

9 Physiological Characteristics of Coastal Dune Pioneer Species from the Eastern Cape, South Africa, in Relation to Stress and Disturbance

B.S. RIPLEY and N.W. PAMMENTER

9.1 Introduction

A characteristic of coastal dune systems is that species diversity and total plant biomass is less than that of the adjoining inland areas, and furthermore, there is generally pronounced zonation of the species present on the dunes (Clements 1916; Lubke 1983). Why are the foredunes inhabited by only few species, and dominated by even fewer?

There are obviously a number of factors controlling plant distribution and productivity, but for the foredunes in particular, adaptations to resource stress and/or disturbance are likely to be very important (Barbour 1992). The resources required by plants for growth include light, water and nutrients, and stress could be a consequence of either deficiencies or excesses of these resources. Adaptations to acquire resources present in low amounts, or to resist those present in excess, may also play a role in competition between species. Disturbance is the process by which part or all of a plant is damaged or destroyed, generally by physical processes. Disturbance is particularly high in coastal foredunes and includes wind, salt-spray, occasional inundation by seawater and sand movement. The latter can lead to burial, exposure, or physical damage from sand-blasting. Salt spray could be argued to be an environmental stress, but because it can lead to direct physical damage, we prefer to consider it a disturbance. However the distinction is unimportant in the discussion that follows. Further complications arise because of adaptations to a combination of stresses and/or disturbance, and because plant response may vary with stage in the life cycle (particularly seedlings in comparison with established plants).

9.2 A Conceptual Model of Resource Limitation and Plant Performance

To consider the adaptations to resource stresses and disturbances, a conceptual model of foredune plant performance is presented (Fig. 9.1). The model describes the relationship between the supply of resources, plant function in relation to the acquisition and use of these resources, and the link to the resultant productivity. This gives insight into the potential limitations created by the particular resources. The effect that disturbance may have is also indicated. Differences among species may explain why species survive on the foredunes and why particular species are more abundant within the particular microhabitats of the foredunes.

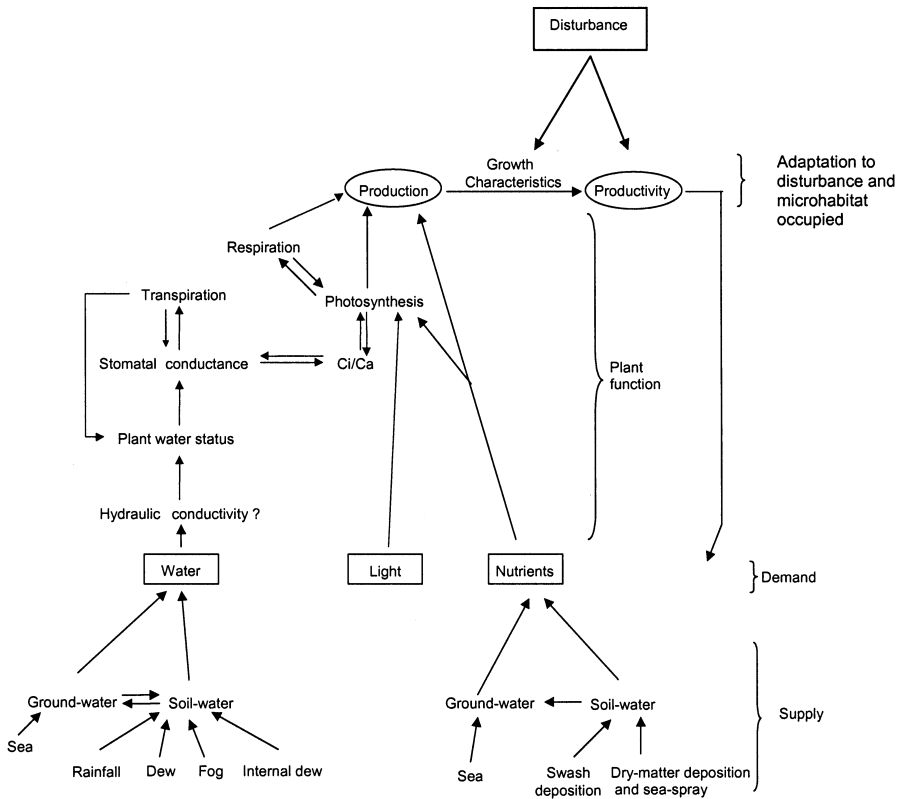


Fig. 9.1. A conceptual model of how plant production and ultimately productivity (model outputs) are related to the acquisition and use of water, nutrients and light (model inputs) and how, in turn, productivity determines the demand for resources. The environment supplies resources and the possible origins of these resources are indicated. Disturbance can influence growth characteristics and productivity, and hence demand. See text for explanation. (Atmospheric fallout refers to the input of nutrients by atmospheric fall-out, such as dust etc.)

Water availability and transpiration rate, in conjunction with plant hydraulic conductance, determine leaf water status (Passioura 1982), which in turn affects stomatal conductance (Mansfield and Davies 1981). Stomatal conductance affects the diffusion of CO_2 into the leaf and influences the ratio of intercellular (C_i) to atmospheric (C_a) CO_2 concentration (Farquhar and Sharkey 1982). C_i , in conjunction with light absorption and the intrinsic capacity of the photosynthetic apparatus (which is dependent *inter alia* upon mineral nutrients) determines the photosynthetic rate, and photosynthetic rate in turn influences C_i . Photosynthate production and respiration determine net carbon gain. Carbon gain, biomass allocation patterns and the acquisition of mineral nutrients determine production. Production per unit land area, as determined by the species growth characteristics, determines productivity. Biomass allocation patterns are likely to differ among species and are also modified by the prevailing stress and disturbance (microhabitat) conditions. Disturbance can reduce standing biomass and hence resource demand.

The relationship between plant growth and resource availability can be complex, although it is often thought that plant growth is limited by the supply of resources. The amount of plant material present as biomass per unit land area or leaf area index (LAI, leaf area per unit ground surface area) is obviously important when considering resource supply and demand. A low standing biomass could be considered as a direct consequence of low resource supply. Alternatively, it could be viewed as a phenomenon that ensures that each unit of biomass is supplied with adequate resources and, consequently, that physiological stress does not occur. This is not a facile argument: restriction of standing biomass by resource supply implies that the plants present exploit the resources available down to some minimum level; restriction of biomass that avoids stress implies availability of resources in excess of those utilised. Avoidance of stress would permit high growth rates per unit plant mass, and concomitant death and loss of plant parts would prevent biomass accumulation, i.e. a low standing crop but high turnover rates. In the study described in this chapter the highest growth rate per unit plant mass actually occurred in the species with the lowest standing biomass. There is considerable biomass turnover, such that these high rates of dry matter production do not lead to high biomass accumulation. To distinguish between the two possibilities is not simple, but adaptations that enable more efficient resource acquisition or reduce resource demand may be taken as indicators that resources are limiting. Similarly, symptoms of stress, such as reduced stomatal conductance, net assimilation rates, photosynthetic electron transport, all leading to reduced growth rates, may also indicate the inadequacy of a resource.

To assess the importance of resource limitation and physiological stress in terms of Fig. 9.1 requires a considerable data set. Certainly with respect to coastal dunes, comprehensive data sets of that nature are not available. This chapter largely describes a study on the foredunes of the coast of the Eastern

Cape, South Africa, in which physiological and growth measurements were made over a number of years (Ripley 2001). The data set is such that it makes it possible to assess the extent and possible consequences of physiological stress in relation to resource availability.

9.3 Study Site, Species and Parameters Measured

The study was conducted at the mouth of Old Woman's River, 30 km northeast of Port Alfred (27°08'49"E; 33°28'59"S) over a period of 3 years, with measurements being taken in every season. Mean annual rainfall is 618 mm, with a peak in summer but winter rains are not unusual. Mean maximum and minimum temperatures for summer are 24.6 and 17.8 °C, and for winter 20.2 and 10.2 °C, respectively.

The species selected for study were *Arctotheca populifolia* (Berg.) Norl. (Asteraceae), *Ipomoea pes-caprae* (L.) R. Br. (Convolvulaceae) and *Scaevola plumieri* (L.) Vahl (Goodeniaceae) (Fig. 9.2). *S. plumieri* is a classic 'dune builder' with semi-succulent leaves, branching and growing up through sand trapped by the expanding above-ground parts of the plant. *A. populifolia*, also with semi-succulent leaves, has a more compact growth form, and occurs as individual plants towards base of the seaward slope of the foredune. *I. pes-caprae* occurs on the more stable sand at the top of the foredune and further inland. The growth form is prostrate, with long stems running across the top of the sand; the leaves, although occasionally semi-succulent, are far less so than the leaves of the other species. These species were chosen because they are the major foredune species along the entire east coast of southern Africa. Water and mineral nutrients are often considered to be potentially limiting factors in sand dune ecosystems (because of the nature of the substrate) (Willis 1965; Morris et al. 1974; Rozema et al. 1985; Hesp 1991). Consequently, the water relations and nutrient status of the plants were studied on a seasonal basis, and these were related to photosynthetic characteristics and growth rates (measured as leaf and stem production).

To assess the availability of resources and to scale up resource utilisation from leaf to ground surface area requires knowledge of the LAI. This was fairly simple to measure for *I. pes-caprae* and *S. plumieri* as these species form fairly uniform 'stands' on well-vegetated foredunes. Individual plants of *A. populifolia* are small and more widely scattered than the other species, and measurement of LAI was more difficult and less reliable. What was important was to assess the area of soil that the roots could exploit, and so the approach used was to randomly throw small quadrats where the plants of this species were growing, ensuring that plants occurred in every quadrat.

Various measurements of physiological and growth characteristics were made (see below for details) on a total of six visits over a three year period,

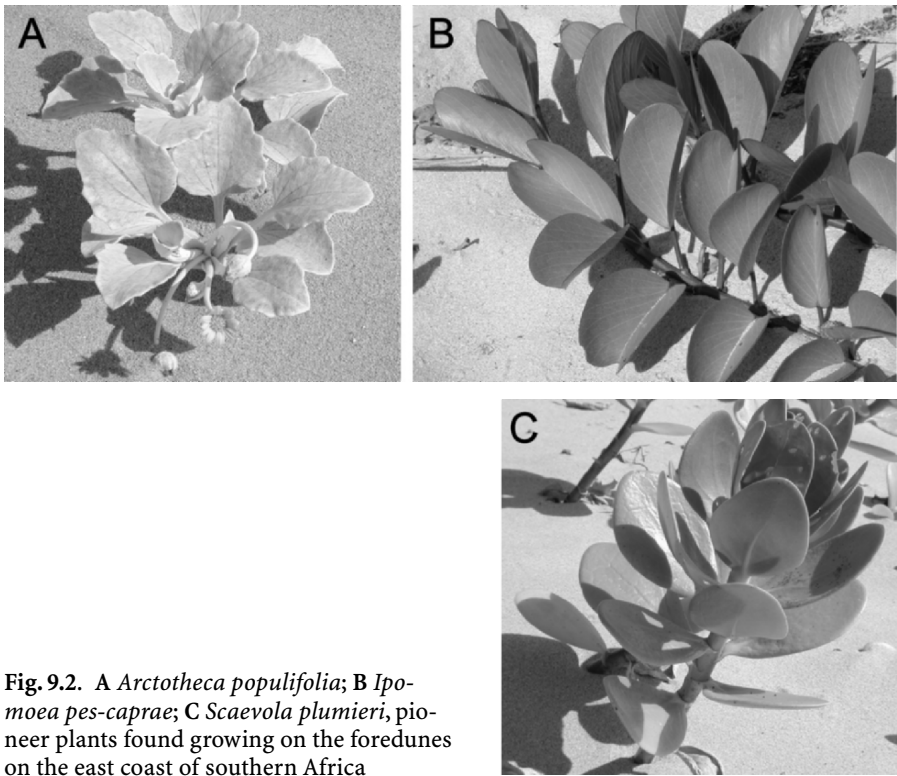


Fig. 9.2. A *Arctotheca populifolia*; B *Ipomoea pes-caprae*; C *Scaevola plumieri*, pioneer plants found growing on the foredunes on the east coast of southern Africa

two in each of the seasons: summer (1997 and 1998), winter (1996 and 1998) and spring (1997 and 1998). Replicate data (see Tables for details) were statistically compared both between experimental days and between species, although only the significance (at the 95 % confidence level) of the species comparison is given in the Tables. For a more complete comparison see Ripley (2001).

9.4 Water Relations

Stomatal conductance and transpiration rates were measured by porometry, stem or leaf water potential with a pressure chamber, and pressure-volume curves were established to assess points of turgor loss and the osmotic component of water potential.

Stomatal conductances for all species showed normal diurnal responses, with only *I. pes-caprae* sometimes showing midday reductions (Table 9.1). Mean maximum values for *A. populifolia* were particularly high, being over

Table 9.1. Interspecific differences in water-relations and transpiration rates measured for *A. populifolia*, *I. pes-caprae* and *S. plumieri*

No.	Parameters measured	Species		
		<i>A. populifolia</i>	<i>I. pes-caprae</i>	<i>S. plumieri</i>
1	Diurnal stomatal conductance, N=15	One-peaked for 15 replicates	Two-peaked for 9 replicates	One-peaked for 15 replicates
2	Maximum leaf conductance ($\text{mol m}^{-2} \text{s}^{-1}$), N=15	1.3±1.1 ^a	0.17±0.05 ^b	0.33±0.19 ^b
3	Midday leaf or shoot water potential (MPa), N=15	-1.01±0.04 ^a	-0.93±0.05 ^a	-1.56±0.08 ^b
4	Leaf water potential where turgor potential=zero (MPa), N=18	-1.31±0.54 ^a	-1.65±0.55 ^a	-1.61±0.41 ^a
5	Osmotic potential when tissue is fully hydrated (MPa), N=18	-1.24±0.53 ^a	-1.48±0.47 ^a	-1.46±0.35 ^a
6	Maximum transpiration rates ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$), N=15	4.2±1.5 ^a	3.7±1.4 ^a	4.1±1.5 ^a
7	Annual water budgets in an average rainfall year (1978–1998)	618±168	618±168	618±168
	Transpiration ($1 \text{ m}^{-2} \text{ year}^{-1}$)	208±12	593±34	430±30
	Difference ($1 \text{ m}^{-2} \text{ year}^{-1}$)	410	25	188
8	Number of months in 1997 (rainfall =546 mm) when predicted volumes of water transpired exceeded volumes of rainfall per unit dune surface-area.	2	6	5

Values with the same superscript letter are not significantly different at the 95 % probability level (*post hoc* ANOVA and Tukey multiple range test)

1 mmol m⁻² s⁻¹, while those of *I. pes-caprae* were much lower (Table 9.1). *A. populifolia* possesses an indumentum of silvery hairs that reduces leaf conductance (Ripley et al. 1999). Mean midday leaf water potentials were characteristic of mesic plants, ranging from -0.93 MPa in *I. pes-caprae* to -1.56 MPa in *S. plumieri*, and values seldom dropped below the water potential corresponding to loss of turgor (Table 9.1). Osmotic potential at full turgor did not differ among the species, with an average of about -1.4 MPa (Table 9.1), and there were no indications of seasonal osmotic adjustment. Mean maximum transpiration rates were high (Table 9.1, with values up to 6.5 mmol m⁻² s⁻¹ being recorded). These values are similar to those of temperate dune species (Pavlik 1983), and higher than those reported from some plants from semi-arid areas (Caldwell 1985; von Willert et al. 1989). In *S. plumieri* there was a strong linear relationship between transpiration rate and evaporative demand (measured as vapour pressure difference, VPD), suggesting little stomatal control of transpiration (see also Peter and Ripley 2000). A similar response was shown by *A. populifolia*, although the relationship was not as good as for *S. plumieri*, possibly as a consequence of fewer data points. In *I. pes-caprae* the relationship was non-linear, suggesting stomatal limitation of transpiration at high VPD. No distinct seasonal patterns were observed in plant water relations; rather, the plants responded to the immediate environmental conditions.

It is possible to make some rough calculations of the water budget of the foredune system. Using the measured relationships between E and VPD, and by calculating VPD from air temperature and relative humidity supplied from weather stations, transpiration rates can be estimated for any point in time (Peter and Ripley 2000). These estimated transpiration rates can be integrated over the year to give annual water use, and from LAI, this can be converted to units of mm water per unit ground area and compared with average annual rainfall. For all three species estimated annual average water utilisation by transpiration was less than annual average rainfall (1.7; although, because of the difficulty of assessing LAI for *A. populifolia*, calculated water use for this species may be an underestimate). Rainfall for 1997 was below average, and these rough calculations indicated a water use exceeding rainfall for a number of months during the year (Table 9.1). Either the plants were not transpiring as rapidly as the model based on measured E and VPD would suggest or they were accessing some other source of water, such as ground water, water condensed within the cold upper depths of the sand dunes (termed "internal dew" by Olsson-Seffer 1909; see Salisbury 1952 for details of this process), or the water stored in the soil column. Isotopic measurements were unable to distinguish between rain- and groundwater as a water supply, because of the rapidity with which the isotopic composition of the ground water reflected that of a particular rain event. The budgeting procedure was altered to incorporate the soil water. From knowledge of rooting depth the volume of soil available to the plants could be calculated, and

from this and the water content of the soil at field capacity, the amount of water available to plants could be calculated. Soil water could then be modelled by estimates of subsequent transpiration and input from rain. When this was done at no point did soil water drop below 0.5%, the value suggested by Salisbury (1952) to be the lower limit at which plants could extract water from the sandy dune soils.

9.5 Mineral Nutrients

Soil nutrient contents and nutrient contents of successive leaves on a stem (thus generating a 'time series'), were measured using standard analytical procedures.

Sand dune soils are generally low in mineral nutrients, and these dunes were no exception, with concentrations of N, P and K being 1.6 ± 1.4 , 0.32 ± 0.02 and 2.57 ± 0.41 mg 100 g⁻¹ dry sand, respectively ($N=6$). Despite this, leaf nutrient concentrations were not particularly low (Table 9.2). These concentrations are well within the range measured on plants growing on less oligotrophic soils (Allen 1989). Measurements on consecutive leaves on a stem generally show that total leaf content of P and K initially rose as the leaf expanded and then declined after full expansion. This indicated that young leaves were net importers of P and K, and older leaves net exporters (Table 9.2); considerable internal recycling was occurring. Similar recycling of N and K has been shown in *S. plumieri* (Harte and Pammenter 1983). Ca accumulated in the leaves of *A. populifolia* and *I. pes-caprae* but remained relatively unchanged in the leaves of *S. plumieri*. In all three species Mg and Na were accumulated throughout the life of the leaves (Table 9.2). Na was accumulated to particularly high levels in *S. plumieri* (on a dry mass, but not wet mass, basis the Na levels in old leaves of this species were higher than those in the leaves of the mangrove *Avicennia marina*; Harte and Pammenter 1983). This accumulation was probably a consequence of a combination of high transpiration rates and long leaf life span. Cl concentrations increased slightly or remained relatively unchanged with increasing leaf age (Table 9.2).

9.6 Photosynthetic Characteristics

Photosynthetic rates were measured using a portable infrared gas analyser (LCA-II and PLC leaf chamber, ADC, Hoddeson, UK, or LI-6400, LI-COR, Lincoln, USA); potential photoinhibition was assessed by chlorophyll fluorescence (PEA, Hansatech, King's Lynn, UK); night-time respiration was mea-

Table 9.2. Interspecific differences in nutrient-relations measured for *A. populifolia*, *I. pes-caprae* and *S. plumieri*. Data from Ripley 2001

No.	Parameters measured	Species		
		<i>A. populifolia</i>	<i>I. pes-caprae</i>	<i>S. plumieri</i>
1	Leaf nitrogen content (mg g ⁻¹ dry wt.), N=6	14.1±2.3 ^{ab}	15.3±1.3 ^a	10.2±2.4 ^b
2	Leaf phosphorus content (mg g ⁻¹ dry wt.), N=6	1.2±0.3 ^a	1.9±0.4 ^b	1.6±0.2 ^b
3	Leaf potassium content (mg g ⁻¹ dry wt.), N=6	7.1±2.5 ^a	19.4±4.0 ^b	16.8±6.8 ^b
4	Remobilisation of indicated nutrients from older to younger leaves, based on a comparison of the slopes of changes in leaf weight and nutrient concentration in response to increasing leaf age. N=6	Yes Yes	Yes Yes	No Yes
5	Accumulation of indicated nutrients. Considered accumulating if average concentration of leaf 20 exceeded that to leaf 5. N=6	Yes Yes Yes Yes	Yes Yes Yes No	No Yes Yes Yes

Values with the same superscript letter are not significantly different at the 95 % probability level (*post hoc* ANOVA and Tukey multiple range test)

sured by enclosing shoots in a chamber and conducting standard gas exchange measurements.

The three species showed a range of photosynthetic characteristics (Table 9.3). *A. populifolia* had a high photosynthetic capacity, measured in terms of CO₂ saturated rates of ribulosebisphosphate (RuBP) regeneration and carboxylation efficiency (Table 9.3; related to rubisco activity; Farquhar and Sharkey 1982). It also had low stomatal limitations and high efficiency of radiation utilisation, the latter probably being related to the high chlorophyll content per unit area (Table 9.3). The hair layer reduced transpiration more than photosynthesis, giving rise to a higher leaf-level water use efficiency than was measured for the other species (Table 9.3). There was only a small reduction in the maximum quantum yield of photosynthesis (Table 9.3), which recovered quickly (ca. 30 min) on darkening, indicating little photoinhibition of photosynthesis. The hair layer contributed to this low photoinhibition (Ripley et al. 1999). Consequent upon the high capacity as well as high stomatal conductance, maximum light saturated rates of photosynthesis were high (up to 34 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Table 9.3). *S. plumieri* showed characteristics similar to those of *A. populifolia*, except that capacities and rates were not as high (Table 9.3). Photoinhibition at midday was slightly more marked, but recovery was rapid (ca. 60 min).

I. pes-caprae showed lower capacities and slower CO₂ assimilation rates than the other species, and this was associated with the lowest leaf chlorophyll concentration (on an area basis, Table 9.3). Photoinhibition was also more marked in this species and recovery of maximum quantum yield of photosynthesis took approximately 120 min. *I. pes-caprae* was the only species that showed stomatal control of water loss, and these reductions in stomatal conductance may have contributed to the generally low photosynthetic performance of the species (Table 9.3).

9.7 Growth Rates

Aboveground growth was estimated by tagging individual leaves on several shoots and counting and measuring new leaves and stems produced subsequent to tagging. Belowground growth was not measured. It is extremely difficult to do this in the field, and our unpublished observations suggest that data derived from pot experiments would be unreliable; growth rates and growth patterns of these species in pots are considerably different from that of material in the field. However, root:shoot ratios are carefully regulated (Farrar 1999) and under constant conditions it is likely that aboveground growth reflects belowground growth. Biomass was measured by harvesting quadrats and structural carbohydrates were measured according to Buysse and Merckx (1993).

Table 9.3. Interspecific differences in photosynthetic characteristics measured for *A. populifolia*, *I. pes-caprae* and *S. plumieri*. Data from Ripley 2001

No.	Parameters measured	Species		
		<i>A. populifolia</i>	<i>I. pes-caprae</i>	<i>S. plumieri</i>
1	Peak assimilation rate from diurnal curves ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), N=15	25.9±6.9 ^a	9.7±5.2 ^b	20.1±4.5 ^c
2	RuBP regeneration rate ($\mu\text{mol m}^{-2} \text{ s}^{-1}$), N=10	37.0±3.4 ^a	23.4±5.4 ^b	24.9±6.0 ^b
3	Carboxylation efficiency ($\text{mmol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), N=10	118.3±20.6 ^a	71.1±14.4 ^b	95.8±17.6 ^c
4	Efficiency of utilisation of incident PPFD ($\mu\text{mol mol}^{-1}$), N=15	55.7±5.0 ^a	39.1±3.0 ^b	42.7±12.0 ^{ab}
5	Chlorophyll content a+b ($\mu\text{g cm}^{-2}$ leaf surface area), N=36	43.0±11.8 ^a	19.0±6.1 ^b	37.0±10.5 ^a
6	Stomatal limitation (%), N=10	16.5±3.4 ^a	45.7±11.0 ^b	26.2±11.4 ^a
7	Instantaneous water use efficiency ($\text{mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$), N=15	5.9±2.4 ^a	2.3±1.1 ^b	4.7±1.8 ^a
8	Midday reduction in maximum quantum yield of primary photochemistry (%), N=15	18.7±9.6 ^a	28.0±21.5 ^{ab}	32.3±16.5 ^b
9	Light saturated assimilation rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), N=15	33.6±2.0 ^a	16.4±3.4 ^b	19.0±3.6 ^b

Values with the same superscript letter are not significantly different at the 95% probability level (*post hoc* ANOVA and Tukey multiple range test)

Amongst the species there was a general relationship between CO₂ assimilation rates and growth rates (compare Tables 9.3 and 9.4, parameter 1), and also between whole shoot dark respiration per unit leaf area (Table 9.4) and growth. Interestingly, dark respiration rates as a percentage of maximum photosynthetic rates (1–5 %, depending on species and season) were lower than recorded in either temperate dune species (4.5–10.3 %; Pavlik 1983) or savanna grasses or trees (9–18 %; Scholes and Walker 1993). As growth rates are high, this low respiration rate is probably a consequence of low maintenance respiration. This is a characteristic that may be expected from short-lived leaves (Table 9.4)

Growth rates may be expressed as new leaf and stem production per shoot, biomass produced per unit land area (primary productivity) or per unit initial biomass (relative growth rate on a biomass basis; Table 9.4). The standing above-ground biomass that gave rise to the measured production varied among the three species (Table 9.4). These values are similar to, although a little higher, particularly for *S. plumieri*, than those reported for temperate dune systems (Barbour and Robichaux 1976). *A. populifolia* showed the highest growth rate in terms of production per shoot, and per g dry matter initially present (Table 9.4). Because of rapid leaf and stem death, there was no marked accumulation of dry matter and mean leaf life span was short (Table 9.4). Total non-structural carbohydrates (TNC) were low, presumably newly assimilated material was allocated directly to growth, with little reserve material being deposited (Table 9.4). Growth in this species was surprisingly non-seasonal. *I. pes-caprae* had the lowest growth rate per shoot, with mean life span being about 176 d (Table 9.4). Leaf and stem TNC was similar to that of *A. populifolia*, but more biomass was allocated to leaves; presumably the creeping habit of *I. pes-caprae* makes considerable allocation to stems unnecessary (Table 9.4). *I. pes-caprae* growth rate expressed per unit biomass was lower than *A. populifolia* (Table 9.4) and most of that initial biomass was leaf, rather than stem and so growth efficiency per unit leaf area would have been low. The production per shoot of *S. plumieri* was intermediate between the other species (Table 9.4), and leaves were longer lived (ca. 217 d). This species had the highest leaf and stem TNC (Table 9.4), suggesting that reserves may be available for non-seasonal growth, or to support the substantial reproductive investment (numerous large fruit) characteristic of this species. Production per unit biomass was lower than in *I. pes-caprae* (Table 9.4). However, *S. plumieri* has substantial stems, and growth efficiency per unit leaf area would be higher than that of *I. pes-caprae*.

Because the three species had different LAI, differences in production at the stem level tended to even out when expressed as a primary productivity (Table 9.4; the caveat about estimating LAI for *A. populifolia* remains). Because the productivity data are strictly gross primary productivity (based on new biomass, rather than increment in biomass, i.e. death and loss of plant parts was not accounted for), comparisons with published values of net pri-

Table 9.4. Interspecific differences in production and productivity measured for *A. populifolia*, *I. pes-caprae* and *S. plumieri*. Data from Ripley 2001

No.	Parameters measured	Species		
		<i>A. populifolia</i>	<i>I. pes-caprae</i>	<i>S. plumieri</i>
1	Shoot primary production (g dry mass shoot ⁻¹ year ⁻¹), N=20	42.4±18.7 ^a	17.8±15.0 ^b	25.3±10.3 ^c
2	Whole shoot respiration rate (µmol CO ₂ m ⁻² s ⁻¹), N=6	0.47±0.15 ^a	0.15±0.03 ^b	0.22±0.01 ^b
3	Leaf production (g dry wt. shoot ⁻¹ month ⁻¹), N=20	1.08±0.48 ^a	1.09±0.76 ^a	1.34±0.61 ^b
4	Stem production (g dry wt. shoot ⁻¹ month ⁻¹), N=20	2.43±1.47 ^a	0.33±0.10 ^b	0.76±0.29 ^c
5	Aboveground primary productivity (g dry wt. m ⁻² year ⁻¹), N=10	479.5±211.6 ^a	386.5±326.2 ^b	541.4±220.6 ^a
6	Aboveground biomass (g dry wt. m ⁻²), N=5	63.1±17.7 ^a	134.6±40.9 ^{ab}	271.4±133.3 ^b
7	Relative growth rate (g g ⁻¹ average initial biomass year ⁻¹), N=5	7.6±3.4 ^a	2.9±2.4 ^b	2.0±0.8 ^b
8	Leaf longevity (days), N=5	ca. 69	ca. 176	ca. 217
9	Total non-structural leaf carbohydrates (mg g ⁻¹ dry wt.)	1.63±0.70 ^a	1.81±0.70 ^a	3.06±1.76 ^b
10	Leaf area index (LAI), N=5	0.23±0.06 ^a	0.78±0.26 ^{ab}	1.05±0.51 ^b
11	Specific leaf area (SLA, cm ² g ⁻¹), N=6	60.6±6.9 ^a	77.3±5.2 ^b	35.8±6.2 ^c

Values with the same superscript letter are not significantly different at the 95% probability level (*post hoc* ANOVA and Tukey multiple range test)

mary production are difficult. Nevertheless, productivity for the species on this dune system (ranging from $380 \text{ g m}^{-2} \text{ year}^{-1}$ for *I. pes-caprae* to 540 for *S. plumieri*) compare favourably with the $250 \text{ m}^{-2} \text{ year}^{-1}$ recorded for *Ammophila arenaria* on a Scottish mobile dune system (Deshmukh 1977), and the range of 280 to $500 \text{ m}^{-2} \text{ year}^{-1}$ for *Spartina alterniflora* in a North American salt marsh (Stroud and Cooper 1968), and are similar to the value of $440 \text{ g m}^{-2} \text{ year}^{-1}$ reported for a South African savanna (Scholes and Walker 1993).

9.8 Stress and Disturbance

To what extent do the data gathered in the investigation described here 'explain' the occurrence of the foredune species? We pointed out the general perception that plants occupying the foredune may be subjected to stresses associated with limitations on resources, as well as to disturbance. Resource utilisation generated by plant growth obviously cannot exceed supply, but the requirement for resources in a resource-limited environment can be generated in different ways. A particular species may have a high standing biomass and low growth per unit biomass, or a species may have a low standing biomass and exhibit high growth and turnover rates: the resource requirement in each case may be similar. Physiological symptoms of stress or adaptations that increase access to resources may indicate a potential resource limitation.

Two of the species investigated (*A. populifolia* and *S. plumieri*) showed no evidence of water stress or limitation at the leaf level: stomatal conductances were high and transpiration responded primarily to atmospheric demand, and leaf water potentials did not drop below the turgor loss point. On a per unit land basis water use by the dune plants would have been lower than that of a well vegetated area, simply because of the low LAI on the foredune. *S. plumieri* had a higher LAI than *A. populifolia*, but rooted deeper, and may on occasions have tapped ground water. *I. pes-caprae* had lower stomatal conductances and did occasionally show a midday depression in conductance, indicating an inadequate water supply. However, leaf water potentials were always higher than those of *S. plumieri* (perhaps indicating a lower hydraulic resistance in *I. pes-caprae*) and did not drop below the turgor loss point.

It is more difficult to assess limitations imposed by nutrient shortages. Although dune soils are low in nutrients, there is a continual input from salt spray, as well as dry-matter deposition, and although the pool size of nutrients in the soil may be low, there may be a fairly rapid through-put. It is possible that high transpiration rates are necessary for the acquisition of sufficient nutrients from the dilute soil solution. Additionally, there is evidence of internal recycling of nutrients, which would obviously be important in the case of high leaf turnover rates. Intuitively, the high rates of leaf production and

growth suggest that, at the shoot meristem level, cell division and growth are not limited by nutrients. More detailed studies of nutrient cycling, with particular emphasis on rates of nutrient input into the system, loss by leaching and utilisation by the plants (on a per plant and per unit ground area basis) are required. Nutrient supplementation experiments were considered, but Barbour et al. (1985) have criticised such experiments, questioning their use in nutrient ecology.

Rates of net CO₂ assimilation were high (although that of *I. pes-caprae* was lower than the other species), suggesting that there were no immediate shortages of resources at the leaf level. Allocation of photosynthate differed in that the proportion of stem in newly produced above-ground dry mass was lower in *I. pes-caprae* than the other species. This reflects the growth habits of the species. The high rates of photosynthesis at the leaf level translated into high rates of growth at the level of individual stems. *A. populifolia* showed particularly high rates of growth, coupled with high rates of death and loss of plant parts, giving rise to very high turnover rates.

The three species have different, although related, growth strategies, and these strategies allow the species to tolerate disturbance. Standing biomass and LAI on the foredune is low, and at the level of the individual leaf or stem, the plants do not appear to be suffering physiological stress or resource limitation. *A. populifolia* occurs predominantly at the seaward base of the foredune, where rates of sand movement are highest. It has the highest growth rate on a stem or initial dry mass basis, but the lowest leaf life span, and shows rapid biomass turnover. A single plant can soon become fragmented into several individual 'daughter' plants. This rapid turnover permits rapid adjustment to changes in the local topography of the dune that occurs with unpredictable sand movement. *S. plumieri* colonises the main dune itself. It is a classic 'dune builder' trapping and growing through accreting sand, and casual observations indicate that the species becomes moribund in stable sand. (Sand burial has been shown to enhance photosynthetic rates and affect leaf morphology in *Ammophila breviligulata* and *Calamovilfa longifolia* as well; Yuan et al. 1993). The high growth rate of *S. plumieri* permits the maintenance of a (relatively) high LAI, and also the production of stem to grow through the accreting sand. In the system studied *I. pes-caprae* is almost an anomaly: it occurs predominantly on the more stable crest and landward slope of the dune, and does not suffer frequent large-scale disturbance. It is the species that shows some signs of water limitation in that stomatal conductances are low, and this appears to negatively impact on its photosynthetic and growth rates. However, seedlings of this species are capable of responding to disturbance, re-allocating resources from roots to shoots (Martinez and Moreno-Casaola 1996) on sand burial. It is not known why it is absent from the front of the foredune in the system we studied.

For all three species, because of limited nutrient and water availability, the high rates of growth can be sustained only because plant cover is low. What is

the mechanism that maintains this low cover? It does not seem to be an immediate resource limitation at the leaf or stem level. There are two other possibilities. Firstly, disturbance could limit the establishment of new individuals (seedlings are the most vulnerable part of the life cycle) and perhaps could limit the extension of existing individuals (sand removal, particularly, would do this). Secondly, it is possible that each species has an inherent leaf turnover rate such that the production of new leaves is, in the long term, in balance with the death of old ones. Detailed long-term growth and demographic studies are required.

It is probably the necessity to tolerate disturbance (including salt spray) that prevents the invasion of other species onto the foredune. It is well established that salt spray has an influence on species zonation on coastal dune systems (Boyce 1954; Donnelly and Pammenter 1983; Davy and Figueroa 1993). The growth strategy adopted by foredune species, largely to tolerate sand movement (Maun 1998), is likely to be a disadvantage in stable dunes, where competition and thus resource sequestration by the plants is important. This probably explains why the foredune species do not occur further inland. It is interesting to note that *I. pes-caprae* does occur further from the high tide line than the other foredune species.

9.9 Conclusions

The success of the species inhabiting the foredune of the system we studied (and probably many other mesic tropical and subtropical dune systems) appears to lie in a combination of three factors. Firstly, the plants of the foredune must, of course, have physical characteristics that can resist salt spray and the physical assault of sand blasting. Secondly, plant cover is low, possibly as a consequence of disturbance, particularly sand movement, such that individual stems do not suffer stress imposed by severe resource limitations. Thirdly, growth patterns are such that there is rapid turnover of biomass, which permits accommodation to the disturbance associated with sand movement, as well as reducing biomass accumulation; growth patterns vary amongst species, and this may contribute to the suitability of a species for a particular microhabitat.

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