. Only where fire has not recurred for more than 20 years are shrub communities able to persist. Drewa and Havstad (2001), however, suggested that the pattern was not necessarily so straightforward, and that it depends on the interactions between fire and other processes such as drought and grazing by large herbivores. Other drylands have C_3 species that have specially adapted, for example by resprouting from the trunk or having fire-adapted seeds, seen in Mediterranean trees such as holm oak (*Quercus ilex*) or aleppo pine (*Pinus halepensis*), respectively. Fire can have important impacts in changing the surface hydrology, in nutrient budgets, and on erosion and sedimentation patterns (see review in Wainwright and Thornes, 2003). The exact nature of fire occurrence in a particular location will depend on the vegetation state, especially the amount of combustible material, its moisture content and the connectivity of the canopy, as well as the weather (wind speed, temperature and relative humidity) and topography (local aspect and slope) (McPherson, 1995). Fire frequencies tend to demonstrate power-law scaling (Malamud et al., 2005), so that small fires are relatively frequent and very large fires infrequent, with important feedbacks for the connectivity of the system (Fig. 3.10).

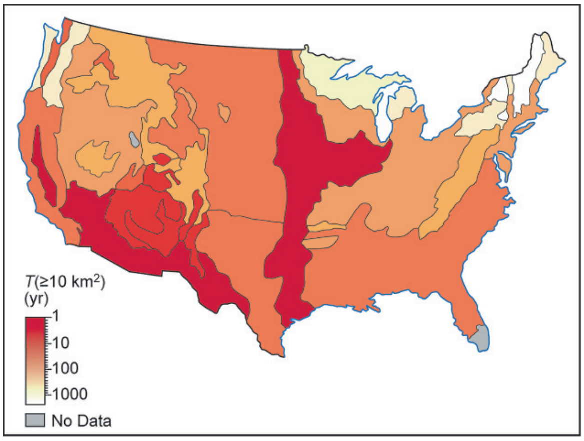


Fig. 3.10 Recurrence intervals mapped by ecoregion for the coterminous United States (Malamud et al., 2005)

Roots

Martinez-Meza and Whitford (1996) used dye-tracing experiments on mesquite, tarbush and creosotebush to demonstrate that water from stemflow is typically channelled along the roots of the shrub to depth, where it is available in periods of drought. The same process has been observed by Wang et al. (2007) for *Artemisia ordosica* and *Caragana korshinskii* shrubs in China, and in *Artemisia tridentata* (big sagebrush) in the US by Ryel et al. (2003; 2004). Decaying and decayed roots can also increase infiltration amount and depth. Devitt and Smith (2002) demonstrated using dye-tracing that plots where creosotebush plants had previously been located produced decaying root pathways that allowed water to reach a depth of more than 40 cm, compared to plots without these pathways where infiltration did not reach a depth of 20 cm. These preferential pathways for water flow may thus persist for significant periods, even once vegetation has been removed or died off, and thus may explain sources of variability in observed infiltration rates and consequently why surface properties are not always a good indicator of variability in infiltration (Wainwright et al., 2000). As well as leading to the development of such macropores, root decomposition also affects soil texture and porosity. Whitford et al. (1988) have demonstrated that roots in desert ecosystems tend to decay more rapidly than in other environments. The rate of decay was found to be highly correlated to the extent of termite colonization, and seems relatively independent of additional moisture supplies. The presence of termites will also enhance the porosity and macroporosity of the soil, providing a further feedback to higher infiltration rates. Decaying organic matter will also provide binding materials leading to the development of soil aggregates with similar consequences. Decomposition does also produce a range of non-water-soluble compounds, and these may be significant in dryland vegetation. The presence of such phenolic, turpene and related compounds may be to increase soil hydrophobicity, and thus lead to a decrease in infiltration rates. It should be remembered that these processes relating to decomposition may occur even if the main plant still survives, as parts of the plant biomass may senesce as a response to drought conditions, or die off due to predation by animals. Whitford (2002) points out that root decomposition is the principal carbon source in desert soils. However, the link between this decomposition and reconstruction of past environments using soil-carbon isotopic composition (see above) is probably complicated by other processes including erosion (Turnbull et al., 2008a).

Roots also have a very high strength and can often penetrate along narrow fissures in bedrock to exploit water resources. Opening up of the fissures in this way provides a further feedback to infiltration, possibly to depth, and in the formation of soils. However, most literature suggests that roots have a very limited ability to penetrate through calcic and petrocalcic horizons (Chapters 5 and 6), resulting in limitations to water availability and consequently plant growth. These limitations affect shrubs (Cunningham and Burk, 1973; Hamerlynck et al., 2002), grasses (McAuliffe, 1995) and succulants (Escoto-Rodríguez and Bullock, 2002) alike (Gibbens and Lenz, 2001; Gibbens et al., 2005). Plant-available water contents have been measured to be higher in petrocalcic horizons than the overlying soils (Duniway et al., 2007) and the structure of the horizons loses strength when wetted (Larsen, *pers. comm.*), so it may be that the explanation for this lack of penetration is more a function of soil chemistry. Buxbaum and Vanderbilt (2007) have related the limitations of vegetation growth to the limitations imposed on the plant due to the high osmotic potential of $CaCO_3$-saturated water. However, this explanation cannot be complete because, as Buxbaum and Vanderbilt themselves point out, creosotebush is more tolerant to these higher potentials than grasses and yet creosotebushes are commonly constrained to a fraction of their potential size above shallow petrocalcic horizons.

Roots affect the vertical flow of water towards the surface as well as away from it. Hydraulic lift occurs when there is a sufficiently high hydraulic conductivity between the soil and root pores to enable flow into plant roots. The phenomenon can only occur if there is sufficient water stored in the soil to produce a hydraulic gradient from the soil to the root during conditions when the plant is not transpiring (and thus generating the gradient by this means). Water then flows upwards through the roots until it reaches levels where the surrounding soil is sufficiently dry to cause a reverse hydraulic gradient, and the water flows out into this soil, where it is available to this and other plants during normal transpiration-driven metabolism.

The process was first observed in big sagebrush shrubs (Richards and Caldwell, 1987), and has been subsequently documented in species of all photosynthetic pathways. Yoder and Nowak (1999) demonstrated its occurrence in C_3 plants with deep (creosotebush), intermediate (*Ephedra nevadensis* [Mormon tea]) and shallow (*Ambrosia dumosa* [white bursage]) roots, as well as the CAM *Yucca schidigera* and the C_4 perennial grass *Achnatherum hymenoides*. While hydraulic lift occurs during the night for the C_3 and C_4 plants, it occurs during the day for the CAM plants in relation to the relative timing of transpiration. However, there is also increasing evidence that some transpiration occurs at night in both C_3 and C_4 plants due to incomplete stomatal closure (and thus conductance of water from the plant) (Caird et al., 2007) and that the conductance mechanism occurs in parallel with hydraulic lift. Snyder et al. (2008) have suggested that night-time transpiration may be a response to nutrient limitation.

Deeper water flow into the vadose zone is heavily restricted if not absent in drylands. Although roots act to channel water to depth, most of this water does not travel beyond the root zone (Walvoord and Phillips, 2004) and is indeed used by plants at a later stage by the mechanisms outlined above. Sandvig and Phillips (2006) cored sites across a vegetation transect in the Sevilleta National Wildlife Reserve in order to evaluate potential water flux. The transect covered creosotebush (1,470–1,590 m asl, mean annual temperature 12.8–13.3°C, mean annual precipitation 230–235 mm), mixed grassland (*Bouteloua gracilis*, *B. eriopoda*, *Muhlenbergia porteri* and *Hilaria mutica* at 1,560–1,900 m asl, 12.0–12.8°C, 230–306 mm), juniper woodland (*Juniperus monosperma*, 1,930–2,050 m asl, 11.5–12.1°C, 306–316 mm) and ponderosa pine forest (2,300–2,380 m asl, 9.2–9.5°C, 327–336 mm). Preferential flow paths were suggested for the juniper and pine sites, usually below a depth of several metres. Limited preferential flow paths were found in the grassland, but none was apparent below about 0.5 m in creosotebush. The chloride mass-balance approach was used to estimate recharge rates. No recharge was found to have occurred beneath the creosotebush sites since 22.0±2.9 ka. Complete flushing of the grassland site soil moisture has probably not occurred for 10.0±1.5 ka, although a slow recharge rate of $0.069\pm0.020\,\text{mm a}^{-1}$ was measured. Turnover of soil moisture under juniper took place since 5.9±1.9 ka with estimated recharge of $0.439\pm0.430\,\text{mm a}^{-1}$, while under ponderosa pine the turnover varied between 300 a and 3.6 ka and estimated recharge was $2.26\pm2.89\,\text{mm a}^{-1}$. While some caution must be expressed in interpreting these differences (the creosotebush is likely to have been much less extensive prior to European settlement; there are large uncertainties due to small sample sizes), the overall recharge rates under present conditions are probably $<1\%$ of precipitation, with most of this recharge coming from upland, wooded areas. Studies using weighing lysimeters with creosotebush vegetation and unvegetated lysimeters in the Mojave Desert found that even during wet periods (El Niño-related winter rainfalls) the creosotebush was very effective in using water that had percolated to depth (1.7 m) (BR Scanlon et al., 2005a). The evaporation from the unvegetated sites was unable on its own to remove all the water at this depth, and thus some deeper percolation could be expected from bare surfaces. Such bare surfaces would be limited for example to cultivated areas in reality, as the root distributions often extend well beyond the canopy into areas with a bare surface, as noted previously. Scanlon et al. interpreted these results as being consistent with chloride-based estimates that no recharge has occurred for the last 10–15 ka. A similar change was demonstrated by Wang et al. (2004) using vegetated and unvegetated weighing lysimeters under *Caragana korshinskii* shrubland in the Tengger Desert in China.

When indigenous vegetation was replaced by irrigation agriculture in the Amargosa Desert and High Plains, recharge occurred once the combined precipitation and applied irrigation water exceeded about 800 mm (BR Scanlon et al., 2005b). Such rates are however clearly unsustainable over broad areas. Seyfried and Wilcox (2006) reviewed the suggestions that removing woody (shrub) vegetation in drylands would lead to increased recharge and streamflow, given that the current literature has broadly varying interpretations of the consequences. By monitoring soil moisture post-fire at Reynolds Creek in Idaho (550 mm annual precipitation), they found that water uptake was much lower beyond depths of about 1 m, suggesting higher potential for recharge under the burnt areas. They suggest that the critical factor leading to a change in recharge under these circumstances is the extent to which the profile can store plant-available moisture. The change in availability is likely to be a complex function of local conditions. In more arid cases, the ability of precipitation to wet the whole profile will also limit the conditions for recharge to occur. Seyfried et al. (2005) carried out a review a model analysis of recharge in the US deserts since the late Pleistocene. They suggest that slow recharge may still be taking place below depths of about 20 m, representing water that infiltrated over 10,000 years ago. Above this zone is a general area of net upward flux (Fig. 3.11).

While recharge from much of the surface area of drylands is negligible at best, the same is not necessarily true of channels and the riparian zone. Riparian vegetation is generally well developed in drylands as the area surrounding the channel is well supplied by water, if only intermittently. The high porosity of many channel-bed materials also enhances infiltration through transmission losses, often by an order of magnitude compared to surrounding areas (see Chapter 11). Atchley et al. (1999) investigated differences in soil water and nutrients and photosynthetic and transpiration rates in *Fallugia paradoxa* (Apache plume), *Prosopis glandulosa* (honey mesquite) both of which grow in the riparian zone and elsewhere, with *Chilopsis linearis* (desert willow), which is an obligate riparian shrub. They found that patterns were highly variable both between and within sites, not least because of the highly variable spatial response to convective storm events. In some locations, the multi-stemmed structure of the Apache plume was able to trap more nutrients and thus not be nutrient-limited. The relative location of the vegetation to rapid flow (straight channel sections) seemed to control the ability of the plant to act in this way via a feedback in the resistance to flow imparted by the vegetation canopy. Mesquite is able to exploit the moisture stored beneath the channel more effectively, and thus transpires more rapidly than mesquite growing away from the arroyos. The desert willow adjusted its transpiration in order to minimize water needs in periods when water was sparse. De Soyza et al. (2004) found this response to be the case even in conditions of extreme drought. At the end of drought conditions, all of the species observed responded quickly. The relative importance of recharge along arroyos will thus relate to the extent to which the additional vegetation and rapid response can increase transpiration rates relative to water supply. Scott et al. (2006) investigated transpiration rates of grassland, shrubland and wooded habitats on terraces of the San Pedro river in Arizona. They found that over a single growing season where precipitation was 233 mm, total evapotranspiration was 407, 639 and 450 mm, respectively (Fig. 3.12). In other words, groundwater use was 227, 473 and 265 mm, respectively, which was clearly observed in the water-table depth (2.6, 6.4 and 9.8 m, respectively) which responded rapidly to biomass growth. These results imply that riparian vegetation can limit or prevent enhanced recharge around channels. Wilcox (2002) reached similar conclusions in relation to a review of attempts to enhance streamflow by mesquite removal. The pattern in juniper rangelands was more equivocal, although Wilcox interpreted these results as being more due to the relatively shallow soils and sediments in the uplands where the juniper is commonly found.

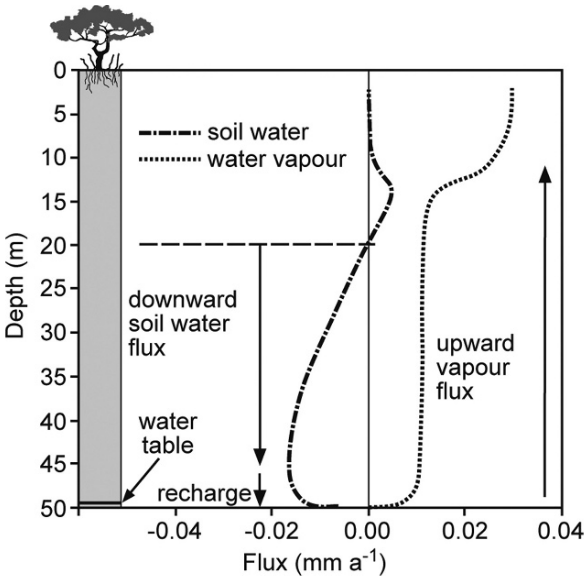


Fig. 3.11 Modelled soil-water and water-vapour fluxes below the root zone 10 ka after the establishment of xeric vegetation, which are compatible with rates observed using tracer studies (Seyfried et al., 2005)

The results of these studies imply that the response of riparian and other phreatophytic vegetation in drylands will be sensitive to changing ground-water levels. However, Naumburg et al. (2005) demonstrate that the consequences of change are not straightforward. Declining water levels may be beneficial in providing more root space and may also provide more beneficial conditions in saline soils. More often they may be detrimental, as the plant needs to exert higher leaf-pressure potentials to raise water from deeper in the soil profile. Threshold potentials before cavitation occurs in the leaves may be anything from –4 to –12 Mpa, so

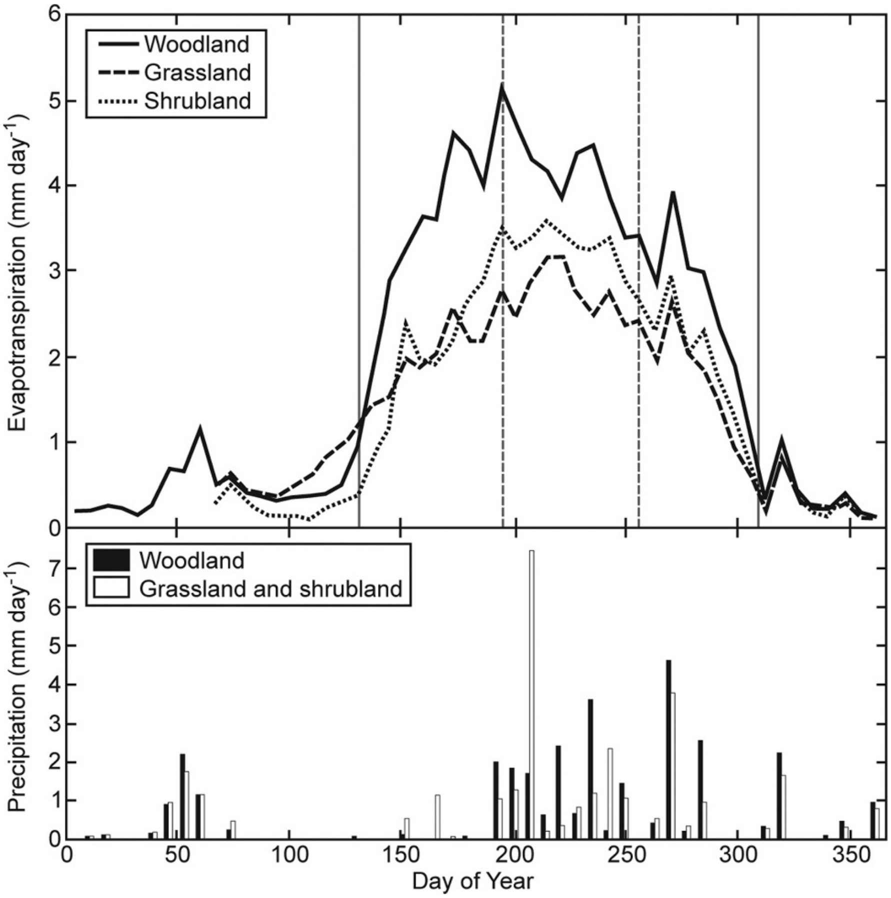


Fig. 3.12 Weekly evapotranspiration and precipitation measured by Scott et al. (2006) for the San Pedro River, Arizona, in relation to different types of riparian vegetation

that responses will be species-specific. The impact on plants will also be a function of the rate of descent, as root growth may be able to keep pace with the drop – measured rates of root growth are between 1–13 mm day^{-1} in riparian species such as *Populus*, *Salix* and *Tamarix* – so that rates of groundwater fall up to 40 mm day^{-1} have been tolerated up to the maximum rooting depth of the species. Some species also maintain shallow roots and thus switch to more readily accessible near-surface moisture under these conditions. To minimize the resistance in the roots and thus maximize the ability to raise water from depth, deeper roots will tend to have a greater diameter, but the ultimate limitation on following declining groundwater will be the ability of plants to produce sufficient biomass to create new roots. Rising water levels also paradoxically affect phreatophytic vegetation. Waterlogging produces anoxic conditions, causing root die-off unless the plant can translate sufficient oxygen to the roots. The relative rate of impact will thus again be species-specific. Root death will also reduce the ability of the plant to extract moisture to supply the above-ground biomass, and so produces a feedback to the ability of the plant to adapt. Plants will usually adapt to rising water tables by growing new roots higher in the profile, or by becoming dormant. These relative effects were evaluated using a numerical model by Naumberg et al. (2005), demonstrating that for an application to Owens Valley, shrubs were less responsive (more resilient) than grasses although the particular response was also a function of soil type. Biomass is typically lower in changing or fluctuating conditions than it is with steady water tables near the surface. Seyfried et al. (2005) suggested that riparian vegetation would have been especially sensitive to changes at the start of the Holocene, but that further studies are required in terms of the carbon costs that the plant incurs in adapting to a declining water table, unknown interactions between species (for example in the presence of hydraulic lift), the link with upland processes and the understanding community dynamics, particularly in defining critical thresholds. For example, Stromberg et al. (1996) demonstrated that well defined species associations along the San Pedro River in Arizona had clear thresholds of tolerance of distance to the water table. The species composition changed dramatically on passing 0.25 m, and then again at 1, 3 and 8 m. These thresholds are further complicated by the variability in the water table through the year (Stromberg et al., 2007). Increased rates of abstraction for agriculture, drinking water and industry in drylands will thus accentuate the sensitivity of riparian vegetation. Anthropic impacts are not limited to extraction; they are also a function of introduced species. Pataki et al. (2006) demonstrate the sensitivity of Fremont cottonwood (*Populus fremontii*) along the Colorado to invasion by salt cedar (*Tamarix ramosissima*). The ability of the latter species to tolerate more highly saline conditions allowed it to transpire more and thus outcompete the cottonwood. More saline conditions will again be a typical response to human intervention.

Roots also have a significant impact in providing a structure to soils and sediments. There are two specific effects. First, this structure imparts cohesion to soils and thus reduces their erodibility, in relation to splash and overland-flow erosion. Such cohesion will also reduce erodibility with respect to wind erosion, although it is likely that the modification of the velocity profile by the vegetation structure as discussed above is more important in this case. Secondly, roots typically have a high tensile strength and thus act as reinforcing elements, thereby minimizing the likelihood of slope or channel-bank failure. Tensile strength is inversely proportional to the root diameter, so that the overall effect is a function of the distribution of roots of different sizes, which is often poorly known, especially in the case of dryland plants (Pollen and Simon, 2005). Graf (1981, 1983a) has demonstrated the importance of vegetation in maintaining stability along the Gila River in Arizona, with thresholds due to extreme events leading to the erosion of stabilizing vegetation and corresponding subsequent increase of active-channel width. Subsequent recolonization and restabilization is a much slower process. Stromberg (1997) investigated a 25-year recurrence-interval flood event on the Hassayampa River in Arizona in January 1993 which created a 50-m-wide expansion of the active channel zone. She found that colonization of the expanded channel occurred very rapidly, with Fremont cottonwood germinating in March-April (i.e. two-three months after the flood event), Goodding willow in April-May, salt cedar in May-September, and arrow weed and seep willow in July-September. Different species were found to colonize different areas, with Fremont cottonwood preferring dry surface sediments, salt cedar and seep willow preferring saturated surface sediments and the other species found in both types of sediment. A second major event in 1995 removed a significant number of the colonizing plants, and reset the revegetation process. However, the more depositional nature of this flood in the study area tended to favour recolonization on the second occasion by Freemont cottonwood. Thus, the relative timing and nature of flood events will strongly interact with the types of riparian vegetation present and thus the likelihood that any particular event will be erosive or be resisted by the effects of vegetation. Diversity of vegetation type will be less in channels with increasingly ephemeral flows – including those due to human modifications – due to the removal of wetter microhabitats (Stromberg, 2001; Stromberg et al., 2007). Therefore, it is likely that the more ephemeral a channel is, the more likely it is to present a major response to extreme flows because of the sparseness and spatial patchiness of riparian vegetation. A further significant interaction between vegetation and channel flow is in the initiation of gullies. Graf (1983b, 1988) analyzed the relationship between vegetation cover and shear stresses generated to initiate gullies in the Henry Mountains in Utah. He found a strongly hysteretic relationship that was well described by a cusp-catastrophe model.

Surface and Near Surface

Vegetation provides a further control on infiltration by reducing the energy and rate of water arrival at the surface. As noted above, Wainwright et al. (1999c) identified a significant reduction in rainfall energy arriving at the surface below creosotebush, and Brandt (1989) measured the same phenomenon under a number of shrub plants. The effect of grass – especially species with a clumped and/or low growth form – can be considered to exacerbate this effect, although direct measurement is difficult. However, such vegetation controls are not universal and depend on the interaction with other surface features. For example, Descroix et al. (2001) demonstrated that on grass slopes in the Sierra Madre of Mexico, runoff and erosion was significantly higher than elsewhere in the area. They attributed this difference to higher proportions of embedded stones and surface crusting than found in association with other vegetation types.

Most discussion thus far has been of macrophytic vegetation. However, microphytes are also an important component of the desert ecosystem. Lichens, mosses, and cyanobacterial and chlorophytal algae have all been observed (Lange et al., 1992; 1994). They may be early colonizers and, in conditions where moisture from rain is sparse, they may be the only form of vegetation present in deserts. Growing at or near the surface because of their need to photosynthesize, they can produce dense mats at the surface, and reinforce the subsurface by the production of filamentous growths. Together, these reinforcing mechanisms produce what are commonly known as biological crusts. The filaments can often be seen in cross section and are a useful way of distinguishing between biological and mechanical crusts. These crusts tend to have low infiltration rates and fewer propensities for runon infiltration due to low roughness values (Belnap et al., 2005), except in cases where frost action is important and rough surfaces are created thus tending to lead to higher infiltration rates (Belnap, 2003). Conversely, Williams et al. (1999) found no measured difference between unsaturated hydraulic conductivity of biological crusts compared to other areas, which may be due to their use of a tension infiltrometer for measurement rather than considering the effect of rainfall. Belnap (2006) summarizes the difference in the literature regarding differential infiltration rates. She suggests that smooth cyanobacterial crusts decrease infiltration, while rugose crusts or lichen or moss surfaces will tend to increase infiltration, suggesting that different crust types in different environments will have significantly different effects on infiltration and runoff processes (Fig. 3.13). Microphytic crusts respond rapidly to pulses of rainfall (Cable and Huxman, 2004; Belnap et al., 2005; Bell et al., 2008; Loik, 2006). For example, Cable and Huxman (2004) found that crusts began photosynthesis within 100 h of a rainfall event and contributed a significant component of carbon flux into soils, especially for small rainfall events. Bell et al. (2008) found a positive correlation between soil moisture and photosynthetic activity. Crust growth may therefore be rapid and able to exploit water sources that are too sparse for other plant activity. Thus, microphytic crusts may be significant in the rapid stabilization of the surface following disturbance due to erosion events or human activity. Belnap and Eldridge (2001) noted a 35-fold decrease in erosion on a well-developed crust surface, and Kidron (2001) and Neave and Rayburg (2007) also highlight the importance of these crusts in reducing erosion. However, once disturbance has taken place, full recovery of microphytic crust function may take decades or centuries (Belnap, 2003).

Microphytic crusts can also provide a significant nutrient input to the soil, with corresponding benefits to other plant life. Belnap (2003; see also Chapter 9) notes that this effect may be indirect in that the polysaccharide sheaths of bacteria are "sticky" and thus trap dust, an effect that may be emphasized where the crust surface is rugose. Bell et al. (2008) measured significant NH_4-N and NO_3-N production by microphytes in soils at Big Bend National Park, Texas. Nitrogen fixation by lichen may be as high as 10 kg ha^{-1} a^{-1}, and that by cyanobacteria as high as 1 kg ha^{-1} a^{-1} (Belnap, 2003).

Certain microphytes inhabit very extreme environments. Schlesinger et al. (2003) note the presence of a range of hypolithic cyanobacteria beneath quartz pebbles in the Mojave Desert. Although most frequent beneath pebbles of 9–10 mm thick, some examples were found beneath 25-mm thick pebbles where light was approximately 0.08% that of ambient. Such cyanobacteria have been found to tolerate temperatures as high as 90°C. It has been suggested that these environments are analogues for where life may be found on other planets, or for the early evolution of plant life in desert systems. Hypolithic cyanobacteria may also increase the stability of pavement surfaces, although detailed research has yet to be carried out on this aspect of their function.

Habitat

A further rôle of vegetation in affecting geomorphological processes comes through its interaction with fauna. Beyond its source as a food supply (e.g. Noy-Meir, 1974; Tivy, 1990; Stafford Smith, 1996; Whitford, 2002) and the resultant redistribution of nutrients across the landscape as faecal matter, the vegetation structure also provides a habitat for animals. Birds nest and roost, often in upper branches away from potential predators, where there is also

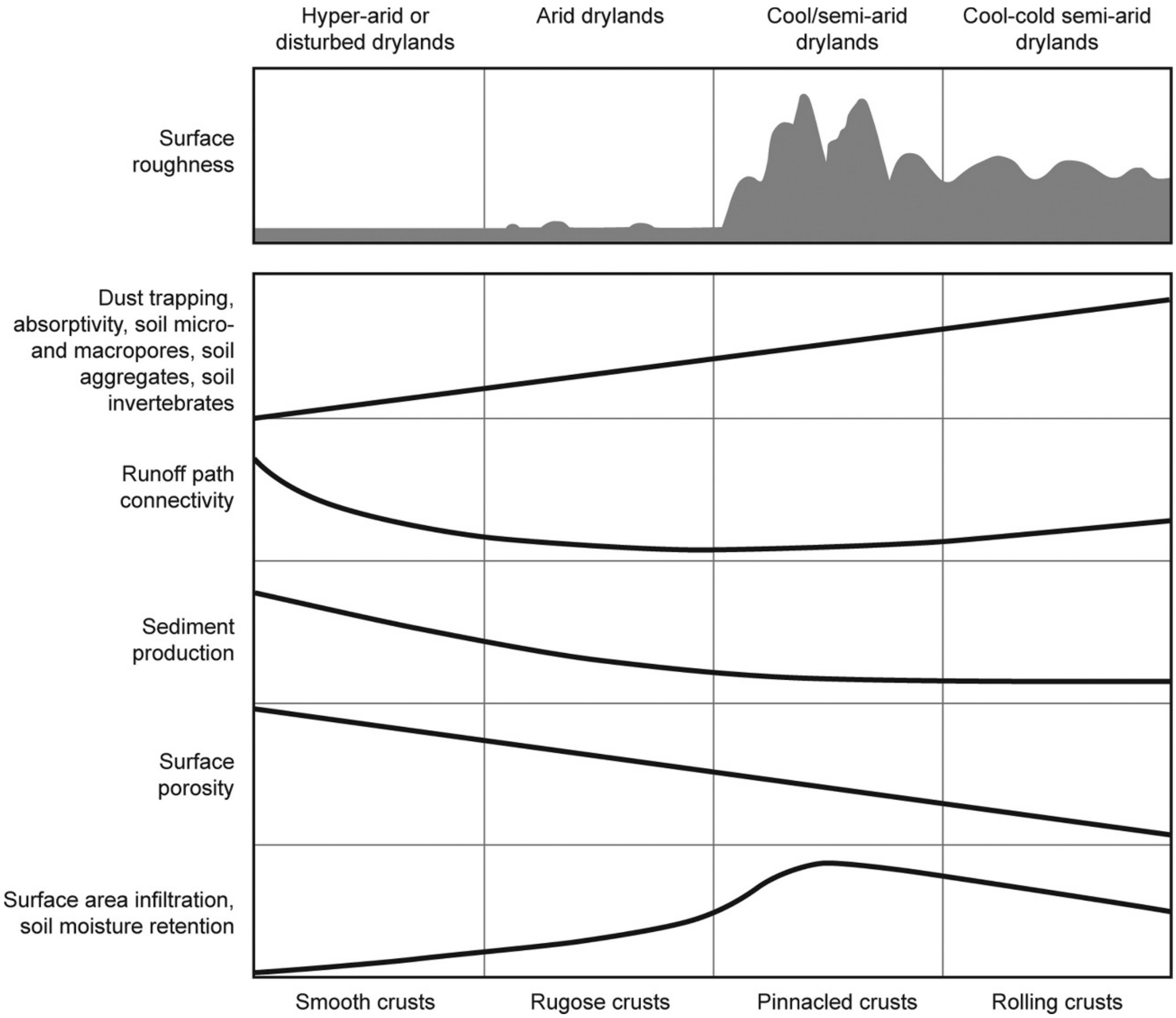


Fig. 3.13 Effects of different crust types on surface hydrology (Belnap, 2006)

the advantage of cooler microclimates. Reptiles may use branches for basking, while amphibians and a range of small mammals burrow beneath vegetation (Whitford, 2002). The vegetation provides a way for the animals to avoid the extremes of the environment, as well as providing protection from predation. One consequence of the burrowing and other digging activity (e.g. for food) is that it disturbs the surface below and around plant canopies. Neave and Abrahams (2001) demonstrated a positive relationship between the extent of such disturbance activity and subsequent erosion in overland flow. The disturbance creates a significant sediment source that is less readily exhausted during runoff events, so that erosion is higher and more prolonged than on undisturbed sites. Concentration of small animals in and around shrub canopies may contribute to the "islands of fertility" phenomenon by recycling of plant material and redeposition of it as faecal matter beneath and adjacent to plants. In contrast, large herbivores may have a more dispersive effect.

Pattern

The discussion of process-interactions above suggests that work on understanding the interactions between desert vegetation and geomorphic processes has focussed on two extremes of scale. The first is the regional scale of thousands of square kilometres or more, where there is reasonable evidence to suggest large scale feedbacks between vegetation and climate. The second is at the scale of individual plants or some component of their structure. This latter approach has been highly influential, not least since the development of the "islands of fertility" concept by Garcia-Moya and McKell (1970) and Charley and West (1975), and used as a basis for understanding dryland degradation by Schlesinger et al. (1990). This oft-cited paper has been used to support a large body of research that has informed our understanding of desert vegetation at the scale of individual plants, and because of the sparse distribution of plants, at the scale of the interspaces between the plants. Research at this scale is frequently carried out, not least because of the relative ease of carrying out experimental approaches at this scale. An implication of this research focus has been an often implicit conceptualization that once the plant-interspace scale has been fully investigated, desert ecosystems and their interaction with the landscape will be fully understood. Four considerations suggest that this logical leap is unfounded.

First, empirical considerations suggest that patterns are not quite so straightforward. When the Schlesinger et al. (1990) paper was published, it contained little in the way of direct evidence to support the concept of islands of fertility; it was more a manifesto for research that would be required to test the hypothesis. Schlesinger et al. (1996) compared patterns of soil N, P and K with distributions of black grama grass plants, and of creosotebush and mesquite shrubs at sites in the Chihuahuan, Mojave and Great Basin Deserts. Geostatistical analyses of 8 × 12-m areas suggested that nutrients were autocorrelated at shorter distances in the grasslands than in the shrubs, and that these patterns could be related to the average distance between plants in the different cases. This analysis was extended by Schlesinger and Pilmanis (1998) who noted changes in spatial autocorrelation as shrubs invade grassland, and that when shrubs are cleared, they tend to be more readily reestablished if the soils are not homogenized. In contrast, Müller et al. (2008) used geostatistical analyses over areas of 90 × 90 m to investigate spatial patterns of nutrients, soil moisture, infiltration and other soil properties in grassland and creosotebush, mesquite and tarbush shrubland. They found that although soil moisture and infiltration was closely related to vegetation size in all cases except for mesquite, other parameters were distributed in a much more complex way (Fig. 3.14). This complexity was attributed to processes that transfer materials over longer distances such as overland flow in concentrated flow paths and rills. Indeed, these results are not incompatible with those of Schlesinger et al. (1996), who noted for example that only 35–76% of variance in grassland N and 35–51% in shrubland N was explained by the pattern of vegetation. More often than not, therefore, factors at larger scales than vegetation variability must explain the variance in N in their results also.

Secondly, and not least, it has long been known that dryland vegetation exhibits distinct distribution patterns and distributions at different scales. On moderate-angled slopes, the plant-interspace patchiness contains features at larger scales, such as concentrations of vegetation along rills and larger channels, and concentrations in splay areas that typically receive high amounts of runon infiltration (termed "beads" by Wainwright et al., 2002). The exact scale of these patterns is a function of local soil and climate conditions, but may induce variability on a scale of tens of metres to several kilometres (Fig. 3.15). At these larger scales, progressive sorting and the development of soil catenas and other evolutionary sequences control the structure of water availability and thus the larger scale patterns of vegetation distribution, including transitions between different dominant vegetation types (e.g. Phillips and MacMahon, 1978; McAuliffe, 1994). Larger scale vegetation patterns have also been observed in environments where wind is considered to be the dominant vector of sediment transport. Okin and Gillette (2001; Okin et al., 2006) have described elongated bare patches parallel to the dominant wind pattern in areas with mesquite nebkhas, so that there is a distinct anisotropy in the vegetation pattern here too. These elongated patches have been termed "streets". In reality, in all but the more hyperarid areas, there are likely to be significant interactions between water and wind movement of sediment along these streets. In areas dominated by more gentle slopes (c.1% is typically considered the threshold, but again the exact value will depend on local conditions), vegetation bands parallel to the slope contour have been described in deserts worldwide (Dunkerley and Brown, 1995). These areas of banded vegetation are known as mulga groves in Australia and vegetation arcs and tiger bush (*brousse tigrée* in Francophone areas) in Africa. The bands are usually associated with a stepped microtopography of about 10 cm. Bands occur dominantly in shrublands but

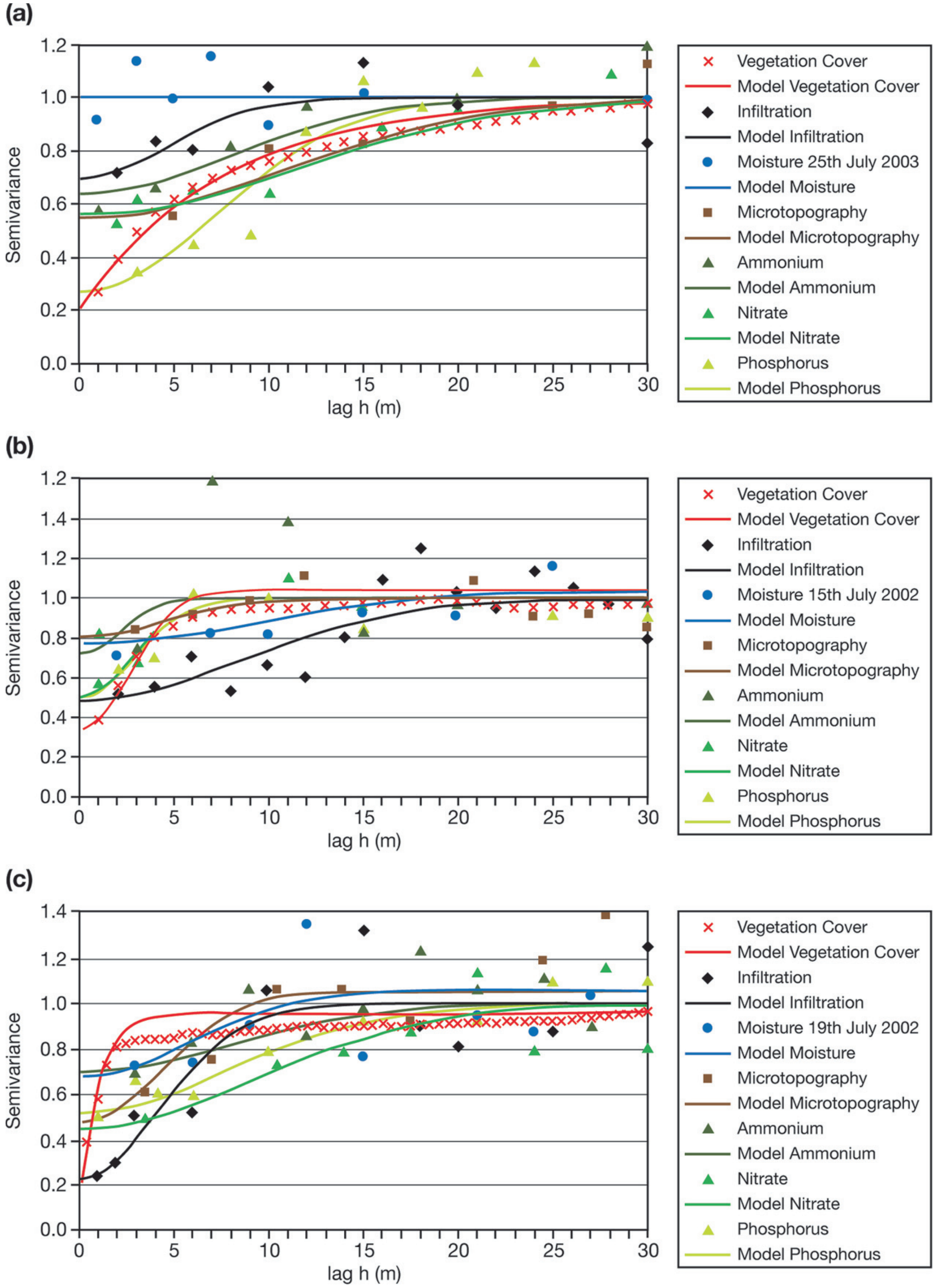


Fig. 3.14 Semivariograms showing different spatial relationships of vegetation and surface characteristics for a range of shrub and grass vegetation types, Jornada Experimental Range, New Mexico (Müller, 2004; see also Müller et al., 2008)

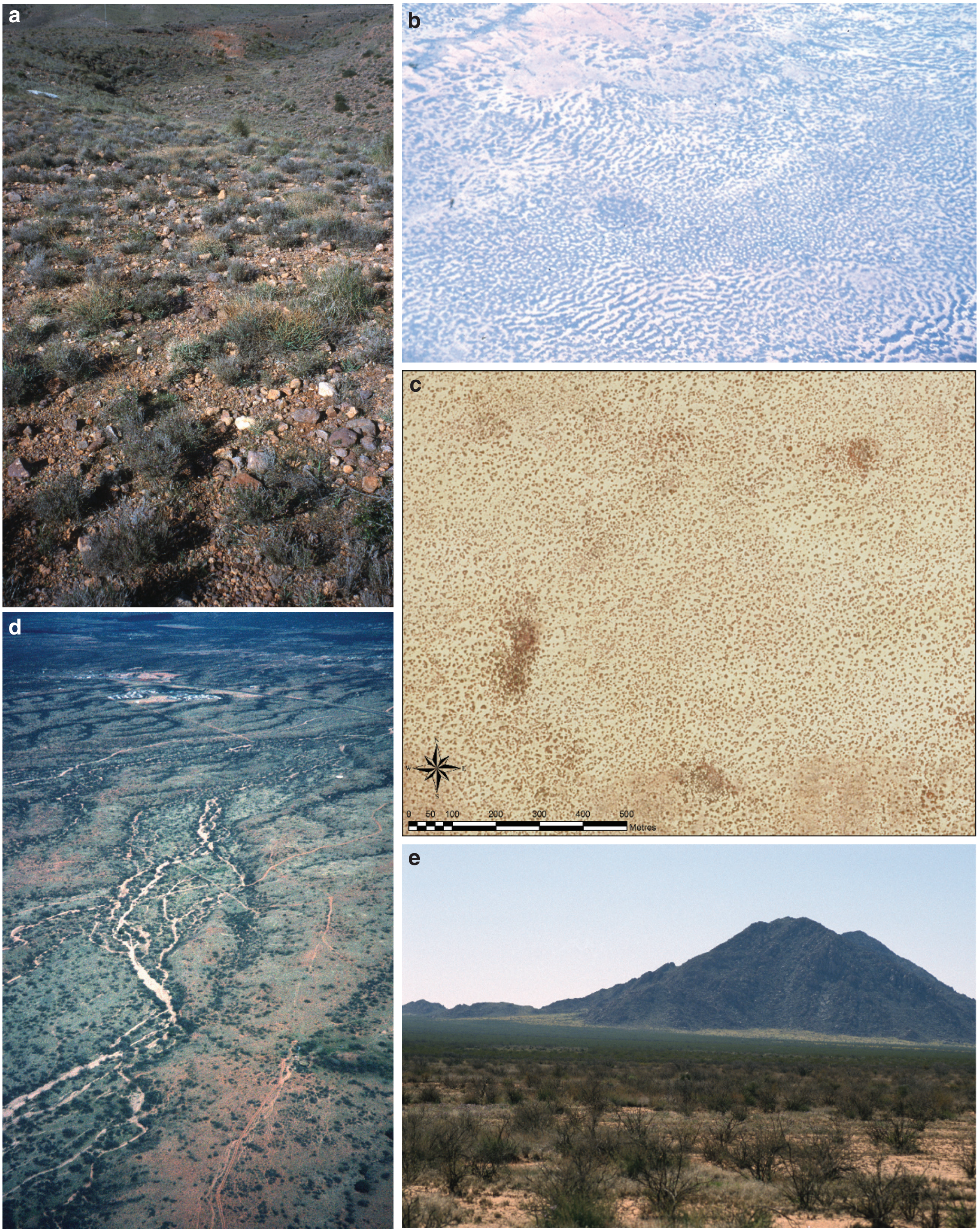


Fig. 3.15 (caption on next page)

have also been observed in grasslands (Worrall, 1959; Montaña, 1992); grasslands may also exhibit similar patterns at smaller scales, with arcuate patches and tread-and-riser topographies. Common explanations of banded vegetation are not dissimilar to those of "islands of fertility" in patchy vegetation. It is argued that runoff from the bare areas transports sediment, nutrients and propagules downslope. Erosion of sediment in this way creates the stepped microtopography and makes the interband areas less likely to be able to support vegetation. When the runoff encounters the vegetation band, it starts to deposit water, sediment and nutrients so that vegetation on the upslope edge of the band receives more resource than vegetation elsewhere. The relative effect of this resource accumulation can be estimated by observing the relative widths of the bands and interbands. Tongway and Ludwig (1990) note that bands are typically 10–20-m wide, and that interbands are 20–50-m wide. Goudie (2002) gives examples of interbands that are 100–200 m in width and generalizes that they are often two to four times as wide as the bands. Propagules will also have a favourable location to start new vegetation growth. Thus, it is often argued that vegetation bands should migrate upslope (but see Dunkerley, 1997 for an opposing viewpoint based on hydrological mechanisms only). Dunkerley and Brown (2002) observed banded vegetation on slopes as low as 0.4%, and there is nothing theoretically to prevent banding on less steep slopes, as long as a mechanism for building a pressure head exists. However, much uncertainty exists in the explanation of banded vegetation, inasmuch as different mechanisms may be in operation in different places. For example, Montaña (1992) demonstrated that banded mesquite-tobosa grass vegetation in the Chihuahuan Desert in Mexico migrated upslope as a result of colonization processes, while Dunkerley and Brown (2002) did not observe this process in relatively stable bands of mixed chenopod shrubs and tussock grasses. The latter study also demonstrated the existence of bands at orientations of 45–70° to the slope direction, which are difficult to explain using the same mechanisms. A further consequence of vegetation patchiness is its effect on biomass productivity. A number of authors (Humphrey, 1958; Buffington and Herbel, 1965; Barbier et al., 2006) have suggested that patchy vegetation produces a greater biomass than uniform vegetation. Aguiar and Sala (1999) have suggested that the reason for this difference is that patchy vegetation is more easily able to exploit all precipitation rather than lose some "ineffective precipitation" below the biomass-production threshold. This theory implies that sufficient ineffective precipitation can be accessed by plants, which may not always be the case for low intensity events (e.g. runoff-runon mechanisms do no occur). The lack of a significant difference in biomass between grasslands and shrublands in the same location (Huenneke and Schlesinger, 2006) may imply that the patchiness at the scale at which it occurs in grasslands is also able to exploit this mechanism, and it is the relative scale of plant to interspace that is important. However, the analysis of Aguiar and Sala (1999) also implies that patchy vegetation is the result of dominant wind and animal vectors of movement, which is clearly contrary to observations elsewhere that show water vectors are highly sigificant in the development of patches. Oksanen (1990) has also suggested that herbivorous animals play a significant rôle in the development of patches in semi-arid environments, but that their impact is moderated in arid conditions.

Thirdly, and often as a response to the difficulties of field-based explanations of pattern, there has been a rash of related modelling studies. These studies either focus just on banded vegetation (e.g. Lefever and Lejeune, 1997; Lejeune and Tlidi, 1999; Klausmeier, 1999; Esteban and Fairén, 2006; Sherratt and Lord, 2007) or attempt to explain pattern in a generic framework, which usually consists of a classification into "patchy"/"spotty"/"leopard", "labyrinthine" and

Fig. 3.15 Spatial patterns of desert vegetation: (**a**) patchy low matorral in Almería, Spain; (**b**) patches, labyrinths and tiger bush near Niamey (bare ground in the tiger bush is 75–100-m in width), Niger; (**c**) patches in mesquite nebkhas (cf. Fig. 3.8b: this figure is in the same area of the M-NORT site of Okin and Gillette, 2001, with evidence of "streets" aligned SW-NE following dominant wind directions; note also the patches of denser vegetation in local topographic hollows); (**d**) patchy vegetation at various scales relating to the presence of riparian vegetation and discontinuous flows in the Sonoran Desert (cf. also Wainwright et al., 2002); and (**e**) vegetation following an altitudinal-catena gradient in the Chihuahuan Desert (the mountain has sparse juniper trees, the base of the mountain has remnant black grama-yucca grassland, which merges into creosotebush and then tarbush shrubland, and finally into a mixed tarbush-tobosa grass) "banded"/"tiger" (e.g. HilleRisLambers et al., 2001; Rietkerk et al., 2002). As with other classifications, its utility is probably more by demonstration of proof by exception. A common feature of this modelling approach is to use the concept of emergence of larger scale properties (the vegetation patterning) as a response to local scale interactions. Many of these studies are conducted implicitly or explicitly within a Turing-instability framework. Stewart et al. (in press) point to the conceptual and practical inadequacies of these approaches and present an alternative modelling framework that incorporates processes that operate at a range of scales within the landscape that produce patterns at a range of spatial scales.

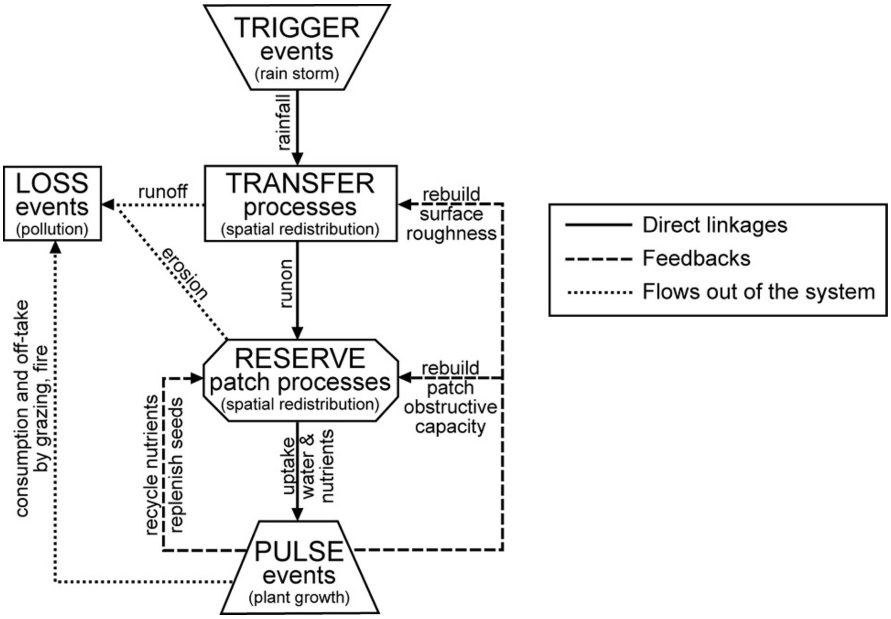
Fourthly, strategies for mitigation of land degradation that have been based on the plant-interspace concept have generally proven inadequate. Rango et al. (2005) demonstrated that areas where shrubs had invaded grassland and where shrubs were subsequently removed were able to revert back to shrubland if no other measures were taken (see also Rango et al., 2006). One aspect of this inadequacy is the failure to incorporate aspects of historical legacies (Foster et al., 2003) on understanding the evolution of systems by affecting the boundary and initial conditions of the problem when observed in isolation. A similar problem is the impact of contingency both in terms of stochastic events and historical development. Allison and Hobbs (2004) have considered the effects of long-term (and large-scale) economic cycles and demonstrated their importance for understanding problems in the management of agricultural systems in arid Western Australia.

Thus, as noted previously, dryland landscapes can be seen to interact with vegetation on a range of spatial and temporal scales. For example, mound formation may be the result of plant-interspace processes at least initially in areas where rainsplash is the dominant mechanism. The presence of mounds starts to concentrate fluvial and aeolian erosion processes that not only concentrate differences at the plant-interspace scale, but also contribute to more advective patterns of redistribution. However, splash-related processes will operate more frequently because of the magnitude of most rainfall events, while advective transfers require larger magnitude events. Vegetation patterns thus evolve at a range of spatial scales on timescales ranging from years to centuries. Cooke and Reeves (1976) have demonstrated how changing hydrological régimes produced during these vegetation changes can cause both deepening and widening of arroyos, which in turn affects and is affected by the presence of riparian vegetation. Consequently, these changes may have impacts on regional groundwater recharge on millennial timescales (see also Wilcox et al., 2006). Graf (1983c) has also demonstrated decadal consequences on patterns of incision and sedimentation, that are consistent with previous episodes in the Holocene (Hall, 1977). All of these changes will produce decadal to centennial variations by feedbacks in the climate. At the longest timescales, there will be feedbacks between landforms and tectonic processes. While this interaction is usually considered unidirectional, in the sense of deserts created in the lee of mountain chains (e.g. Chapter 28) or of structural controls (e.g. Campos-Enriquez et al., 1999; Schlemon and Riefner, 2006; Dill et al., 2006), Willett (1999) has demonstrated that there is a dynamic feedback between pattern of climate (e.g. pro- versus retro-wedge aridity in convergence zones) and uplift via isostatic adjustment following erosion. There are thus likely to be complex feedbacks in the presence, evolution and pattern of dryland vegetation at timescales of millions of years.

Implications

Understanding the complexity of the interaction of desert vegetation with landforms is not a trivial exercise. As noted by Newman et al. (2006), it requires both top-down (systems-based) and bottom-up (complexity-theory and evolutionary) approaches. A range of conceptual models has been proposed to try to explain different aspects of these interactions, and for the most part they are undergoing evaluation and refinement. The two-layer hypothesis of Walter (1971) that attempts to explain the coexistence of grasses and shrubs or trees in the same apparent niche has been demonstrated to be too simplistic, and temporal as well as spatial variability needs to be accounted for. This variability was central to the classic overview by Noy-Meir (1973). The trigger–transfer–reserve–pulse (TTRP) model of Ludwig et al. (2005) provides one means of accounting for both sources of variability (Fig. 3.16), with examples relating to runoff-runon dynamics and patterned vegetation in Australia and

Fig. 3.16 The trigger-transfer-reserve-pulse (TTRP) conceptual model of Ludwig et al. (2005). Direct consequences of a trigger event are shown as solid arrows, feedbacks as dashed lines and flows out of the (local) system as dotted lines



the USA. Loik et al. (2004) have used a similar pulse-based framework to consider vegetation-climate linkages from local to regional spatial scales and from timescales of individual storm events to decadal variability of climate (principally series of drought cycles). One emergent property of landscapes that undergo these processes with those driven principally by aeolian processes is that of connectivity, or in other words, the extent to which spatial patterns emerge that allow the effective transfer of resources across the landscape (Stewart et al., in press; Okin et al., 2009, and more general reviews in Bracken and Croke, 2007). The extent to which structural and functional connectivity link the dynamics of process with form in desert environments seems to be a useful concept allowing the understanding of changes from plant-interspace to landscape scales (Turnbull et al., 2008b).

One apparent paradox with desert vegetation is that it can both exhibit highly resilient characteristics and undergo very dramatic, rapid changes. The resilience of an ecosystem can be defined as its ability to withstand major disturbances without significant change (Holling, 1973). At the plant level, desert vegetation is resilient because it has had to develop mechanisms for adapting to extreme and highly variable environmental conditions, as discussed above, and in some conditions, the interaction between plants in producing favourable environments for each other can lead to the operation of this resilience at larger spatial and temporal scales. Catastrophic changes are also well known (DeMenocal et al., 2000; Scheffer et al., 2001; Liu et al., 2007) and can be interpreted in terms of the non-linear and threshold behaviour of vegetation-vegetation and vegetation-landscape interactions. Models using catastrophe theory to explain different aspects of these interactions have been relatively widely employed (e.g. Graf, 1983b, 1988; Thornes, 1980; Lockwood and Lockwood, 1993; Rietkerk et al., 1996; Scheffer and Carpenter, 2003), and Turnbull et al. (2008b) have suggested that these conceptual approaches can be combined with those relating to connectivity as discussed above. Given that vegetation is a strong control on the types and rates of landscape evolution that occur in drylands, it seems reasonable to hypothesize that a TTRP model for geomorphic processes is appropriate, and explains some of the current difficulties in understanding the complexities of dryland landscape evolution.

As noted in the introduction, conceptual models that assume (simple) equilibrium conditions are particularly inappropriate to dryland environments, and there has been much debate about the existence of multiple stable states in savannah ecosystems, for example (Scoones et al., 1993; Sullivan and Rohde, 2002). Gillson (2004) has demonstrated that such conditions are likely to have persisted in Kenya for at least the last 1,400 years. It is thus unlikely that ecohydrological approaches that are based on assumptions of tendency towards equilibrium, such as those of Eagleson (2002), will provide strong explanatory mechanisms for understanding the evolution of dryland vegetation (see also the discussions on optimality from an ecological perspective in Hatton et al., 1997, and Kerkoff et al., 2004). Adding geomorphic processes increases the number of degrees of freedom in the system and the subsequent difficulty of demonstrating equilibrium conditions (Bracken and Wainwright, 2006), even if they do exist. Multiple equilibria or non-equilibrium systems are one reason why semi-arid geomorphic systems exhibit complex responses both spatially (Schumm, 1973) and in time (Wainwright, 2006b). They also help to understand why explanations of certain phenomena may fall foul of the problem of equifinality (e.g. Cooke and Reeves, 1976). Overall, the interactions of dryland vegetation and geomorphic processes, with their multifarious scales, delays, emergence, thresholds, catastrophic changes, nonlinearities and non- or multi-equilibrium states, are one reason why the reconstruction of environmental change in drylands (Chapter 28) is problematic.

Conclusions

Progress in understanding the interactions of desert vegetation with geomorphic processes over the last two decades or so has been considerable. In part, this progress has been due to a shift in perspective away from empirically based studies to more conceptually sound frameworks that often take on multidisciplinary perspectives. However, this shift needs to continue and to take on a more holistic perspective that allows the integration of process understanding and employ models of a range of complexities.

At the same time, it is important not to lose sight of the wood (as it were) from the trees. Although advances are being made, most dryland environments remain poorly understood, and the variability in understanding of different environments and systems is considerable. It is fundamental that new empirical studies are carried out in parallel with the development of new models and theories, in order to evaluate their general usefulness.

In so doing, it is important to build on the recent advances in research in dryland ecogeomorphology. Underpinning much of this work are various concepts of scale and scaling. In particular, there is a convergence in perspectives from ecological moves from individual leaf or plant scales to a focus on landscape, and geomorphological moves from small-scale processes again to a landscape perspective. Work on the "islands of fertility" concept over the last two decades has demonstrated that while the idea is useful for understanding behaviour at individual plant scale, it does not offer sufficient explanatory power for the emergence of vegetation patchiness and patterns at hillslope to landscape scales, nor for the longer term behaviour of landscapes at decadal and longer timescales. More work is required to elucidate how vegetation "islands" interconnect with other landscape elements; indeed, given their leakiness, it may be appropriate to stop using the island metaphor in the sense that it may impede further developments in understanding integrated vegetation-landscape systems. At present, the change in scale has tended to be driven from the bottom up, i.e. from a perspective of employing small-scale process understandings to interpret landscape-scale pattern. However, as shown above (Fig. 3.1), ecogeomorphic processes operate over multiple time and space scales, and so there is great scope for driving understanding in the opposite direction, from geological or Quaternary science perspectives for example. At a global scale, deserts produce significant feedbacks on climate systems, and there is also a greater need for understanding the rôle of these feedbacks within broader debates on climate change and Earth-System Science (Wainwright, 2009). A number of empirical observations and modelling results also suggest that dryland ecogeomorphology is particularly susceptible to initial conditions and to past trajectories, again emphasizing the need for integration with work carried out at longer timescales. This integration needs to operate in both directions, with a recognition that reconstructing past climate or vegetation patterns is not straightforward, but needs to be informed by ongoing process-based work. A significant aspect of contingency and path-dependence in the system is the impact of human activity, and new methodologies are being developed for the analysis and interpretation of these impacts (Wainwright, 2008; Wainwright and Millington, in press). However, there is also a need for historical and archaeological work to underpin these approaches with data to assess the integrated human-landscape interactions and their evolution. Along with human activity, the impacts of other animals and of fire, all of which have only been considered briefly within the scope of this chapter, need to be fully incorporated into studies of dryland ecogeomorphology. As more holistic or whole-system approaches are developed, there needs to be an evaluation of these processes as interrnal to the system, rather than as being external "disturbances", a perspective that tends to draw the focus away from their importance. By so doing, significant advances may also be made in understanding one of the key questions of dryland ecogeomorphology, namely why individual plants and plant components can exhibit such degrees of resilience while plant assemblages and landscapes are highly sensitivite. The development of these holistic approaches also requires a clearer recognition of the interactions between different processes, and in particular the removal of barriers imposed by the imposition of narrow geomorphic process domains. There are many advantages to interpreting aeolian and fluvial processes within the same framework, for example, and in all but the more hyper-arid or temperate extremes of drylands, both sets of process tend to operate to varying degrees. There is also the rather false split between hillslope and fluvial geomorphology, which has tended to hinder the understanding of whole catchment behaviour. Recent management as well as scientific developments will hopefully begin to remove this division. There needs to be a continued development of new techniques for understanding process, and for evaluating patterns over large areas. Continued improvements in Earth-Observation techniques are required in this respect, and there needs to be an ongoing evaluation of how such observations fit into a continuum of measurement from the point scale upwards. Given the extent to which desert vegetation concentrates resources below ground, there is a major need for improving techniques that can evaluate the subsurface, preferably non-destructively. Such improvements are vital to make advances from current techniques that base estimates on surface proxies. Finally, as we have previously noted (Wainwright et al., 2000), all of the above developments will require a move away from empiricism to general, conceptually underpinned approaches that recognize the need to move away from plant-/plot-based methodologies, and the need for better framing of individual case studies to relate their specific context to the bigger scientific picture.

Whither desert ecogeomorphology? Conceptual developments over the last decade suggest that the topic is a prime area for understanding non-equilibrium dynamics, complexity theory and spatio-temporal connectivity of process and form in whole-systems perspectives. Taking these conceptual models forwards employing integrated modelling and field approaches within an inter- and multidisciplinary framework is likely to provide fertile ground for future discoveries.

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