

CLIMATE CHANGE

Impact on Coastal Habitation

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LEWIS PUBLISHERS

Boca Raton Ann Arbor London Tokyo

Climate Change Impact on Coastal Habitation, p. 189-207

Impact of Climatic Change on the Ecology of Temperate Coastal Wetlands, Beaches, and Dunes

Vera Noest, Eddy van der Maarel, and Frank van der Meulen

INTRODUCTION

The possible impact of global climatic change, usually indicated as the greenhouse effect, on the coast and its ecology has caught the attention of the general public, mainly because of the fate of low-lying countries such as lowland Bangladesh or the Maldives facing a catastrophic rise in sea level. Even in countries such as the Netherlands with relatively strong protecting dunes there is much concern for the safety of the western part of the country. Apart from the immediate threat to lives and social organization there are many probable and possible changes in coastal ecosystems to be mentioned. Unfortunately, in most cases our assumptions about the general, i.e., global changes are still rather vague, and, moreover, the possible response of coastal ecosystems and landscapes can hardly be indicated because we lack historical data from which future changes could be derived. This chapter will treat some changes about which a prediction is not entirely unrealistic.

Among the effects put forward in the general discussions on global change the following processes are both of general and of direct interest within the framework of this contribution: an increase of the atmospheric CO₂ content, a general rise in air temperature, and a rise in sea level. From these general changes further changes can be derived, which will be discussed below. Estimations of the intensity or size of the global effects, and of their interrelations, vary largely between experts. In this contribution, global climatic changes are assumed to take place according to the predictions of the Intergovernmental Panel on Climate Change (IPCC).¹

The main features are

- An increase in atmospheric CO₂ content to 450 ppm by the year 2050 and to about 520 ppm by the year 2100
- A rise in temperature of 1°C by 2025 and 3°C before the end of the next century
- A rise in sea level of 18 cm by 2030 and of 44 cm by 2070

Regional climate changes will differ significantly from these global mean values and predictions on a regional scale are much less reliable than the predictions on the global scale. Changes in regional precipitation (total amount and seasonal variation), wind velocity and direction, storm incidence, and the variability of the future climate (i.e., the incidence of extremes) are really hard to predict with a reasonable amount of confidence. However, these factors, in addition to the regional rise in temperature, will have a strong impact on the regional ecosystems, particularly on the interaction between abiotic and biotic processes.

For coastal ecosystems this list has to be extended with changes in storm incidence and changes in tidal range, in addition to a regional rise in sea level.

SPECIAL FEATURES AND MAIN TYPES OF COASTAL ECOSYSTEMS

Coastal ecosystems are all characterized by the proximity of the sea, the relatively strong influence of wind and airborne salt, and a maritime climate, i.e., a climate with smaller differences between summer and winter temperature than further inland. A second factor that distinguishes coasts from many other terrestrial ecosystems is their human use. In order to specify the special features of coastal ecosystems we will adopt a main division into types of coastal landscapes. In accordance with the structure developed in the series *Ecosystems of the World* we first distinguish between wet and dry coastal ecosystems,^{2,3} which are further subdivided into:

- Salt marshes and mud flats
- Mangroves
- Coastal wetlands
- Coastal dunes and beaches
- Sea cliffs
- Raised reefs
- Skerry coasts

This contribution will concentrate on salt marshes and particularly on dunes and beaches. Effects on sea cliffs and skerries are presumably small, but the effects of a rising sea level on coastal wetlands may be large, especially through the loss of flat, low-lying land. The most extensive coastal wetland system is the coastal tundra, which borders much of the Arctic Ocean and the Canadian arctic waters. Indirect implications for the flora and fauna of this zone are difficult to appreciate. Regarding

coastal wetlands in the tropics, we dare not say anything specific. Effects on raised reefs, and on coral reefs in general, will certainly be considerable, but this lies outside the expertise of the authors and, therefore, will not be treated here.

SALT MARSHES AND MUD FLATS

Salt marsh and mud flat systems widely occur in shallow seas or bays. They form mosaics and zonations of ecosystems, which are very important, both economically and ecologically. The main feature of a salt marsh is its zonation in relation to the tidal regime: a gradual transition from bare mud or sand flats at the line of low tide, through a variety of plant communities on the intertidal flat, to either a freshwater marsh or a dry terrestrial community. Each zone can be defined in terms of the frequency and duration of submergence, intensity of mechanical disturbance, and other components of the tidal regime. This often leads to a distinct zonation of communities parallel to the shore, although a more mosaic-like pattern can also be observed.

Salt marsh vegetation is characterized by low species diversity. It consists mainly of low-growing, salt-tolerant herbs, especially grasses. The prime colonizers of the lower flats are generally species of *Salicornia* and *Spartina*. Other typical genera with a global distribution include *Suaeda*, *Plantago*, *Juncus*, and *Puccinellia*.

The marsh is built up and grows seaward by the accretion of sediment. As the surface of the marsh rises, the frequency and duration of submergence decreases, which leads to a seaward shift of vegetation zones.

Impact of global change on distribution patterns will be mostly caused by temperature changes. There is a clear relationship between the isotherms of the coldest month and the geographical limits of salt marshes and mangroves: salt marshes occur in general in mid- and high latitudes, while mangroves are confined to the equatorial regions.² Maximum temperature rise (beyond the global mean) is predicted for high-latitude regions. This might well cause a shift in the distribution of mangroves from subtropical to temperate zones, notably along the eastern coasts of North America and Asia, and the southeastern coasts of South America, Africa, and Australia.

Regional salt marsh and mangrove systems will probably be affected most of all by changes in sea level and in tidal range, but such effects are still difficult to predict in detail. We will summarize here information on two well-known areas.

The Wadden Sea is one of the major salt marsh areas of the world, and well known through many studies (e.g., Reference 4). Moreover, some attention has already been given to the possible changes of the area as a result of global changes. We will therefore take this area as a case study.

Extensive salt marshes occur in the Wadden Sea area, both on the islands and on the mainland. Clear zonation patterns can be distinguished (see Reference 4 for historical notes) and on most of the Wadden islands transitions between the salt marshes and beach plains and dune slacks occur; they have a relatively high species

diversity and harbor many rare plant species. The tidal flats contain few higher plants but huge numbers of lower plants (benthic diatoms) and animals, especially worms, molluscs, and crustaceans. Therefore, the area is extremely important as a nursery for many fish species. In addition, numerous bird species use the Wadden Sea as a breeding, feeding, moulting, and/or wintering area. Large parts of the world populations of species of ducks, geese, waders, gulls, and terns are largely dependent on the area.⁵ Economically important are fisheries for shrimps and cockles, and aquaculture of mussels. Agricultural exploitation is mainly restricted to the mainland coast.

Present sedimentation rates on the island marshes in the Wadden Sea area are keeping up with the ongoing relative rise of sea level (0.44 cm/year over the last decades). A higher sea level rise of 0.5 to 1.0 cm/year may cause a reduction of the present island marsh area from 2800 to 450 ha.⁶ Even if the marshes could compensate sea level rise by increased sedimentation, fluctuations in the tidal range are bound to induce changes in the vegetation composition. Olf et al. found distinct changes in species cover of the major species of the salt marsh of Schiermonnikoog, which could be correlated to fluctuations of the tidal inundation frequency.⁷

The Mississippi Delta has experienced a long-term relative sea level rise mainly due to regional subsidence, and offers valuable information about the impact of sea level rise on coastal wetlands. The current local rate of relative sea level rise is about 1.2 cm/year of which 85 to 90% is due to subsidence.^{8,9} In the past several thousand years, the Mississippi Delta expanded considerably, despite the relative sea level rise.¹⁰ During the last century, however, this accretion trend was reversed and land losses of 100 km²/year have been reported.¹¹ The main cause of these losses of coastal wetlands and marshes is not the relative sea level rise in itself, but the diminishing of sediment input.¹² Channeling, dam construction (for navigation and flood control purposes), and other management activities have effectively stopped both the influx of riverine sediment and the accumulation of resuspended sediment. Salt marshes that are cut off from their sediment source can no longer keep up with the relative sea level rise and are eventually drowned. Given sufficient input of sediment, both vertical and lateral expansion of the marshes may occur, even during periods of considerable sea level rise. Using a process-based spatial simulation model (CELSS), Constanza et al. computed a slight gain in total land area (10 km², or 0.7% of the total land area) for the Atchafalaya-Terrebonne marsh-estuarine complex, even when local rates of sea level rise were doubled to 0.46 cm/year (leading to a total rise of 1.03 cm/year, including subsidence).¹³ The Mississippi River is at present changing from its current channel to the Atchafalaya River, thereby supplying the Atchafalaya-Terrebonne area with sufficient sediment. A second scenario, with a sea level rise of 1.67 cm/year (2.24 cm/year including subsidence) showed a net loss of land (19 km², or 1.3% of the total land area). These results are supported by earlier research by Baumann et al., who found that the marshes in the Atchafalaya area were able to maintain their surface elevation despite the ongoing subsidence and sea level rise.¹⁴

Other large coastal marsh systems we know of include the Camargue in southern France, the Marismas in the Coto Doñana National Park in southwestern Spain, the Banc d'Arguin off the Mauritanian coast, and the Mississippi Delta.¹⁵⁻¹⁸

Table 9-1 Human Influences Present in Coastal Areas Arranged According to the Ecosystem Component They Affect

Ecosystem	Human influence	Land use type										
Substrate	Appearance of artificial structures	X	X	X				X				X
	Accretion of sand	X										
	Removal of sand	X			X				X			
	Mobilization of sand				X				X			X
	Fixation of sand	X									X	
Soil structure	Ploughing up						X	X				X
	Compaction				X	X	X					
Soil water	Lowering phreatic water table		X									
	Raising phreatic water table			X								
Nutrition	Inundation		X									
	Eutrophication		X	X	X	X						
	Calcification				X				X			X
Plants	Mineralization		X		X							
	Removal	X			X	X				X		
Vegetation	Introduction	X			X						X	
	Removal	X			X				X			
Animals	Treading				X	X	X					
	Planting	X									X	
	Removal					X					X	
	Introduction										X	
	Disturbance				X	X		X				X
	<u>Coastal defense</u>											
	<u>Water catchment-extraction</u>											
	<u>Water catchment-infiltration</u>											
	<u>Recreation-substrate</u>											
	<u>Recreation-landscape</u>											
	<u>Recreation-nature, research</u>											
	<u>Production of petroleum, gas</u>											
	<u>Extraction of sand</u>											
	<u>Collection of fruits</u>											
	<u>Forestry</u>											
	<u>Military training</u>											

After van der Maarel.²⁰

COASTAL DUNES AND BEACHES

GEOGRAPHICAL DISTRIBUTION AND SIGNIFICANCE

Dunes are even more important than salt marshes, both economically and ecologically. They occupy large areas along the shore all over the world and are particularly extensive along the Atlantic coasts of Europe, eastern and northwestern North America, southeastern South America and southeastern Africa, Japan, and most coasts of Australia.^{2,3,19}

Probably the main function of dunes, at least for low-lying countries, is coastal defense. Several densely populated areas are protected from the sea by dunes (e.g., the Netherlands, southwestern France, eastern Spain, and the U.S. East Coast). Other important functions are water catchment and tourism. Table 9-1 lists the different types of land use of coastal dunes, together with the impact they have on different

Table 9–2 Main Gradients and Processes in Coastal Dune Ecosystems and the Major Climatic Factors Affecting Them

Component	Gradient	Process	Climate factor
Sand budget (foreshore)	Pos./neg.	Accretion/retreat	Sea level rise, marine currents
Sand budget (inland)	Pos./neg.	Erosion/accumulation	Wind climate, storm incidence
Moisture	Wet-dry	Humidification/desiccation	Precipitation, groundwater level
Chloride	Fresh-salt	Desalination/salination	Salt spray, groundwater level
Carbonate content	Poor-rich in CaCO ₃	Acidification/calcification	Sand budget, wind climate
Organic material	Humic-mineral	Decomposition	Temperature, moisture
Vegetation			Elevated CO ₂ , temperature, precipitation

After van der Maarel²¹ and van der Meulen and van der Maare.²²

ecosystem components.²⁰ Nature conservation as an alternative important land use is often in conflict with these land use functions.

GRADIENTS AND PROCESSES

Coastal dune ecosystems are characterized by the occurrence of many small-scale gradients, forming complexes. Table 9–2 lists the main gradients and processes acting on coastal dune ecosystems.^{21,22} The fourth column lists the main aspects of climate change that will have a significant impact on these processes.

The gradients and processes in Table 9–2 may be considered in a hierarchical way^{21,23} (Figure 9–1). Processes higher in the table are dominant over processes lower in the table. Vegetation will not only be influenced directly by climate change, but also by all processes on higher levels, either directly or indirectly.²⁴

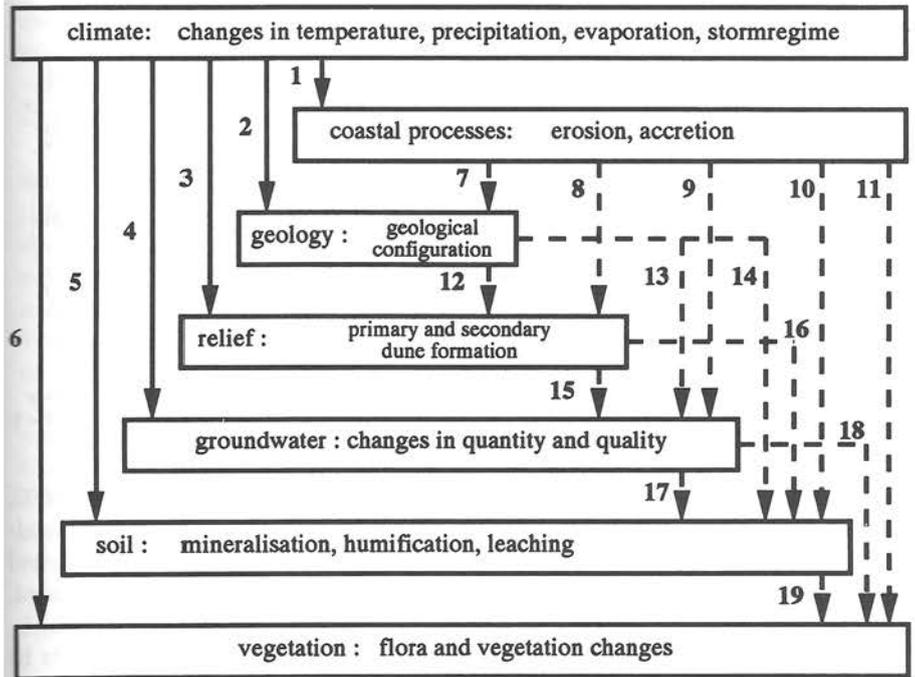
Influences of factors on lower levels on those on higher levels occur as well. An example on a small scale is the impact of rabbits on vegetation and on the soil surface (erosion). An example on the global scale is the fixation of CO₂ by plants and thus the influence of the phytosphere on the CO₂ concentration in the atmosphere.

In the original scheme of this hierarchy of spheres, the noosphere, the sphere of human activities, was placed lowest, because it is energetically dependent of the other levels. However, at the same time human activity has an ever-increasing ability to influence processes higher up in the hierarchy. The very problem of global change is the result of an essentially human impact on the atmosphere.

The following sections deal with the processes listed in Figure 9–1 in more detail.

COASTAL ACCRETION AND RETREAT

Sea level rise will in many places result in increased erosion and a trend toward landward movement of the coastline (transgression). This trend can be counteracted by reinforcement of natural (sand dune) or artificial (dike) barriers.²⁵ On sandy coasts,



- > / - - - -> = direct / indirect relation
- 1 = temperature, relative sealevel rise, change in storm regime
 - 2,7 = speed of sealevel rise, erosion or accretion
 - 3,8 = storm regime, phases of dune formation
 - 4 = change in amount and/or distribution of yearly evaporation
 - 5 = change in effective precipitation, temperature, sunshine, air humidity, soil formation
 - 6 = change in all climate factors
 - 9 = change in width of dunes causing change in groundwater level and influence of salt spray
 - 10,11 = drift-sand activity / wind erosion, change in sea spray
 - 12,14 = lime content, mineral composition of sand, grain size
 - 13 = hydrogeology
 - 15 = microtopography of groundwater table
 - 16,17 = changes in groundwater regime, soil and vegetation
 - 18 = inundation or desiccation of valleys
 - 19 = succession, (de-)eutrophication, decalcification and acidification

Figure 9-1 Main relations between landscape components, starting with climate. Feedback relations not shown. (After van der Meulen.²⁴)

however, the impact of sea level rise is largely dependent on the sand budget of the foreshore-beach area, with a negative sand budget leading to erosion of the beach and foredunes.²⁶ The formation of the recent dune coast of the Netherlands has taken place during a period of relative sea level rise, but with enough sediment being available.^{27,28}

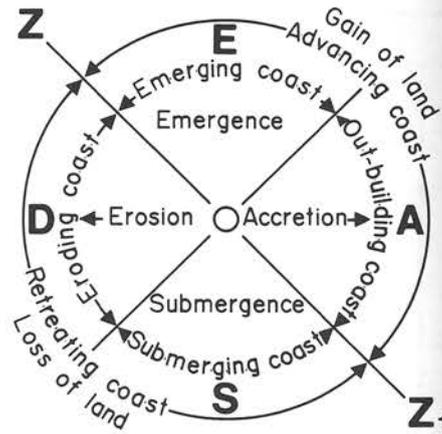


Figure 9-2 Valentin's scheme of coastal classification. (After King.²⁹)

This dune landscape, the "Younger Dunes", was formed between 1000 and 1600, during a period of marine transgression, and partly covered the existing dune landscape. This former landscape, the "Older Dunes", was formed between 6000 and 3000 B.C. and can still be recognized on topographical maps by its elongated, parallel ridges with the troughs in between now filled with peat.

At emerging coasts, like in parts of the Gulf of Bothnia, sea level rise might be compensated by isostatic uplift. In other regions, however, such as the Wadden Sea area, the predicted sea level rise is superimposed on the relative rise of 15 to 20 cm per century as the result of isostatic lowering of the land.

Valentin's scheme of coastal classification (Figure 9-2) shows the combined effects of submergence or emergence and coastal accretion or erosion.^{22,29} The line ZZ_1 represents the line along which two processes compensate each other.

Dune Erosion/Formation

A full vegetation cover of the dune surface will effectively control all erosion in the inner dune area. But where patches of bare sand occur at the surface, erosion processes can and will modify the geomorphology. Erosion by water tends to flatten the surface, while erosion by wind leads to the formation of both blowouts and accumulation dunes. Erosion by water can be far more important than by wind, measured in the amount of sand that is displaced.³⁰

Moreover, Jungerius³¹ found an intricate connection between the two processes: deflation patches are most likely to arise on the upper parts of slopes, after erosion by water has washed away the humic, water repellent sand and exposed the yellow sand underneath. Changes in the annual distribution of rainfall may influence the effects of water repellency of the sand. The effects of changing wind regimes on the development of blowouts is discussed by Jungerius et al.:³² deflation of six blowouts in the Blink (the Netherlands) was found to be most highly correlated with SW winds with velocities between 6.25 and 12.5 m/s, which are the critical wind velocities for the particle sizes in the area (0.15 to 0.42 mm). Extreme events, e.g., NW storms,

showed a tendency to fill the blowouts, which is interpreted as a first step of adaptation to a higher energy level. A shift in wind regime towards higher effective velocities may lead to a breakdown of the whole blowout-accumulation dune system, especially if this shift were accompanied by a change in wind direction.

Under the present climatological conditions, wind erosion very seldom leads to the formation of extensive deflation plains. Nearly all blowouts are stabilized spontaneously by either algae or vegetation;^{33,34} hence, there is no need for expensive stabilization measures. If changes in wind, climate, and precipitation would enhance eolian erosion, species that can withstand considerable sand burial, such as *Ammophila arenaria* (marram grass) and *Salix arenaria* (creeping willow), would be favored. The survival of other pioneer plants in relation to increased sand burial will depend on the growth rate of such plants.

Changes in vegetation cover, caused by direct effects of climate change will probably be more important. When increased CO₂ levels lead to an increase in plant biomass and cover (see later discussion), this could reduce both wind and water erosion, and lead to a less dynamic dune landscape, both geomorphologically and ecologically. The interaction between abiotic and biotic processes in the dune environment then shifts toward a situation in which the biotic processes prevail.²⁴

Humidification/Dessication

Underneath most dune areas lies a dome of fresh water, which is "floating" on top of the salt water. The fresh water table is raised above sea level due to the effective precipitation and the topography of the dunes.²³ A decreased width of the dune belt (as a result of a rising sea level) will in principle lead to a lowering of the water table in the remaining area. Sea level rise in itself has the opposite effect and will counteract the lowering of the water table.³⁵ Changes in annual precipitation have to be superimposed on this interaction, and even if total precipitation does not change, the effective precipitation may do so when vegetation cover and structure are changing.

For a coastal dune area with a length of 7 km in the Netherlands, Noest calculated net changes in groundwater level to vary from +36.5 to -21.0 cm, depending on the position with regard to the coastline and the amount of coastal retreat, assuming a sea level rise of 30 cm in 2050 and of 60 cm in 2090.³⁶

Subsequently, a vegetation model was used to predict the expected species composition of 23 plots in the area. In the vegetation model a number of hydrological, climatological, and site variables were used to estimate the probability of occurrence of 100 dune valley species. Predictions were made for the 2 years under study (2050 and 2090) and for two management options: option 1 allows a coastline retreat of 25 m at most for 2050 and 50 m for 2090, and option 2 allows maximum coastline retreat of 50 m and 100 m, respectively. Canonical correspondence analysis was used to evaluate the changes in species composition of the plots.³⁷ With this ordination technique a number of independent (orthogonal) axes of maximal floristic variation are obtained, which are correlated with the environmental gradients included in the analysis.

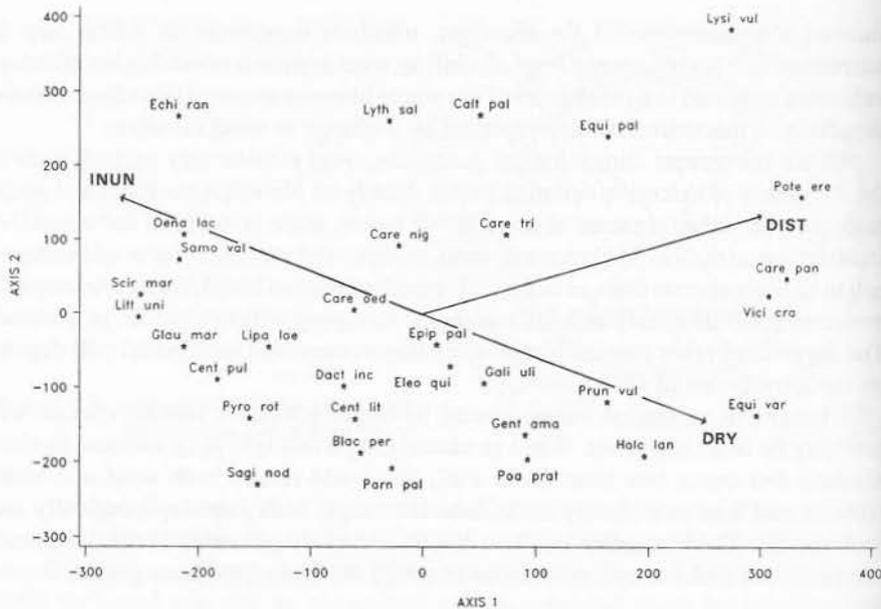


Figure 9-3 The position of the species centroids and the main environmental variables along the first two axes of maximal floristic variation from CCA. The projection of a species point onto the arrow of an environmental variable indicates the position of the species curve along the environmental gradient. See Appendix for abbreviations of species names. (From Noest, V. *Landscape Ecology* 6(1/2):89-97 (1991). With permission.)

Figure 9-3 shows 32 typical dune valley species and the 3 main environmental variables in an ordination diagram. The main variation in vegetation (on axes 1 and 2) is related to the variation in moisture as expressed by the parameters "duration of inundation" (INUN) and "duration of period with groundwater level >30 cm below surface" (DRY). A second gradient is based on distance to the foredunes (DIST).

Figure 9-4 shows the position of nine plots in the starting year (1989) and with the predicted vegetation in 2050 and 2090, for both management options. The connecting lines between the positions of one plot indicate the direction of change. The restricted coastline retreat under management option 1 leads for most plots to much wetter conditions, because the rise in phreatic level caused by sea level rise dominates the fall in phreatic level caused by the coastline retreat. There is a change in the direction of species occurring in wet valleys near the foredunes, which partly are indicators of brackish conditions. Under management option 2, the situation becomes reversed for many plots (notably plots 9, 13, 17, 12, and 10). Coastline retreat now dominates sea level rise, leading to drier conditions and a corresponding shift in species composition. The magnitude of this shift decreases from plot 9 toward plot 10 because of the increasingly inland positions of the plots.

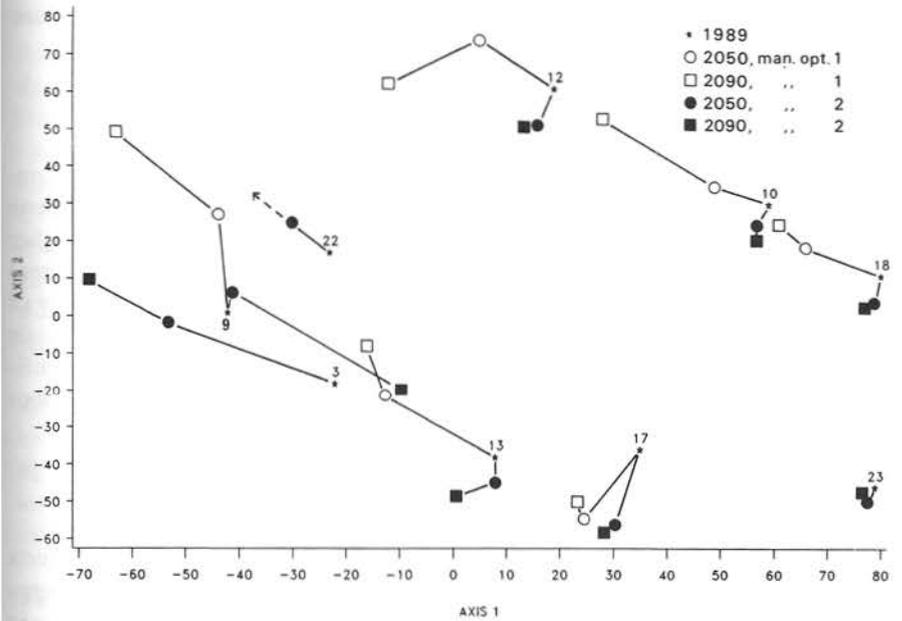


Figure 9-4 Sample scores (weighted average species scores) from CCA for nine plots. See main text for explanation. (From Noest, V. *Landscape Ecology* 6(1/2):89-97 (1991). With permission.)

Desalinization and Salinization

Airborne salt spray and intrusion of salty groundwater result in a higher chloride content of the dune sand. Salt spray is dependent on the speed and direction of the prevailing winds and the incidence of storms, and decreases exponentially with distance from the sea.^{38,39} Coastal retreat will expose formerly inland parts of the dunes to increased salt spray, which may induce the return of salt-tolerant species. When the freshwater dome underneath a dune area is diminished by coastal retreat and sea level rise, the groundwater can become mixed with brackish water, especially in low-lying dune depressions (dune slacks, swales) behind the foredunes.

Acidification and Calcification

The current carbonate content of the superficial layers in a dune area is mainly a function of the initial lime content of the dune sand and the duration of leaching since the formation of the dunes. Decalcification of the top soil to a level of <0.3% CaCO₃ will lead to a sharp increase in pH, since the buffering capacity diminishes.^{40,41} This acidification can be halted by the input of fresh sand with a high initial lime content. One source of fresh sand is the foreshore-beach system, but this only occurs when the sand budget is at least temporarily positive. A second source is the

dune body itself: wind erosion and the formation of blowouts and secondary dune valleys will bring new, not yet decalcified sand to the surface.

Decomposition

The decomposition rate of surface litter and soil organic matter is largely controlled by temperature, soil moisture, and soil texture. In sandy, well-drained dune soils an increase in temperature and decrease in precipitation will lead to higher decomposition rates, lesser leaching, and lower acidification rates, at least in areas with a relatively large precipitation surplus.⁴² In more arid regions, the hydrology of these soils may change from leaching to accumulative, while poorly drained soils may show a sharp increase in salinization. Where climate change leads to a significant change in composition of the vegetation and the litter produced, soil development may change drastically.

Vegetation Responses to Elevated CO₂ Concentrations

Climate change has both direct and indirect effects on plants. The direct effects include responses to increased atmospheric CO₂, higher temperatures, and changes in precipitation. Climate change will indirectly affect vegetation through changes in the above-mentioned processes, notably changes in moisture, nutrients, salt spray, and CaCO₃ content.

Elevated CO₂ levels have been shown to stimulate growth through enhanced photosynthesis, although this effect may decrease after some time, probably by starch accumulation and/or size constraints (self-shading).⁴³⁻⁴⁵ Effects of elevated CO₂ concentrations will be physiologically different for the two main groups of photosynthetically active plants: C₃ and C₄ plants. The main difference between the groups lies in the biochemical pathways they use in photosynthesis. C₄ plants make very efficient use of the available CO₂, while CO₂ is a limiting factor for photosynthesis in C₃ plants. Effects of elevated CO₂ levels are therefore stronger on C₃ species than on C₄ species. Most coastal plants are C₃ species; examples of coastal C₄ species are *Salsola kali*, *Suaeda fruticosa*, and *Spartina townsendii*.

Increased CO₂ will reduce stomatal conductance, thereby increasing water use efficiency.⁴⁶ It may also lead to a decrease in stomatal density,⁴⁷ which may enable plants to withstand water stress slightly better than with present CO₂ levels.⁴⁸

CO₂ enrichment of the atmosphere stimulates symbiotic nitrogen fixation in many agricultural legumes, as well as in some woody plants.^{49,50} This can increase nutrient availability in infertile habitats. Especially in dunes, this can be an important factor.

However, most of the present knowledge stems from controlled experiments on single species.^{51,52} Resource (light, nutrients) deficiencies are likely to modify the effect of CO₂ fertilization.^{44,46} Moreover, the magnitude of the effects of elevated CO₂ concentrations differs considerably between species, thereby affecting species competition and, hence, community structure and species composition.⁵³

Tracing increased biomass production may be difficult in many areas where the dunes are rich in nutrients, and/or are subjected to air pollution, notably the dry deposition of nitrogen compounds. In the relatively young dunes of Vorne (the Netherlands), near the big harbor and industry area of Rotterdam, which show a natural vegetational succession, a detailed vegetation map was made in 1959 and repeated in 1980.⁵⁴ Comparison of the maps and the accompanying floristic inventories showed an increase in nitrophilous and ruderal species and an overall trend towards a scrub/woodland complex. In other places — probably with more acid, leached soils — dry deposition may lead to dominance of grasses. Effects of succession, eutrophication by nitrogen deposition, and (future) CO₂ fertilization might be hard to quantify separately.

In summary, the main theoretical effect of increased CO₂ concentration is a larger total biomass, especially in dunes in temperate zones, where the C₃ pathway dominates. However, if there are limiting factors, notably moisture and nutrient availability, this effect may be much less in reality, while in nutrient- and humus-rich dune areas effects of a higher CO₂ level will be hard to separate from (natural) succession and eutrophication effects.

Vegetation Responses to Higher Temperature

The geographical distribution of vegetation types on a global scale is mainly defined by climatic variables. An obvious response to a temperature rise would be a general migration of plant species, including dominants, to higher latitudes and/or altitudes. However, past migration rates, especially of trees, have been much slower than the expected shift of isotherms (100 to 200 km poleward per degree of warming). Inadequate seed dispersal, a lag in soil development, and competition from persisting vegetation would force species to adapt to a different climatic regime.⁵⁵ Dispersal rates and adaptive abilities are extremely variable between species. Natural or man-made barriers to dispersal might cause local or even global extinction of some species (polar, montane, and island communities; isolated nature reserves), leading to a decrease in global species diversity.

The effects of elevated CO₂ on photosynthesis, stomatal conductance, and transpiration are generally enhanced by increasing temperatures.⁴³ A rise in mean temperature may cause insufficient hardening against colds and severe damage during incidental frosts. Insufficient winter chilling of buds may increase the required thermal time (accumulated day degrees >5°C) in some species (e.g., *Fagus sylvatica*), causing failure to take advantage of early springs. Species with low chilling requirements (e.g., *Crataegus monogyna*) may show early budburst and benefit from a prolonged growing season, albeit with an increased risk for subsequent frost damage.^{56,57} Forest fire regime is closely correlated with climate and available fuel.⁵⁸ Higher temperatures, especially when combined with drought, will lead to an increase in fire frequency. When the forest understory is denser, due to direct CO₂ effects, fire intensities may also increase. This is likely to cause considerable changes in community structure and composition.

Vegetation Responses to Changes in Precipitation

An increased seasonality of precipitation, even when total annual precipitation remains constant, may result in prolonged flooding during winter and extensive periods of relative drought during summer, particularly in wet dune valleys. Most dune valley species are extremely sensitive to even small changes in groundwater level.⁵⁹

Reduced summer precipitation, which may accompany rises in summer temperature, could well be the most important cause of change, the change being toward more open vegetation and a higher level of sand mobility. Temperate dune systems could become more semidesert-like. It is still impossible to say which species would be involved in such shifts of species composition.

Effects on Fauna

Few direct effects of changes in climate on mammals and birds of dune ecosystems are to be expected. They will, however, be affected by food availability and loss of habitat. Meeke has discussed the possible impact of climate change on bird species and concluded that of about 25 selected species only 3 or 4 may be threatened, whereas two species may even benefit from possible changes.⁶⁰

Insect development, survival, growth, and reproduction increases linearly with temperature.⁶¹ This may lead to increased frequencies of insect pests. Moreover, drought stress on plants tends to lead to more severe pest outbreaks (due to reduced chemical defense and increased nutrient levels).⁶² Leaves of plants grown under elevated CO₂ conditions have a higher content of carbohydrates, resulting in lower leaf nitrogen concentrations and a higher C/N ratio.^{63,64} This means that the nutritive value to herbivores is decreased, which can cause both increased feeding on C3 plants and reduced growth of insect herbivores.^{65,66}

CONCLUSION

The overall conclusion is, not unexpectedly, that it is very difficult to predict any change, even a major one in coastal ecosystems as a result of global change. If sea level rise would occur to the extent predicted, this will doubtless cause the biggest overall changes, because both larger parts of salt marshes and low dune systems may disappear altogether. Changes as a result of increased temperature and CO₂ concentrations are much more difficult to predict and will depend very much on the species composition of the vegetation and the associated fauna composition.

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APPENDIX: LIST OF SPECIES ABBREVIATIONS AND NAMES

Species of young, wet slacks near the foredunes (partly brackish):

Cent pul	<i>Centaurium pulchellum</i>
Echi ran	<i>Echinodorus ranunculoides</i>
Glau mar	<i>Glaux maritima</i>
Litt uni	<i>Littorella uniflora</i>
Oena lac	<i>Oenanthe lachenalii</i>
Samo val	<i>Samolus valerandii</i>
Scir mar	<i>Scirpus maritimus</i>

Species of open, calcareous slacks:

Blac per	<i>Blackstonia perfoliata</i>
Care oed	<i>Carex oederii</i>
Cent lit	<i>Centaurium littorale</i>
Dact inc	<i>Dactylorhiza incarnata</i>
Eleo qui	<i>Eleocharis quinqueflora</i>
Epip pal	<i>Epipactis palustris</i>
Gali uli	<i>Galium uliginosum</i>
Gent ama	<i>Gentianella amarella</i>
Lipa loe	<i>Liparis loeselii</i>
Parn pal	<i>Parnassia palustris</i>
Pyro rot	<i>Pyrola rotundifolia</i>
Sagi nod	<i>Sagina nodosa</i>

Species of older slacks with a well-developed moss and humus layer:

Calt pal	<i>Caltha palustris</i>
Care nig	<i>Carex nigra</i>
Care tri	<i>Carex trinervis</i>
Equi pal	<i>Equisetum palustre</i>
Lysi vul	<i>Lysimachia vulgaris</i>
Lyth sal	<i>Lythrum salicaria</i>

Species of relatively dry slacks, with a mown vegetation:

Care pan	<i>Carex panicea</i>
Equi var	<i>Equisetum variegatum</i>
Holc lan	<i>Holcus lanatus</i>
Poa prat	<i>Poa pratensis</i>
Pote ere	<i>Potentilla erecta</i>
Prun vul	<i>Prunella vulgaris</i>
Vici cra	<i>Vicia cracca</i>