ECOLOGICAL PROCESSES AND PLANT ADAPTATIONS ON COASTAL DUNES

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INTRODUCTION

This paper attempts to review some of the major adaptations of coastal plants to physical (abiotic) stresses imposed in the coastal dune environment. In doing so it struggles to carry out three tasks, firstly, to list and partially discuss the stresses and adaptations which take place in the highest stress zone (generally), the beach/foredune zone; secondly, to analyse the magnitude and range of these stresses in the various coastal dune landform types; and thirdly, to present an initial attempt at analysing stress and adaptation patterns and magnitudes for different coasts of the world. It concludes with a brief comparison of coastal and desert dune stresses and adaptations.

THE INCIPIENT FOREDUNE/FOREDUNE ZONE

The zone above the high spring tide line on the backshore of beaches may be one of the most physically stressful places in which a plant can begin life. Here seed, seedling, and plant growth and survival can be affected by aeolian sand burial, swash erosion, swash inundation and ponding, high temperatures, high light intensity, heat stress, and moisture and nutrient deficiencies.

Seed morphology may operate to produce considerable differences in germination success and plant distribution in this environment. For example, female Spinifex species have a seed head which forms a spikelet ball capable of rolling along the ground at quite high speeds. This seems to be a useful mechanism for promoting fertilization, and enhancing spread of the plant since spikelets fall out as the balls roll across dunes and beach. Cakile edentula enhances its propagation and vegetative spread by producing a fruit containing two segments with one seed in each. The lower segment

remains with the plant falling into the dead plant/shadow dune mass remains with the plant falling into the dead plant/shadow dune mass following autumn-winter die-off (Barbour, 1970; Keddy, 1980). It thus falls into a locally nitrogen and nutrient rich environment which is somewhat protected from deflation because of dead plant material and trapped sand lying on the surface. The other portion of the fruit readily falls from the plant following ripening and will survive swash and seawater inundation and has been known to float for several days. The success of the latter method can be gauged in N.S.W., whereby in 1976, <u>Cakile maritima</u> was found on a few beaches straddling the N.S.W./Victorian border. At the time of writing the plant had spread to Sydney, a distance of some 400 kms in 12 years.

The requirement of some seeds for minimum temperatures (or stratification), for minimum burial depths, and for optimal temperatures to obtain maximum germination may all be regarded as adaptive tactics, but only certain species require all these tactics (Seneca and Cooper, 1971; Van der Valk,1974). Some seeds do not require stratification (and hence may actively compete with seeds needing cold temperatures), and may germinate across a relatively broad range of temperatures and burial depths. As Barbour et al (1985) notes, it is difficult to assign ecological significance to such an array of responses.

Once plants are established on the backshore zone and incipient foredune zones develop, a large range of environmental stresses are present and a variety of plant adaptations and responses to these stresses are possible. Table 1 summarizes some of these stresses and adaptations as they occur particularly in the incipient foredune/foredune zone. It is beyond the scope of this paper to review each adaptation listed here. Rather, I will briefly examine a few examples to illustrate some of the processes operating in this environment, and commonly, within the coastal dune environment in general.

SALT SPRAY

Salt spray aerosols produced by breaking waves are ubiquitous to shorelines and are considered a primary determinant in species succession and growth habit in the immediate beach-dune environment (Oostings and Billings,1942). Salt spray loads and intensities are correlated with distance inland from the beach (e.g. Cartica and Quinn, 1980; Avis and Lubke, 1985), wind speed, height above the ground (Barbour, 1978; Barbour et al, 1985), site microtopography (Barbour,1978; Salisbury,1952) and beach-surfzone type (Short and Hesp,1982; Hesp,1988a).

Where plants receive continuous deposition of air-borne salt they typically respond by enlarging their cells (leaf hypertrophy). This results in a doubling or tripling of leaf thickness (Boyce, 1951; Barbour et al, 1985). Rozema et al (1982) found the application of salt spray to species such as _Cakile maritima_ and _Salsola kali_ increased the fresh weight of the species, and that the majority of this increase was due to an increased degree of succulence (expressed as H_2O cm^{-2} leaf area). They found that the degree of succulence in _Cakile maritima_ due to salt spray increased by a factor of 2 or 3, and that the spray may stimulate growth under low soil fertility (see also Beer et al, 1975).

In contrast to species which increase the degree of succulence and hence increase Na and Cl levels in their shoots as _Cakile_ does

(Rozema et al, 1982), some species (e.g. Elytrigia junceiformis) are highly resistant to intensive seawater spray. Such species have a reduced Na and Cl uptake as well as high levels of potassium in shoot tissue as opposed to the species described above (Rozema et al, 1982).

SAND BURIAL

Individual plant species may react quite differently to varying degrees and rates of sand inundation and burial. Some species (e.g. Spinifex sp., Ammophila sp.;e.g. Hesp, 1983; Travis, 1977; Disraeli, 1984)react positively to sand burial and may become depauperate if there is a low rate of sand burial, whilst other species react mildly to negatively to sand burial rates above a critical minimum (e.g. Moreno-Casasola, 1986, her table 2;Maun and Lapierre, 1986).

The rate of sand inundation and the degree of sand burial can be very important for the establishment of annual species since seed burial at certain depths can result in germination failure (Lee and Ignaciuk, 1985; Maun and Lapierre, 1986). Of three strandline species tested (Atriplex laciniata, Cakile maritima, and Salsola kali) Lee and Ignaciuk (1985) found that maximum germination occurred at the shallowest depth (1 cm). At 16 cm burial depths, minimal germination occurred in Cakile (5%) and zero germination in the other two species. Although few experiments appear to have been conducted on seed germination across a range of plant species within any one coastal environment, the ability of some species to produce a 50 - 80% germination success rate in burial depths of 1 - 8+ cm depth may be an important adaptation tactic. As Barbour et al (1985;p313) note, "beach and foredune species appear to have larger seeds than dune species, implying an ability to successfully send up a seedling from a deeply buried seed" (cf.Van der Valk,1974).

Since strandline and pioneer plants germinate in a region where maximum sand transport and deposition takes place, they are capable of responding to accretion once established (Ranwell,1972; Anderson and Taylor, 1979; Disraeli,1984; Hesp, in press). Figure 1 illustrates the effects of temperature regime and sand accretion on Spinifex sericeus, a 25 cm high, perennial native grass with stout rhizomes and stolons (Hesp, 1983). The growth curves for Spinifex (expressed as number of shoots per square metre) parallel the temperature regime quite closely, and similar relationships have been found for other dune plants (e.g. Watkinson et al, 1979). However, this seasonal growth cycle is tempered by the degree of sand burial/accretion. Whilst the 14 - 15 m, 17 - 18 m and 23 -24 m locations were all actively accreting (although at different rates) the 5 - 6 m location experienced slight erosion (a total of 20 cm vertical change) over the monitoring period. Plant numbers were low and barely responded to a seasonal regime. The 14 - 15 m zone initially displayed the greatest number of shoots, but as the locus of maximum sand deposition shifted seawards, as indicated by the topographic profiles, the 17 - 18 m zone replaced the former zone as the area with greatest plant numbers. This zone was itself replaced by the 23 - 24 m zone as the area of maximum sand deposition and hence maximum shoot development. Thus, there exists a positive feedback mechanism, whereby in the zone where sand deposition is greatest, plant growth is encouraged, the aerodynamic roughness is increased, and as long as seaward colonization processes are limited, sand deposition within this higher density zone is enhanced (Hesp, 1983; Hesp, in press).

It has been observed that some plant species may show an ecotypic response to varying rates of sand burial (de Jong and Barbour, 1979). In other cases it seems that very similar species within a genus may evolve or adapt to varying stress levels. For example, Spinifex sericeus and Spinifex hirsutus were, until recently, considered the same species (i.e.S.hirsutus);(Craig, 1985). However, S. sericeus principally growing on the east coast, is characterized by a fine stem, thin leaves and is around 25 cm high. On this coast, daily onshore sand transport rates are moderate and the climate is relatively mild. S. hirsutus, growing on the west coast, is taller (~35 cm +), much more robust (triple the stem thickness of S. Sericeus), and the leaves are much broader and more hairy. On the west coast, seabreezes may be the strongest in the world and summer afternoon sand transport rates are considerable. The climate is considerably more arid than the east coast. Are these morphological differences between the species a response or adaptation on the part of Spinifex hirsutus (W.coast) to increased sand transport, abrasion and deposition rates and greater aridity compared to S. sericeus (E.coast)? If the answer is yes, then hybridity in this genus (2 - 3 hybrids occur) may be the best adaptive strategy for species occupying environments in between the east and west coast species!

Several theories have been proposed to explain how metabolic behaviour may interact with sand burial (e.g. Marshall, 1965). These include competition, plant age, soil pH, allelopathy, soil microflora and aeration, rate of root growth and nutrient supply (Barbour et al, 1985). "Whatever the cause of the stimulation, the ability to respond to accretion and to withstand abrasion from sand grains are undoubtedly important parts of the adaption to growth on sandy strands....." (Lee and Ignaciuk, 1985,p.322).

DRYNESS

The term 'dryness' is preferred to drought since in many dune systems, a drought is a nearly year round event compared to many non-dune ecosystems.

There are three sources of non-saline water available to vegetation, namely, precipitation, fog and dew, the water table, and so-called 'internal dew' formation (Barbour et al, 1985). Rainfall and fog are probably the most important, fog uptake and/or ordinary dew perhaps increasing with a trend towards semi-arid and arid coastlines (Craig et al, 1983). According to Salisbury (1952) soil moisture storage is rapidly exhausted during dry periods because of the low-water holding capacity of "coarse" sand. However, storage also depends on grain size and compaction, and surface or near-surface drying acts to produce a thermal over-blanket which protects deeper layers (10 cm +) from moisture loss (e.g. Hyde and Wasson, 1983; Hesp and Thom, in press). Moisture loss may therefore be somewhat over-stated in some cases.

Nevertheless, the lack of, or limited availability of water is a primary stress in the coastal dune ecosystem, and many plants have adapted in many various ways to water stress (Table 1). These adaptations include (i) leaf rolling, which as Pavlik (1983) shows, not only increases the osmotic adjustment at the expense of photosynthesis, but is complimented by the partitioning of resources into the development of a more extensive and dense canopy; (ii) leaf orientation or phototropism where plants operate to have a minimum surface area to the sun; (iii) leaf hairiness which occurs in many species, and which can increase the surface area for heat dissipation, protect the plant surface from direct sunlight, increase the reflectance of the surface, and produce a boundary layer of still air next to the stomata which acts to trap moisture and reduce evaporation (Crawley, 1986); (iv) an epicuticular wax layer which increases the plants albedo and reduces overheating of the leaves; (v) succulence which may be achieved by a variety of means; (vi) mechanical resistance (or sclerophlly) which acts to support the leaf structure during dessicated periods, and may reduce the abrasive effects of blowing sand; (vii) efficient water use; (viii) root adaptations such as developing deep tap roots which are capable of tapping water from the capillary fringe above the permanent water table (phraetophylly), or developing shallow, wide spreading roots which maximize absorption of periodic rainfall; (ix) an aerodynamic growth form whereby, for example, a "cushion" morphology allows an aerodynamic resistance layer to form over the plants thereby reducing temperature and vapour pressure gradients between the plant surface and the air and hence decrease evaporation; (x) C4 and CAM photosynthesis; (xi) increased heat tolerance; and (xii) various osmotic adaptions.

C_4 and CAM Photosynthesis

C_4 and CAM photosynthesis are important adaptations whereby efficient water use is maximised. Plants lose water as they take up CO_2 from the atmosphere, and must approach a compromise between CO_2 uptake and water loss to survive (Mooney, 1986). Photosynthetic rate decreases with increasing water stress due to either stomatal closure or desiccation, and a starvation effect may result if the

CO_2 evolved in respiration exceeds that fixed in photosynthesis (Ashenden, 1978). C_4 species possess mechanisms for maintaining the site of carboxylation at high CO_2 concentrations, thus C_4 plants are able to saturate net photosynthesis at higher internal CO_2 concentrations than C_3 plants, and they therefore lose identical amounts of water but the C_4 plants have a higher water use efficiency since they will fix more carbon (Mooney, 1986). A C_4 photosynthetic system continues to function up to 45° - $60^\circ C$ compared to a C_3 system which only operates up to 35° - $45^\circ C$ (Crawley, 1986).

CAM (Crassulacean acid metabolism) plants also occur in the coastal environment. These plants open their stomata at night rather than during the heat of the day. CO_2 diffuses into the leaf at night by using stored energy, and during the day, when the stomata are closed, the stored CO_2 is refixed via the C_3 pathway using light energy. CAM plants have an even higher water use efficiency than C_4 plants because they only open their stomata at night when evaporative water loss is minimal (Mooney, 1986).

Xylem-sap Tensions and Tap root Development

De Jong (1979) indicates that beach species may have evolved unique tactics to utilizing water resources. In a study comparing _Ambrosia chamissonis_, _Abronia maritima_, _Atriplex leucophylla_ and _Cakile maritima_, De Jong found that _Atriplex leucophylla_ (a C_4 plant) exhibited a marked seasonal pattern of dawn xylem-sap tension, developed relatively high midday tensions (on clear days), recovered slowly from high midday tensions, and had a small taproot with an extensive development of fine shallow roots (<40 cm deep). In contrast, Ambrosia chamissonis exhibited little seasonal fluctuation in dawn xylem-sap tension, maintained relatively low tensions, by dusk was able to recover almost completely from the maximum midday tensions, and had one central taproot extending down more than 100 cm before producing extensive fine branches. De Jong (1979) states that the summer-autumn loss of leaves by Ambrosia may also reduce water loss and explain the non-seasonality of xylem-sap tensions. Abronia and Cakile appeared to occupy an intermediate position to the above species with regard to water relations. Thus, at least three tactics of water use in addition to succulence and C_4 photosynthesis are being utilized here : tap-rooted species utilizing the water table (e.g. Ambrosia), shallow-rooted perennials utilizing precipitation and possibly internal dew (e.g. Atriplex), and moderate to shallow rooting annuals (Cakile) which can complete their life cycle prior to the onset of drought (De Jong, 1978;1979; Boorman, 1982; Barbour et al, 1985).

Accumulation of stress metabolites

Solutes may accumulate in plants as a response to water stress and salinity (Stewart et al, 1979; Aspinall and Paleg, 1981; Smirnoff and Stewart, 1985). The solutes include proline, betaines, amino acids, sugars and polyols (sugar alcohols), and have been termed stress metabolites or compatible solutes (Smirnoff and Stewart, 1985). In halophytes, stress metabolites are "thought to act as cytoplasmic osmotica to balance the low osmotic potential of the vacuoles where NaCl is stored, as well as to balance the low water potential of saline soil solutions by increasing the plants heat tolerances" (Smirnoff and Stewart, 1985,p.273). Whilst the adaptive significance of stress metabolites is not fully accepted, Smirnoff and Stewart (p.277) argue cogently that "any small increase in enzyme heat stability caused by the accumulation of stress metabolites would then lead to a shorter lag period in the resumption of full metabolic rates when favourable conditions return". On an ecological level, this would lead to enhanced growth and greater competitive ability and reproduction.

SAND SALINITY

Salt spray is semi-continuously supplied to dunes in most coastal environments, and whilst a proportion of this spray is intercepted by plants (see previous section) much of it is also taken into the sand surface. Plants have developed a variety of ways to cope with or adapt to sand salinity (Table 1). These include (i) developing a resistance to salt (e.g. Salsola kali; Lee and Ignaciuk, 1985); (ii) actually utilizing salt whereby the growth of many annual seedlings is stimulated at low NaCl concentrations (~50 mM NaCl; Lee and Ignaciuk, 1985); (iii) development of salt bladders, whereby epidermal trichomes transfer salt to the bladders which burst leaving a matt of salt crystals and waxy bladder fragments as a reflective coating on the leaf. This also increases the albedo of the plant; (iv) succulence (e.g. Cakile sp.; Carpobrotus sp.), and (v) various osmotic adaptions (e.g. De Jong, 1978).

NUTRIENT DEFICIENCY

Seawater contains every element essential for plant growth (Table 2) and the composition of seawater remains remarkably constant over time (Rozema et al., 1985).

Table 2: Mineral composition (mmol/l) of seawater (from Goldberg, 1963, as reported in Rozema et al., 1985).

Element	Seawater	Element	Seawater
Na	460	P	0.002
Cl	560	B	0.400
K	10	Li	0.024
Ca	10	F	0.07
Mg	55	Br	0.800
S	28	Si	0.100
N	0.035		

Thus, in terms of actual availability of mineral nutrients there is, if anything an overabundance, (except N,P,K), and it could well be that stress is due to an excess of some seawater elements (e.g. Na^+, Cl, Fe^{2+}, Mn^{2+}, SO_4^{2-}, S^{2-}, B and other micronutrients) (Rozema et al., 1985). This, of course, depends on the degree to which plants can actually obtain these nutrients via direct foliar uptake (see van der Valk, 1977).

Once the spray, precipitation, dew and fog delivered nutrients are deposited on the sand surface, rapid leaching takes place, the rate increasing with increasing grain size. Nutrients may also be delivered to the foreshore via swash deposition (seaweeds etc.) and sand movement (Ridley, 1930; Bond, 1952; Gemmell et al.,1953; Laing, 1958; Olson, 1958a,b; Cooper, 1958; Steers, 1964; Leatherman, 1979; Hesp, 1984, in press).

Plants in this environment respond to nutrient deficiencies by (i) having flexible allocation patterns (e.g. by plasticity with the root system such that the plant is able to proliferate lateral roots in localized zones of higher nutrient availability (Pemadasa and Lovell, 1974); (ii) redistributing nutrients (see below); (iii) take up nitrogen via rhizosphere bacterial activity; (iv) obtain phosphorus via endomycorrhizae fungi (see below); (v) enhance their competitive stance in the presence of localized higher nutrient supplies (van Dijk et al., 1985); restricting or enhancing the use of various ions, especially inorganic ions (Stewart et al., 1979); and having a range of ways by which to uptake nutrients (e.g. Cakile maritima and Salsola kali depend on spray for their supply of Mg, whilst Atriplex hastata and A. littoralis absorb Mg from the sand; Rozema et al., 1982).

Nutrient Translocation

Some coastal plants (particularly annuals ?) are capable of translocating nutrients from ageing leaves and from stems to developing leaves and fruits (Pemadasa and Lovell, 1974). Noble and Marshall (1983) found that growth development in Carex arenaria was closely correlated with a gradient of nitrogen concentration within the clone, the result being that the region of active vegetative growth displayed a significantly higher nitrogen concentration than any other part of the clone. Ernst (1983) found that Phleum arenarium was characterized by a notable internal translocation of N and P from vegetative to generative organs. He noted that this was not only related to nutrient deficiency of the habitat but that the seed is the only efficient nutrient sink (i.e. the next generation).

Nitrogen Fixation and Endomycorrhizae

Many studies conducted in coastal dunes have found that nitrogen appears to be the major nutrient limiting plant growth (Willis, 1963, 1965; Willis et al., 1959; Stewart et al., 1973, 1979; Skiba and Wainwright, 1984), although phosphorus and potassium are also regarded as critical, and are often in low quantities (see Table 2; Kachi and Hirose, 1983; van der Valk, 1974; Anderson and Taylor, 1979).. Thus it is important for some plants to have methods by which N, P, K and other nutrients may be fixed or accumulated. Nitrogen fixation by rhizosphere bacteria has been found in some dune plants (e.g. Hassouna and Wareing, 1964; Ahmad and Neckelmann, 1978; Abdel Wahab and Wareing, 1980), but not in others (e.g. Holton, 1980 cited in Barbour et al., 1985).

Endomycorrhizae have also been found in sand dunes (Nicholson, 1960; Ernst, 1983). In a study of fungal hyphae in sand dunes, Jehne and Thompson (1981) found that there was a strong correlation between the presence of sesquioxide coatings of phosphorus around sand grains and the presence of fungal hyphae. They suggest that the fungal hyphae are involved in the uptake of nutrients from the sand grain coatings, and that since the hyphae are associated with the roots of colonizing plant seedlings, the seedlings may have the capacity to obtain these nutrients.

It is difficult to attach adaptive significance to nutrient gathering processes such as nitrogen fixation and fungal hyphae, but it may be that certain plants have adaptations which allow them to utilize these sources whilst others have not.

VARIOUS STRESSES

All the stresses listed above may combine in various ways that are not at present clearly understood to induce adaptations in coastal plant species (Table 1). Some of these apparent adaptations include (i) hygroscopic leaf movement whereby e.g. the outer leaves of mosses (which can be quite common pioneer plants) curl around the apical buds protecting the plant from dessication, increasing the plant's albedo, and allowing the moss when buried by sand to 'wriggle' and shed sand (Dilks and Proctor, 1974; Moore and Scott, 1979); (ii) variation of the plants' life cycle and flowering times, whereby e.g. the timing of flowering may be accelerated during times of nutrient deficiency (e.g. Phleum arenarium; Ernst, 1983), flowering times may be extended (Herrera, 1986), or delayed (van der Meijden and van der Waals-Kooi, 1979); (iii) mechanisms of seed dispersal (see above); (iv) seed morphological variations such that increases in seed weight correlate with germination depth and rate of sand inundation (Platt, unpub. cited in Barbour et al., 1985; van der Valk, 1974); (v) germination strategies whereby e.g. some plants complete their life cycles prior to the onset of summer drought stress (Boorman, 1982); (vi) plant morphology may be varied (see discussion on Spinifex sp. above); (vii) stand density may be varied to cope with competition (e.g. Festuca rubra, Pemadasa and Lovell, 1974) and (viii) some plants may reduce their leaf size (Ernst, 1983).

ADAPTATIONS TO PHYSICAL STRESS IN THE HIND DUNE ENVIRONMENT

In the previous section I attempted to list and outline many of the beach-foredune plant adaptive tactics. Many of these adaptive tactics are also common in plants which inhabit dunes lying landward of the foredune complex.

In general, if one follows the typical European system of dune classification (one, incidentally, in dire need of change), i.e. embryo, white or yellow dune (sometimes mobile, sometimes less so) grey dune and brown dune phases, there is a very general tendency to find that with increasing distance landwards (or increasing age) organic matter increases, pH decreases, the percentage of $CaCo_3$

decreases, salt spray fallout decreases, and sand transport and deposition decreases (Salisbury, 1952; Ranwell, 1972; Hundt, 1985). These trends apply only to the stable (relatively well vegetated) dune systems and in areas in which there is a reasonable rainfall. Such trends are often accompanied by various plant successional trends, where pioneer plants are gradually replaced by others as soil nitrogen and other nutrient levels increase or stress levels decrease. Total plant biomass typically increases landwards and plant structure changes from pioneer herbs and forbs to shrubs to trees (Ranwell, 1972). These trends are exemplified in studies on coastal dune successions (e.g. Smith, *et al.*, 1985; Kirkpatrick and Hassall, 1981; Migahid *et al.*, 1971, van Tooren *et al.*, 1983; Moreno-Casasola and Espejel, 1986; Johnson, 1982; Barbour and Johnson, 1977; Cowles, 1899; Olson, 1958a, 1958b; Robertson and Vitousek, 1981; Weisser and Backer, 1985; Weisser *et al.*, 1982; Hobbs and Grace, 1981; van der Laan, 1985; Cramer and Hytteborn, 1987, Hundt, 1985) and will not be dealt with here.

Whilst sand transport and deposition and salt spray deposition may decline markedly with distance away, or downwind of the beach (Figure 2; Boyce, 1954; Edwards and Clayton, 1964; van der Valk, 1974; Cartica and Quinn, 1980; Rozema *et al.*, 1985) the incidence of drought (localized or seasonal), high sand surface temperatures and a wide temperature range, high solar radiation, wind exposure, water-logging (particularly in slacks and deflation basins) and low nutrient levels may still be significant across the hind dune system. Thus, many of the adaptive tactics employed by beach and foredune plants (Table 1) are also utilized by, or characteristic of the hind dune plants.

Adaptations to competition, nutrient gathering, growth habit and performance, and saline and water-logged sands can also be important in this environment.

Perennial species are common in the dune system. For many of these species propagation by budding is an essential tactic in an environment where sand movement and seasonal water-logging endanger seedling survival (Cordazzo and Seeliger, 1988). Such a tactic also enhances propagation since it is common to find relatively sparsely vegetated areas which experience a considerable range of daily air and surface temperature changes (Hundt, 1985; Watkinson and Davy, 1985; Boaden and Seed, 1985).

Competition for limited resources is common. For example, a vigorously growing dense population of established plants of Festuca rubra is quite effective in reducing the change of survival of adjacent annual plants. Vegetative growth of four annuals examined by Pemadasa and Lovell (1974b) was greatly reduced in the pressence of F. rubra, and this reduction was intensified with increasing density and soil fertility (Pemadasa and Lovell, 1974b). Plasticity in plants is therefore an important adaptive tactic.

Annual species are very common in many sand dune systems. Of several dune annuals, biennials and perennials examined by Boorman (1982), the annuals displayed very high initial growth rates, whilst the perennial species displayed variable, but rather low relative growth rates. The winter annuals tended to be drought-avoiders by completing their life-cycle prior to the onset of summer drought. Biennials such as Cynoglossum and Lactuca widely differ in their growth form, adaptive tactics and behaviour. Cynoglossum has a low growth rate, grows in disturbed, more open areas, has a large seed, and overwinters as a hemicryptophyte with a robust tap root, whilst Lactuca displays a high growth rate, grows in dense

Ammophila or Festuca rubra swards, and has a fibrous root-system with a semi-persistent winter rosette.

Annuals are generally restricted to the drier areas of the semi-fixed and fixed dune systems and are very rare or absent from wet stands in the slacks (Watkinson *et al.*, 1979). It appears that the annuals are present where drought prevents a full cover of perennials (Pemadasa *et al.*, 1974; Pemadasa and Lovell, 1974a). Different annual species occupy characteristically different habitats, some species being favoured by moderate soil moisture regimes and some being more successful in low moisture regimes (Pemadasa and Lovell, 1974c).

In a study of Dactylis glomerata, Ashenden (1978) found that populations of Dactylis growing in dry sites were well adapted to growth in drought-prone periods. Compared to wet sites, dry site populations were able to maintain high relative water contents with low transpiration rates, displayed low stomatal frequencies (driest sites), had a higher density of leaf cuticular waxes and had narrower leaves (thus reducing total transpiring surfaces of the plants).

Annual species appear to compete for space and nutrients and commonly flower in a well-defined sequence (Pemadasa and Lovell, 1974; Watkinson and Davy, 1985).

There is also ranking within the annual species. Mack and Harper (1977) described an ordering of the aggressiveness of the species Vulpia fasciculata > Phleum arenarium > Mibora minima > Cerastium atrovirens > Saxifraga (cf. Rogers, 1980). Dune annuals have low competitive indices as defined by Grime (1974) with small size, limited lateral spread and little or no litter accumulation (Boorman, 1982). Watkinson *et al.* (1979) believe the hierarchy above is a direct function of the length of the growing season of the species. They state that Vulpia fasciculata is relatively larger than the other annuals and more completely dominates these "presumably" through competition for nutrients. Thus, competition is inextricably mixed with adaptive tactic here since root adaptations or greater nutrient gathering abilities increase the competitive edge of the plant. A characteristic feature of the annuals is their depauperate form; Many bear only a single shoot. Watkinson *et al.* (1979) reason that this may be because the limited nutrient capital available is transported from one leaf to another and finally to the inflorescence. Additionally, it is of interest that the whole life cycle of the small annuals is completed during the period of the lowest flux in shoot nodules in the perennials (Watkinson *et al.*, 1979).

The ability to translocate nutrients can be very important in the dunes. Restricted growth of many species is caused mainly by the limitations of the major nutrients rather than the minor elements, with nitrogen being especially important (Pemadasa and Lovell, 1974a). The sparseness and dwarfed growth form of much of the coastal vegetation has been attributed to severe deficiencies of the major nutrients (Willis and Yemm, 1961; Willis, 1963, 1965).

An adaptive ability to alter flowering time or maximise seed output enhances plant viability and germination. Studies conducted in a Spanish (Mediterranean-type) coastal shrubland showed that uninterrupted flowering activity took place throughout the year, heavy flowering occurred at times of good moisture status (e.g. after winter rains, as in most Mediterranean ecosystems), but varied according to species groups (Herrera, 1986). Typical Mediterranean taxa flowered in the wet to dry season transition period. This species group have shallow roots, lack storage organs and tend to occupy the driest sites. Herrera (1986) believed that since seed dispersal in this group is by inanimate vectors, summer is as good a dispersal time as any. In contrast, a species group which depended on vertebrate dispersal and therefore needed to match fruiting season with abundance of avian dispersers, invariably were long-lived, deep-rooted perennials (often with lignotubers or burls) having access to longer lasting water supplies.

Adaptive tactics to fire are common particularly in the Mediterranean coastal shrublands and heaths. Adaptations of reproduction strategies can be important with plants growing flowers attracting animal, bird and insect life providing a food source of pollen and seed dispersal by the development of colourful, fragrant reproductive structures (e.g. Soutamire, 1983; Gould League, 1984).

Wind exposure can be quite high in the hind dune environment and leads to reduced leaf growth due to shaking, leaf damage due to collision with other plant parts, increased transpiration rates and water loss and leaf tip burning (Grace, 1981; Grace and Russell, 1982). Adaptations and responses to this stress include closing of stomatas in the presence of wind (due possibly to shock sensitive guard cells) and hence a reduction in plant water stress.

The extend of leaf dessication that does occur is influenced by the canopy of the species in question. A plant possessing an upright open crown would have a high salt deposition efficiency, whereas a closed heath-like canopy, presents only a small proportion of its foliage to the sea wind. This efficiency is exemplified by the habits of many coastal plants, in which the windward shoots and leaves are effectively desiccated or absent, while the more protected leeward shoots grow relatively unhindered. Translocation of chloride ions (in damaging concentrations) to the leeward shoots, does not occur, thus resulting in a coastal species exhibiting a wedge shaped habit, angling upwards away from the sea. The angle of canopy depends on the intensity of the wind and its salt content. The higher the wind and salt spray intensity, the lower the canopy angle (Boyce, 1954).

Slacks and deflation basins are common in the coastal dune environment. They may be moist (relatively dry) to very wet, and may experience salt incursion in some cases. Slacks typically display a high species richness (Ranwell, 1972; Lubke, 1983; Thalen, 1971; Hope-Simpson and Yemm, 1979; van der Maarel and Leertouwer, 1967) but exeptions do occur (Sykes and Wilson, 1987). Organic contents and nutrient status can be considerably higher than in adjacent dunes (Ranwell, 1972). As Sykes and Wilson (1987) note, slacks often contain a mosaic of plant communities, and the balance of submergence to drought, related to microtopography, is the main environmental influence in all slacks.

A variety of adaptive tactics may be utilised by plants in the slack environment. These include (i) avoidance of germination at unfavourable salinity levels by a strong enforced dormancy (Schat and Scholten, 1985); (ii) seed polymorphism leading to extended periods of germination, which could act to reduce the potentially catastrophic effects of unpredictable fluctuations in salinity; (iii) high juvenile salt resistance (Schat and Scholten, 1985); (iv) an ability to acquire salt resistance with age; (v) xeromorphy, which in this environment may be utilized to reduce the velocity of water movement to the root surface (Armstrong, 1975); (vi) development of the "shaving brush" effect where in an area with a fluctuating water table, root apices are destroyed but root bases remain healthy and new laterals grow from these at the new level (Armstrong, 1975); (vii) explosive germination in combination with extensive seed dispersal (Schat, 1983); (viii) small seed size, which may increase the life-span of buried seeds and prevent seed mortality due to stagnating water (Schat, 1983); (ix) having a well-developed system of intercellular lacunae (aerenchyma) with which shoots can be provided with oxygen via the shoot (Armstron, 1975; e.g. Juncus sp., Schat, 1984); and (x) radial oxygen loss which may prevent excessive uptake of iron and manganese and hence reduce toxicity (Armstrong, 1975).

Levels of Stress in Dune Terrains

The foregoing provides only a limited discussion of the kinds of adaptations to physical stress that may occur in the whole dune ecosystem. This is at least partly because there appears to have been far less research done on the adaptive tactics of higher life forms on dunes, especially on relatively stable dunes, compared to foredunes. The discussion does not provide any indication either, of the levels or types of stress that occur on different dune types. Because of centuries of use, and animal and man-induced change, it is not always easy to distinguish dune type (or evolutionary history) on the European dune terrains. Hence the use of non-genetic terms to describe dune "types" (e.g. white and grey dunes) and the resulting incomparability between dune systems (I would defy many ecologists to accurately define the soil nutrient status, degree of organic accumulation and podsolization in e.g. a 'grey' soil across European dune systems). This is much less of a problem in the Americas', Africa and Australasia, and it is usually relatively easy to define dune types.

In the following, I will briefly outline the levels and degree of physical (abiotic) stress in the major coastal dune types, (apart from foredunes) in order to provide a rough idea of the degree of adaptation to physical stress that might be required within each type.

Blowouts

Blowouts are wind-eroded troughs and hollows and are particularly common in the foredune, but may also occur in all other dune types. Whenever or wherever they occur, they disrupt the local floral patterns and successional trends by surface erosion and substrate undermining, by sand inundation, wind acceleration and local enhancement of salt aerosol transport further inland from the beach. Where blowouts are eroded down to the water table or some other base level (e.g. a calcrete horizon), water-logging, ponding or virtually impenetrable surfaces may be produced. Thus, many of the beach-foredune stresses are locally produced within or immediately adjacent to the blowout, and plant pioneers or colonizers and survivers display many of the foredune plant adaptations.

Relict Foredune Plains

Where beaches are prograding (or accreting seawards) new incipient foredunes and established foredunes are formed and the previous foredune becomes relict (Hesp, 1984). Over time (decades to thousands of years) a plain of foredunes, now relict, may be formed. These are particularly common in Australasia but occur in all parts of the world (e.g. Thom, 1983; Thom *et al.*, 1981). In regions of moderate to high rainfall, and where the percent of carbonate sand is low, these plains commonly display classic zonation patterns in the flora (herbs to large trees) and soil such that the degree of podsolization increases landwards, moisture and nutrient status increases landwards, and apart from the incidence of fire, most stress factors decrease dramatically with distance away from the beach. However, in Mediterranean and semi-arid regions, a low heath typically represents the final successional stage and low rainfall, moisture stress, low nutrient availability and where $CaCo_3$ % is high, a cementing substrate all add physical stresses. These do not typically reduce with dune age landwards (Hesp, pers.obs.).

Parabolic Dunes

Parabolic dunes are upsiloidal or U-shaped or hair-pin shaped dunes which often evolve from blowouts. Two types are common, imbricate (nested) types (Tinley, 1985) and long-walled types (Hesp *et al.*, in press; Pye, 1982). Active parabolic dunes display three main morphological elements: a central deflation basin; elongate, trailing lateral ridges; and a depositional lobe (sometimes extensive and covered by transverse dunes). The upwind edge of the depositional lobe is eroded by the wind, and sand is transported over the lobe and deposited on the downwind (advancing) slipface. Here most vegetation (often heath or forest) is buried and destroyed. As the windward edge of the depositional lobe is eroded, a deflation basin forms, the base of which is determined by the lowest seasonal water table or by a calcrete layer. Once eroded to base level, plants can re-establish and a reversed successional sequence is formed. That is, pioneer species colonize the base first, then low shrubs, tall shrubs and possibly trees (depending on climatic zone). The successional trend is reversed, because here the pioneers are furtherest from the coast and the latter successional flora closest to the coast. The trailing ridges are formed where plants growing along the margins of the depositional lobe manage to trap some of the lobe sand and retain it as the lobe advances away downwind. In Australia, such species are typically Acacias, in which root and shoot development is encouraged by some sand burial.

Thus, in the active parabolic dune environment there are a range of stresses which are applied discreetly at different places on a parabolic dune. On the downwind axial edge of the depositional lobe, sand burial is the greatest stress. Along the lateral margins of the lobe, sand burial is still relatively high but some plants (e.g. Acacia sp.) are adapted to cope (and may even be encouraged by) some burial. As the parabolic lobe moves downwind the inside edge of the partially-stabilized lateral ridges are eroded and undermined. On the developing deflation basin, all fine-grained material, nutrients and previous soils may have been removed. Either water-logging or a hard, cemented surface may add further stress to a pioneer plant in this region of the parabolic dune (Hesp and Pelham, 1984); Figure 3).

Transgressive Dunefields

Transgressive dunefields are broad, relatively free-moving or mobile, sand sheets or fields when active (Hesp and Thom, in press). They commonly display a wide variety of sub-environments including extensive deflation basins, plains and slacks, large migrating transverse and oblique dunes, a (sometimes massive) precipitation ridge or long-walled slipface extending along the landward margin of the dunefield, various erosional dune forms including remnant knobs, and various depositional dune forms including coppice dunes, shadow dunes, depositional knobs and bush pockets (Hunter *et al.*, 1983; Hesp and Thom, in press).

Physical stress levels are high in many places since sand transport, deposition and erosion dominate the environment. Soil moisture and nutrient levels may be very low, and stresses associated with ponding, water-logging and highly variable daily and seasonal moisture status may be high. Nearly all the stresses outlined for the beach/foredune complex apart from high salt spray levels may be present, with sand deposition/erosion rates being greater in many circumstances (Figure 3).

Overall, the degree of physical stress (and therefore the degree of plant adaptations to these stresses) is probably very high in the beach-foredune environment, (and hence also very high in the overwash-dominated barrier types), high in foredune blowouts and on active transgressive dunefields, moderate in the parabolic dune environment and relatively low across relict foredune plains.

GLOBAL PATTERNS OF COASTAL PLANT ECOLOGY AND ADAPTATIONS

It has been established in a limited way, that there exist regional variations in species richness and other variables in coastal beach-dune environments (e.g. Barbour and Johnson, 1977; Barbour et al., 1987; Cordazzo and Seeliger, 1988). Here, I wish to speculate on the wider implications of studies such as these, and attempt to define some global patterns in dune ecological systems. I do so with considerable temerity, but in the hope that it may stimulate further discussion and research.

Where studies of regional coastal ecological patterns have been conducted within a narrow range of latitudinal gradient, limited correlations between beach-dune vegetation composition and latitude have been found (e.g. Barbour et al., 1976; Barbour and Johnson, 1977; Barbour et al., 1987). However, studies of coastal plant community structure across a relatively wide range of latitude show that there is a reasonable correlation with latitude and climatic regime (e.g. Johnson, 1977, 1982; Espejel, 1987; Cordazzo and Seeliger, 1988).

In 1985, Henk Doing made a noble attempt to synthesize coastal foredune zonation and succession around the world. Figure 4 is a plot of Doing's species richness data extracted from his Table 1. Some set of Doing's data, that for SW and S. Africa (24° - 34°S) and tropical W. Austrailia (17° - 25°S), has been omitted because it covers too broad a latitudinal gradient, and additional data have been added by the author. Although there is reasonable variation in the data, a general trend is evident which indicates that maximum species richness occurs in the Meditterranean ecosystems around 34° - 45°N and 35°S. A clearer pattern is evident in the northern hemisphere compared to the southern hemisphere. The notably lower values within the data set occur in N. Africa, Namibia and Brazil. In the N. African case and the Namibian case especially, increasing aridity is probably the reason. There are, however, other problems with this data (e.g. Brazil) which are discussed further in Appendix 1, and to which the reader is referred.

Given that we accept for the moment that the data in Figure 4 may not be directly comparable because of the problems outlined in Appendix 1, let us examine the wider ecological implications of the data shown in Figure 4 and subsidiary data.

Figure 5 provides an indication of the global trends in a range of variables across a climatic gradient ranging from boreal to arid coastal sites. In the broadest general fashion we can possibly identify the following trends:

(i) Species richness decreases as the level of environmental stress increases, such that the lowest number of species are found in the coldest and driest/most sandy regions of the world (e.g.central Namibia; Norway and Iceland; Figure 4).

(ii) Species richness decreases in areas where the degree of aeolian sand movement increases (McAtee and Lynn Drawe, 1981; Avis and Lubke, 1984; Hesp, 1988a), and in general the potential for sand movement increases with increasing aridity;

(iii) The number of annual plants decreases and the dominance of perennial plants tends to increase as one trends from the Mediterranean to arid ecosystems. The percentage of annuals in the total flora in Great Britain e.g. tends to be moderate-high (around 40%; Ranwell, 1972; Chapman, 1976), high in Israel (64%), moderate-low in Californian Mediterranean sites (30%; but many introduced species; Barbour et al.,1981), and low-zero in arid to hyper-arid coasts (e.g. Baja California, Mexico coast; Peru; central Namibia);

(iv) The degree of succulence, sclerophylly and heat resistance, and the number of drought-deciduous plants increases with increasing dryness (Barbour et al., 1987; Smirnoff and Stewart,1985). Within a bio-geographical region the same plant species will increase in degree of succulence, and will change its response to sand burial as dryness and the rate of sand inundation increases (De Jong and Barbour, 1979; Barbour et al., 1985; Lee and Ignaciuk, 1985);

(v) The incidence, or numbers of C_4 plants tends to increase with increasing solar radiation and temperature (Johnson, 1982; Barbour et al., 1985; Moreno-Casasola and Espejel, 1986). De Jong (1979) indicates that water stress (as indicated by xylem-sap tensions) increases as aridity increases;

(vi) Shallow, fibrous-rooted taxa with more pronounced xeromorphies predominate in regions of high precipitation and where internal or external dew formation are favourable, and tap-rooted species tend to predominate in drier areas with fresh water table access (Barbour et al., 1985).

(vii) An increasing degree of desert affinity in the coastal flora might be expected as one trends from warm temperate to arid coastal regions. This trend would be increasingly important where coastal regions abut deserts (e.g. Peru, Baja California, N. Africa, Namibia). Barbour et al., (1981) found that 16% of the Israeli dune flora is influenced by flora with desert affinities compared to only 6% of the Californian flora.

(viii) The number of endemic species as a percentage of the total flora would tend to increase with increasing aridity. (Such a trend may of course be tempered by the age and degree of isolation of the flora).

(ix) The list of features above suggests that on a global scale (and ignoring local variations) either the number of adaptations of coastal plants to physical (abiotic stress) and/or the degree of adaptation to physical stress would increase as one trends from warm temperate to arid and sub-polar coastal environments (Figure 5).

A BRIEF COMPARISON BETWEEN COASTAL AND DESERT PLANT ADAPTATIONS

A number of the main adaptive tactics in coastal plants is outlined in Table 1. One would expect that many similar adaptive tactics may exist in desert plants since many of the same environmental stresses occur in both environments. A notable difference is in the occurence of salt spray (except for very near-coastal desert strips).

Desert arid to semi-arid zones are characterised by high evapotranspiration, high average temperatures, high insolation levels, low water/nutrient availability, an excess of evaporation over rainfall, in some instances moderate-high soil salinity, and a substrate which may range from very stable (e.g. stony deserts) to highly mobile (e.g. upper dune slopes) (e.g. Ash and Wasson, 1983). Desert plant responses to this environment and a comparison with coastal flora are briefly outlined below.

(i) In general, desert species richness and density decreases with increasing aridity (see refs. below). This appears to also be th case for coastal dune ecosystems;

(ii) Many desert plants are probably more truly xerophytic than coastal plants. Zohary and Fahn (1952) noted that transpiration rates are higher and cell-sap concentrations are lower in coastal plants compared to desert plants. Whether coastal dune vegetation may even be classified as halophytic or not is in question since the salt content of many beaches is quite low (Barbour et al., 1985; De Jong, 1979);

(iii) Desert perennials may either resist or evade desiccation. Resistance mechanisms include (a) various leaf form/structural adaptations including reduced leaves (= low surface : volume ratio), sunken stomata, trichomes adjacent to the stomata, a thick waxy cuticle (sometimes reflective), heat resistance, sclerophyllous photosynthetic organs (e.g. cladodes, phyllodes); and pubescence; (b) root adaptations and (c) succulence. Many of the coastal species display similar traits. Desert examples include (a) Casuarina sp. which resists desiccation by having a cladode needle form (stem acting as a leaf), leaves which are whorls of tiny scale-like elements at nodes, and stomates sunken in the grooves of a cladode; (b) Acacia sp. which has a petiole acting as a leaf, a low number of stomata and utilizes leaf orientation. Both species possess root nodules containing nitrogen fixing bacteria. Root adaptations include having higher osmotic pressures of root cell solutions allowing increased moisture absorbtion, deep tap roots or wide shallow spreading roots. Succulence in plants such as cacti and Euphorbia sp. provides a low surface to volume ratio of stem and surface roots, leaves which display thick cuticles, few stomata, a predominance of C_4 and CAM photosynthesis, and where the form is often reduced to a spine (see references below);

(iv) Desert plants (particularly shrubs) also evade desiccation. A woody shrub such as e.g. creosote bush (Larrea tridentia) survives 12 months drought, loses leaves and many branches, tolerates considerable dehydration, has small dormant leaf buds, and a widely spreading shallow root system. Whilst some coastal species display one or two of these traits, Larrea and other shrubs appear to be expert at evasion since some individual Larrea plants are considered to be 11,700 years old. Perennial herbs may evade desiccation by having underground storage organs (bulbs, tubers and corms), by remaining dormant for most of the year, and by reactivating shoot growth following rainfall. Mosses, club mosses, ferns and lichens ("resurrection" plants) may be particularly adept at desiccation avoidance (see earlier discussion on mosses). My guess would be that drought evaders make up a higher proportion of the desert flora than the coastal flora (see references below);

(v) Many desert perennials display considerable salt tolerance. For example, Atriplex sp. have epidermal trichomes which transfer salt to bladders. As noted above, the subsequent production of a matt of salt crystals and waxy bladder fragments acts as a reflective coating on the leaf and reduces the albedo of the plant. Many of the Atriplex coastal species also display this ability but few other coastal plants appear to (see references below).

(vi) Ephemeral plants are widespread in the desert flora constituting up 50 - 60% of the flora. Tactics for evading desiccation (ephemerals, when growing, are no more drought resistant than typical mesophytes) include completing a life cycle rapidly following rain (8 days - 8 weeks), surviving dry periods as seeds; germinating in orderly sequences over years from the same seeding episode, releasing seed over time when the fruit is moistened, and impeding long distance dispersal of seed (hygrochasy) to ensure seeds remain in a favourable environment. These tactics are clearly different from those of plants in many coastal environments where the number of ephemeral plants is generally very low (Table 1) (van Tooren et al., 1983; Loria and Noy-Meir, 1980; Bannister, 1970; Beard, 1984; Cowan, 1981; Crawley, 1986; Dilks and Proctor, 1976; Grime, 1979; Noble and Mulham, 1980; Tivy, 1982; Winter et al., 1981; Danin,A. 1983).

(vii) Desert annuals tend to have a very low seed output but a high probability of survival (Went, 1973). Coastal annuals vary considerably, some having a high seed output and a very high death risk, and others the reverse (Symonides, 1974; Watkinson et al., 1979).

In conclusion it appears that desert plants have far fewer adaptive tactics to salt spray aerosols compared to coastal plants, but that in terms of dealing with saline soils, desert plants may have a greater number of salt resistance mechanisms. Desert plants may have less adaptations overall to sand burial compared to coastal plants, but appear to have developed a greater number of adaptations to heat, high light intensity and water and nutrient stress.

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APPENDIX 1 : FOREDUNE SPECIES GLOBAL VARIATION

Why is there the degree of variation in terms of the number of species per 10° latitudinal band in Figure ? For example, in the northern hemisphere, the Meditterranean, N. Africa data displays considerably less species (17) than adjacent Meditterranean sites such as Greece (31), West Portugal and W. Spain (23). Cordazzo and Seeliger's (1988) data (5 - 11 species; 42° S - 26° S) displays a reasonably good trend in isolation, but does not fit the general trend indicated in the remainder of the southern hemisphere data in Figure . The answer is given, in part, by Barbour and Johnson (1977) when they state that (at least across limited latitudinal gradients) general climatic factors (e.g. rainfall, temperature, etc.) are less significant than local, microenvironmental factors such as incidence of salt spray, substrate mobility, presence of introduced taxa, and exposure. Additionally, and perhaps most importantly, the foredune morphological state, its age and its relationship to the landward dune terrain are critical here. Foredune type (or state), size, volume and vegetational status are strongly correlated with surfzone-beach type (Short and Hesp, 1982; Hesp, 1988a, 1988b). Eroding, previously unstable or destabilizing foredunes display considerably less vegetation richness, cover and community diversity than stable, prograding or older foredunes. Dissipative, wide, low-gradient, high energy, fine-medium grained beaches display higher rates of aeolian sand transport, higher salt spray aerosol levels and potentially greatest storm damage over time compared to reflective, low-energy, steep, narrow beaches which display low rates of aeolian sand transport and low levels of salt spray aerosols (Hesp, 1985a). Thus, in figure 1, we are comparing foredunes for which we are ignorant of critical site information such as beach type, beach state (stable, eroding or prograding), foredune state, landward dune state, and even whether the site sample is a one-off sample or a mean of many transects.

These factors may account for the variability in the southern hemisphere data (e.g. Brazil versus the Austrailian data). Hesp (1988a; 1988b) has demonstrated that foredune vegetation richness may vary considerably along one beach. In addition, the status of the more landward dune systems may be important in determining successional trends and species presence. For example, foredunes fronting large, active transgressive dunefields (which may be the case in the Brazilian data) usually display considerably less species (~3 - 6 species) than do foredunes fronting more stable, well vegetated dune systems supporting tree and shrub forms. These may, depending on the energy and nutrient status of the system, eventually colonize the foredune, giving rise to a dune with 23 - 25 species.

CAPTIONS FOR FIGURES

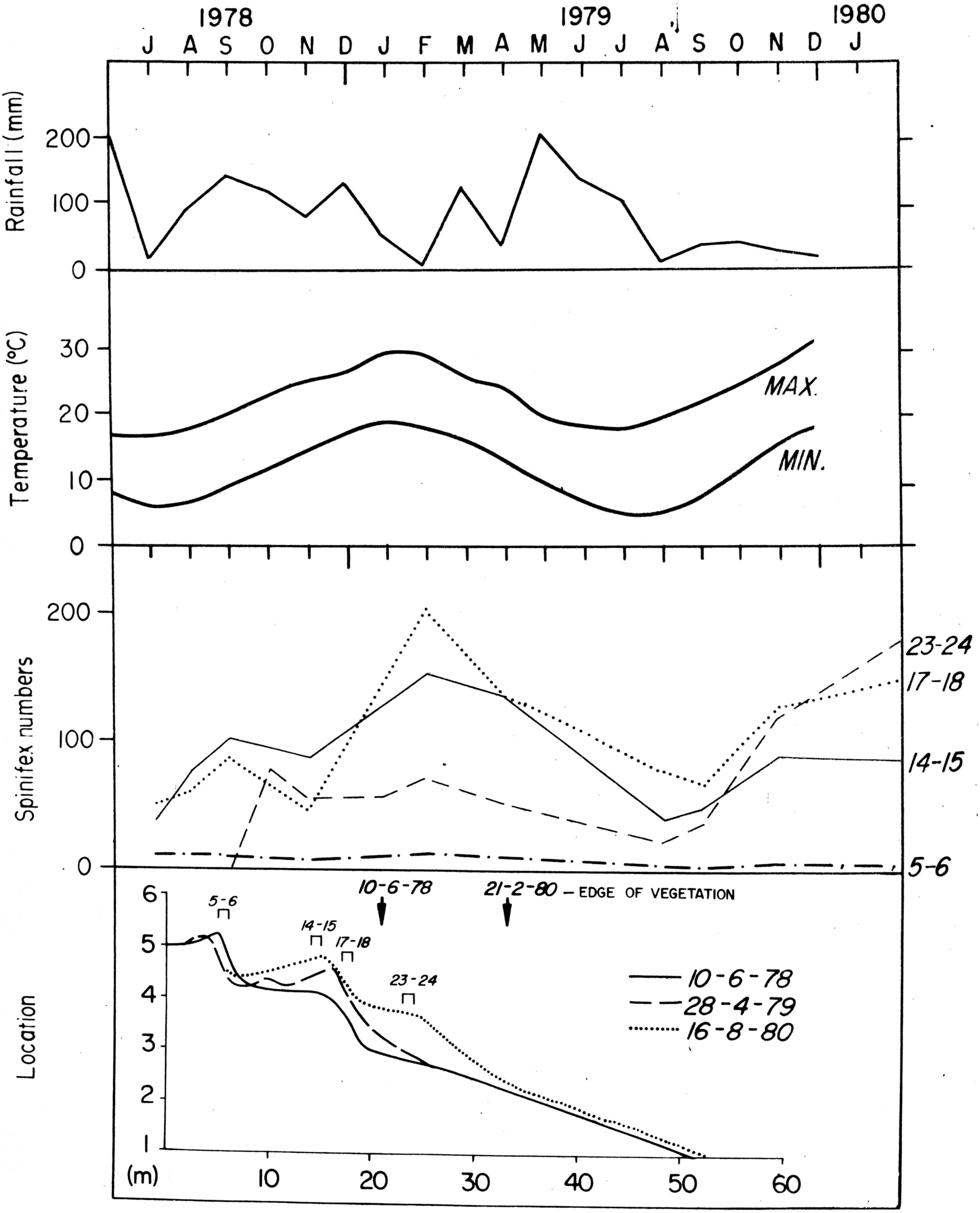
Figure 1: Monthly mean temperature and rainfall data for Williamstown, N.S.W. (the nearest station) and monthly Spinifex numbers measured within four one metre square locations (as indicated) on an incipient foredune in the Myall Lakes region, N.S.W. As the locus of maximum sand deposition shifts seaward as indicated by the foredune profiles, so too does the maximum number of Spinifex shoots recorded. Seasonality is markedly reduced in areas of limited sand deposition or erosion.

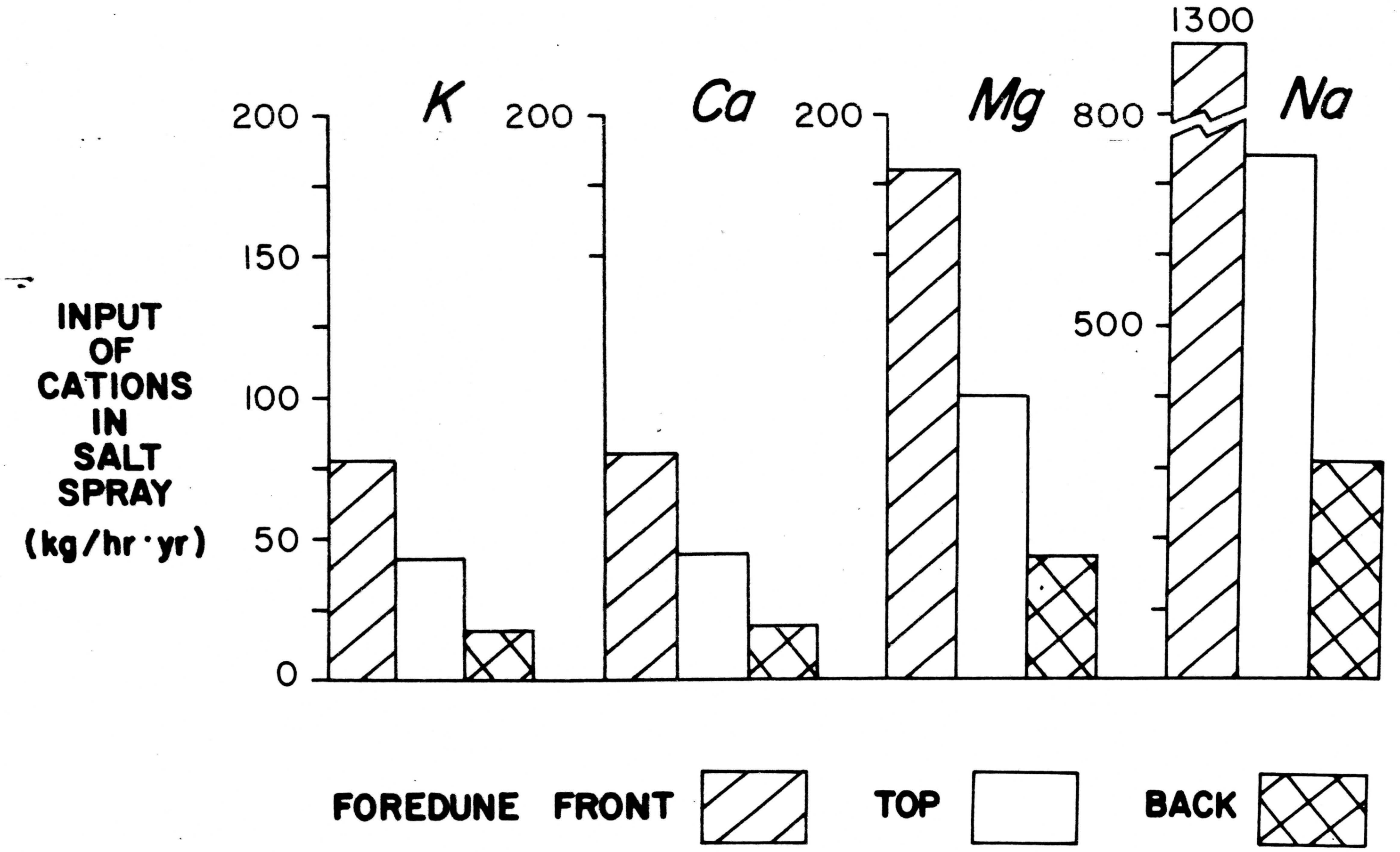
Figure 2: Estimated or calculated annual inputs (kg/ha.yr) of cations in salt spray falling on the front, top and back of a foredune at Bodie Island. Data from van der Valk, 1974.

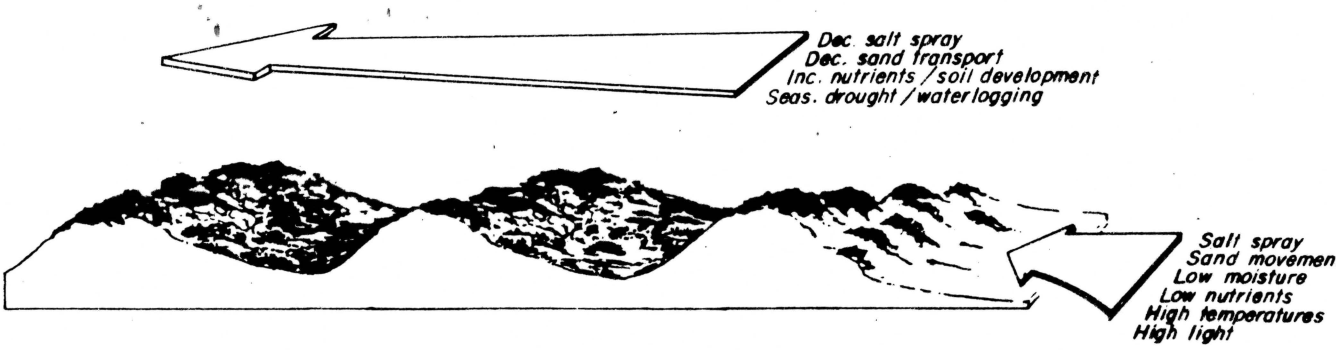
Figure 3: Schematic diagrams of the major coastal dune types, the foredune, relict foredune plain (uppermost), parabolic dune (middle) and transgessive dunefield (lowest), and the types of stress that each dune type incurs. The transgressive dunefield diagram has been modified from Alpha *et al.*, 1983.

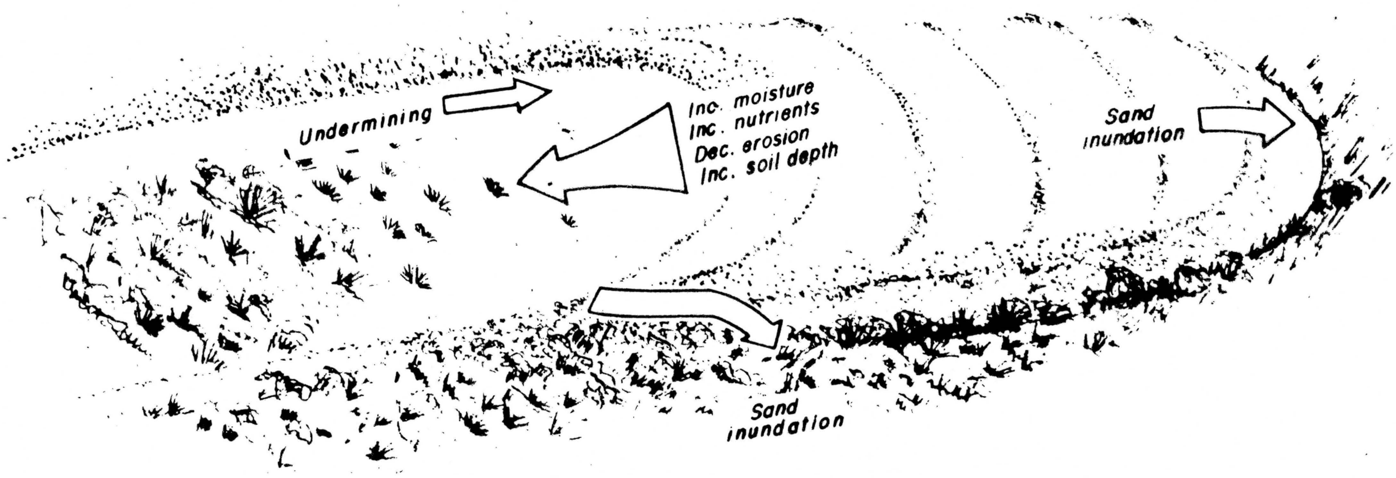
Figure 4: The number of foredune plant species which are found at different latitudes around the world. All data is adapted from Doing (1985) except " Namibia, * central N.S.W., E. Aust., + Ceorong region, S. Aust. (all Hesp obs.); £ Perth, Cresswell and Bridgewater (1985); = S. Island, N.Z., Smith *et al.* (1985); o-o average from: Johnson (1977, 1982), Moreno-Casasola and Espejel (1986), Espejel (1987); x Cordazzo and Seeliger (1988).

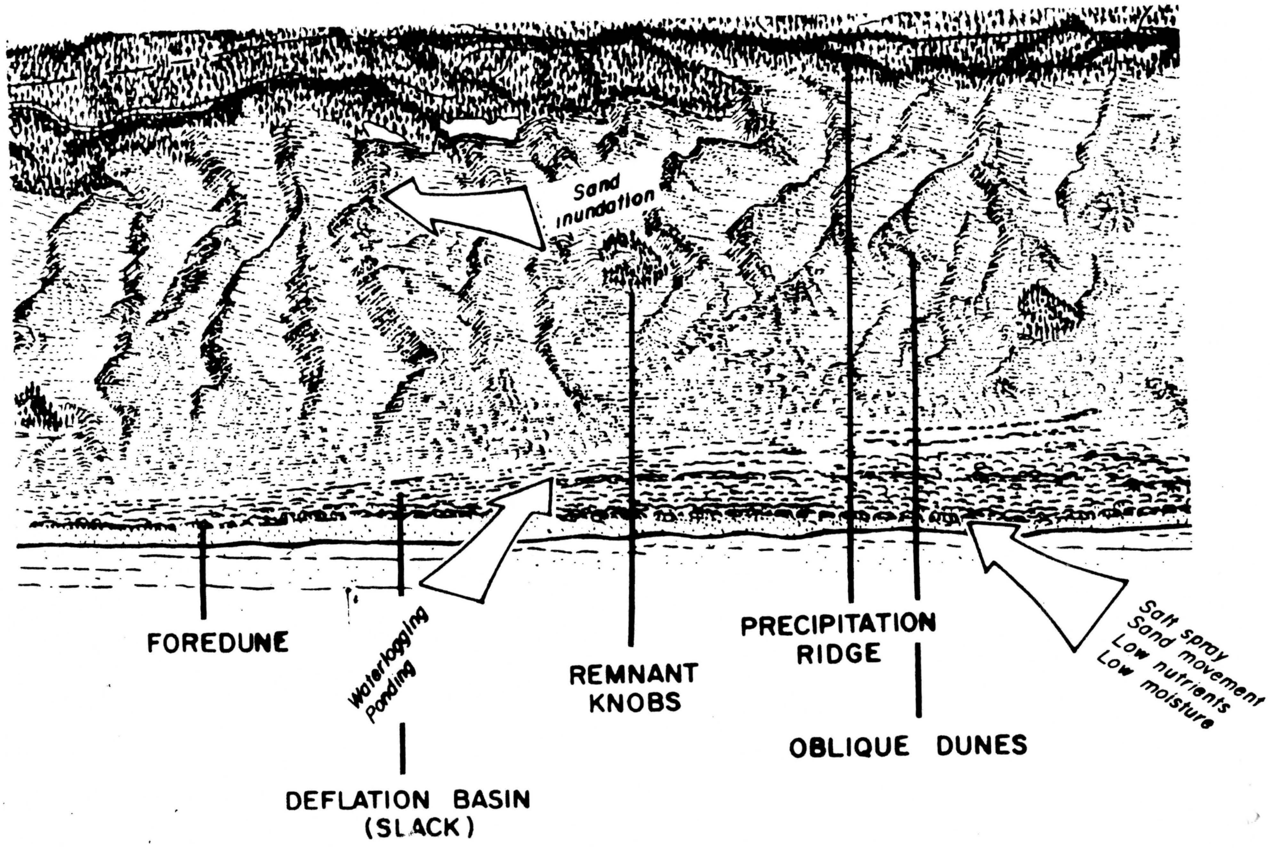
Figure 5: Global ecological trends on coastal dunes.

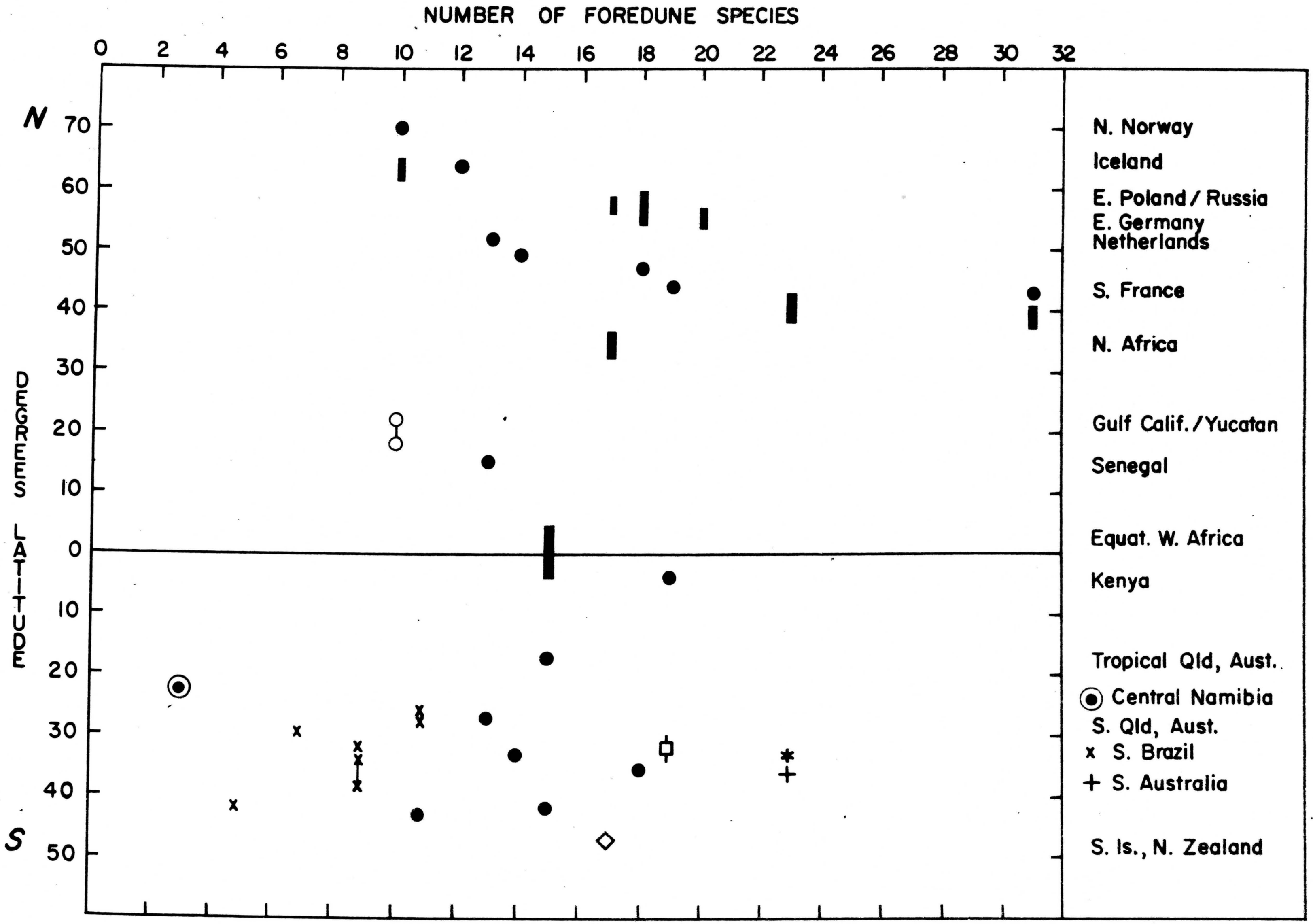

1978
1979
1980
J A S O N D J F M A M J J A S O N D J
Rainfall (mm)
200
100
0
Temperature (°C)
30
20
10
0
MAX.
MIN.
Spinifex numbers
200
100
0
23-24
17-18
14-15
5-6
Location
6
5
4
3
2
1
(m)
10
20
30
40
50
60
10-6-78
21-2-80 – EDGE OF VEGETATION
5-6
14-15
17-18
23-24
10-6-78
28-4-79
16-8-80

INPUT OF CATIONS IN SALT SPRAY (kg/hr·yr)
K
Ca
Mg
Na
200
150
100
50
0
200
200
800
500
1300
FOREDUNE FRONT
TOP
BACK


Dec. salt spray
Dec. sand transport
Inc. nutrients / soil development
Seas. drought / waterlogging
Salt spray
Sand movement
Low moisture
Low nutrients
High temperatures
High light


Undermining
Inc. moisture
Inc. nutrients
Dec. erosion
Inc. soil depth
Sand inundation
Sand inundation


Sand inundation
FOREDUNE
Waterlogging
Ponding
DEFLATION BASIN (SLACK)
REMNANT KNOBS
PRECIPITATION RIDGE
OBLIQUE DUNES
Salt spray
Sand movement
Low nutrients
Low moisture


NUMBER OF FOREDUNE SPECIES
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
N
70
60
50
40
30
20
10
0
10
20
30
40
50
S
DEGREES LATITUDE
N. Norway
Iceland
E. Poland / Russia
E. Germany
Netherlands
S. France
N. Africa
Gulf Calif. / Yucatan
Senegal
Equat. W. Africa
Kenya
Tropical Qld, Aust.
Central Namibia
S. Qld, Aust.
x S. Brazil
+ S. Australia
S. Is., N. Zealand

GLOBAL ECOLOGICAL TRENDS ON COASTAL DUNES