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Environmental limits to the distribution of *Scaevola plumieri* along the South African coast

Peter, Craig I.[1*]**; Ripley, Brad S.**[1**] **& Robertson, Mark P.**[2***]

[1]*Department of Botany;* [2]*Department of Zoology & Entomology, Rhodes University, P.O. Box 94, Grahamstown, 6140, South Africa;* [*]*Corresponding author; Current address School of Botany & Zoology, University of Natal, Private Bag X01, Scottsville, 3209, South Africa; E-mail peterc@nu.ac.za;* [**]*E-mail b.ripley@ru.ac.za;* [***]*E-mail m.robertson@ru.ac.za*

Abstract. *Scaevola plumieri* is an important pioneer on many tropical and subtropical sand dunes, forming a large perennial subterranean plant with only the tips of the branches emerging above accreting sand. In South Africa it is the dominant pioneer on sandy beaches along the east coast, less abundant on the south coast and absent from the southwest and west coasts. Transpiration rates (E) of *S. plumieri* are predictably related to atmospheric vapour pressure deficit under a wide range of conditions and can therefore be predicted from measurement of ambient temperature and relative humidity. Scaling measurements of E at the leaf level to the canopy level has been demonstrated previously. Using a geographic information system, digital maps of regional climatic variables were used to calculate digital maps of potential transpiration from mean monthly temperature and relative humidity values, effectively scaling canopy level transpiration rates to a regional level. Monthly potential transpiration was subtracted from the monthly median rainfall to produce a map of mean monthly water balance. Seasonal growth was correlated with seasonal water balance. Localities along the coast with water deficits in summer corresponded with the recorded absence of *S. plumieri*, which grows and reproduces most actively in the summer months. This suggests that reduced water availability during the summer growth period limits the distribution of *S. plumieri* along the southwest coast, where water deficits develop in summer. Temperature is also important in limiting the distribution of *S. plumieri* on the southwest coast of South Africa through its effects on the growth and phenology of the plant.

Keywords: Coastal sand dune; Predictive biogeography; Predictive modelling; Seasonal water balance; Water deficit.

Nomenclature: Dyer (1967).

Abbreviations: E = Transpiration; ISSR = Inter Simple Sequence Repeat; *LAI* = Leaf area index; *RH* = Relative humidity; *SVP* = Saturation vapour pressure; *VPD* = Vapour pressure deficit.

Introduction

Climate has been recognized as a fundamental determinant of the distribution of plants for almost two centuries (e.g. Woodward 1987; Woodward & Williams 1987). Several studies have investigated relationships between species distributions and various climatic variables (Panetta & Mitchell 1991; Prentice et al. 1992; Richardson & McMahon 1992; Beerling et al. 1995; Sykes et al. 1996; Stephenson 1998). Predictive models have been developed to investigate the potential impacts of climate change on distributions (Schulze et al. 1993; Sykes et al. 1996) or to obtain potential distribution maps for management of selected species (Panetta & Mitchell 1991; Richardson & McMahon 1992; Robertson et al. 2001).

The models used in these studies have been divided into two broad categories, namely *correlative* and *mechanistic* (Beerling et al. 1995, reviewed by Guisan & Zimmermann 2000), although the distinction between categories is often not clear (Stephenson 1998). Correlative models rely on strong, often indirect links between species locality records and predictor variables to make predictions (e.g. Busby 1991; Carpenter et al. 1993; Robertson et al. 2001). Mechanistic models, which have also been termed *ecophysiological models* (Stephenson 1998) and *process models* (Carpenter et al. 1993), attempt to simulate the mechanisms considered to underlie the observed correlations with environmental attributes (Beerling et al. 1995). Mechanistic models use a detailed knowledge of the target organism's physiological responses to environmental variables as well as life history attributes to make predictions (Stephenson 1998).

Scaevola (Goodeniaceae) includes over 400 mostly Australian species (Dyer 1967). Two species are important components of tropical coastal vegetation in the Indo-Atlantic (*Scaevola plumieri*) and Indo-Pacific (*S. sericea*; Jeffery 1979). *S. plumieri* has large obovate succulent leaves randomly arranged on erect stems up to 80 cm in length. As the stems become buried by accreting

wind-borne sand, they branch and the stems produce adventitious roots. The result is a large 'underground trunkless tree' with only the tips of the 'branches' emerging above the sand dune. Each individual plant can be quite massive as shown by invariable Inter-Simple Sequence Repeat (ISSR) sequence data for individual shoots collected from a large single foredune (Barker et al. 2002).

S. plumieri is found in the atlantic region on the east coast of the Americas (Guppy 1917; Espejel 1987) and the north west coast of Africa north of Angola (Doing 1985; Tinley 1985). In the western Indian Ocean region it occurs from Sri Lanka to eastern and southern Africa (Doing 1985; Ridley 1930; Tinley 1985). *S. sericea* is found throughout the tropical regions of the Indo-Pacific from Hawaii (Alpha et al. 1996) to east Africa (Dyer 1967; Jeffrey 1979), overlapping with *S. plumieri*. *S. plumieri* is an important plant on subtropical South African dunes wherever suitable sandy beaches occur (Tinley 1985; Avis 1992; Lubke et al. 1997). Dominant on the east coast, the distribution of this species becomes patchy as the southern limit of its distribution is approached at Arniston near Cape Agulhas. *S. plumieri* is also probably an important pioneer on many tropical sand dunes throughout the Indo-Atlantic region (Doing 1985).

The physiology of *S. plumieri* has been investigated previously by Pammenter (1983, 1985), Harte & Pammenter (1983) and Steinke & Lambert (1986). Pammenter (1983) notes that *S. plumieri* has high rates of transpiration and he presents a preliminary water budget for a *S. plumieri*-covered dune, suggesting that rainfall meets the plant's water requirements. In addition, he presents data on the photosynthetic characteristics, internal nutrient cycling and phenology of this species. Phenological data of Pammenter (1983) agree with that given by Steinke & Lambert (1986). Peter & Ripley (2000) measured transpiration rates (E) of *S. plumieri* leaves in the field using an infrared gas analyser, and showed that E is predictably related to atmospheric vapour pressure deficit (VPD; see Fig. 2 of Peter & Ripley 2000) at the leaf level. These data were collected between dawn and dusk in all seasons over three years, on different positions on sand dunes and at two remote sites. Soil water status was therefore not specifically measured, but is included in this empirical relationship as a result of the broad sampling. When measured, soil water status of Eastern Cape beach sands (below the dry surface layer and above the free water), measured in a number of seasons, is remarkably constant (mean = 4.0 %; stdv = 0.7; n = 4). VPD is calculated from measurements of ambient temperature and relative humidity, allowing for prediction of E when these two variables are known. Peter (2000) and Peter & Ripley (2000) confirmed gravimetrically that it is possible to scale up leaf level measurements of E to the canopy level. Peter (2000) gives possible explanations of the relationship between E and VPD.

The water requirements of *S. plumieri* possibly account for its observed distribution. We investigated the role of water availability and temperature in defining the distribution limits of *S. plumieri* along the South African coast.

Material and Methods

Coastal climate and dune vegetation in South Africa

The coastline of Southern Africa traverses a number of climatic regions from the moist, tropical east coast through the warm, temperate regions of the southern coast to the hyper arid tropical west coast (Tinley 1985). The southwest coast (Cape Agulhas to Cape Columbine) experiences a distinct mediterranean climate with cool, wet winters and hot, dry summers. The east coast receives rain in summer, on the south coast the rainfall is year round, and the west coast receives less than 200 mm of winter rainfall (Schulze et al. 1997). Rainfall exceeds 1000 mm on the east coast, parts of the south coast and on the southwest coast near Cape Town. The other parts of the south coast receive as little as 500 mm annual rainfall (Schulze et al. 1997).

Tinley (1985) surveyed the coastal dunes of South Africa. Vegetated sand dunes occur on all sections of the coast. The coast between East London and Durban is steep and rocky with small dunes confined to bay heads and river mouths. The sand dunes in different parts of southern Africa are colonized by various assemblages of species strongly influenced by the vegetation types of the adjacent inland areas (Lubke & van Wijk 1998). The east coast is strongly influenced by the Tongoland-Pondoland flora, the Afromontane flora (Lubke & van Wijk 1998) and, to an extent, the Madagascan flora (Tinley 1985). The vegetation of the southern coast is dominated by elements of the Cape fynbos flora and, to a lesser extent, the Karoo-Namib flora. These floras mix along the southeast coast (Lubke & van Wijk 1998). The west coast of South Africa (north of Cape Columbine) is dominated by the Karoo-Namib and Cape floras (Tinley 1985; Lubke & van Wijk 1998). Along many sandy coasts, strong successional gradients are evident from pioneer communities near the high water mark to some form of mature community on stabilized sands inland. Lubke et al. (1997) and Tinley (1985) give detailed accounts of vegetation zonation and succession on different sections of the South African coast.

Digital climatic maps

Digital maps of mean monthly maximum (T_{max}) and minimum (T_{min}) temperatures (ºC), mean monthly relative humidity (RH_{ave}; %) and median monthly rainfall (R_m; mm), developed by Schulze et al. (1997), were used to produce maps of water balance. Each of these climatic maps was interpolated from point data obtained from a network of weather recording stations distributed throughout South Africa to produce continuous digital maps at a resolution of 60 pixels per degree. Each pixel is one minute of latitude by one minute of longitude and has an associated value for a specific climatic variable (Schulze et al. 1997).

Production of the water balance maps

Peter & Ripley (2000) have predicted E of *S. plumieri* from VPD which, in turn, is determined from temperature and relative humidity (RH) (Fig. 2 of Peter & Ripley 2000). They note that leaf level transpiration rates may be scaled to the canopy level and validate predictions of transpiration rates made from both instantaneous VPD and mean VPD calculated for entire days (Peter & Ripley 2000).

The regression of E to VPD for *S. plumieri* (Fig. 2 of Peter & Ripley 2000) is the basis of the model for predicting the distribution of *S. plumieri* along the South African coast. The calculation of monthly regional water balance from the relevant climatic maps is given in Fig. 1. A digital map of mean monthly temperature (T_{ave}; ºC) was calculated from T_{max} and T_{min}. A map representing saturation vapour pressure (SVP; kPa) was then calculated from T_{ave} according to the equation of Goff & Gatch (1946):

$$SVP_{T_{ave}} = \frac{6.1375 \exp\left(T_{ave} \times \left[18.564 \pm \left(\frac{T_{ave}}{254.4} \right) \right] \right)}{T_{ave} + 255.57} \times \frac{1}{10} \quad (1)$$

$SVP_{T_{ave}}$ is SVP at mean temperature (T_{ave}).

Using maps of SVP and RH_{ave} (%), a map of vapour pressure deficit (VPD; kPa) was calculated:

$$VPD = SVP_{T_{ave}} \pm \left(SVP_{T_{ave}} \times \frac{RH_{ave}}{100} \right) \quad (2)$$

The monthly VPD map was used to calculate monthly potential transpiration rates according to the regression relationship of E to VPD established for *S. plumieri* (Fig. 2 of Peter & Ripley 2000):

$$E = -0.38VPD^2 + 3.55VPD - 0.73 \quad (3)$$

The map of potential transpiration (mmol.m^{-2}.s^{-1}) was converted to an intermediate map (l.m^{-2}.mo^{-1}) and then multiplied by the leaf area index (LAI, m^2 of leaf area per m^2 of sand dune area). LAI in this case is 0.95 ($n = 21$; Peter 2000), producing a map of potential transpiration (l.mo^{-1}) per m^2 of vegetated sand dune. The map of mean monthly potential transpiration was subtracted from the corresponding median monthly rainfall map (also expressed as litres of rainfall per m^2 of vegetated sand dune) to produce a map of mean monthly water balance on the basis of one m^2 of vegetated sand dune. The 12 monthly water balance maps were summed to produce a cumulative map of annual water balance. The calculations were performed using the Geographic Information System (GIS) software; IDRISI for Windows (Eastman 1997).

Water balance (e.g. in Fig. 2) is the predicted potential amount of water transpired by one m^2 of *S. plumieri* canopy subtracted from the input of water as rain expressed on a square metre basis. This is described as the 'potential water balance' as potential transpiration rates are estimated for the entire coast, including sections

Fig. 1. Simplified schematic representation of the calculation of water balance maps. Input maps are given by ▢, intermediate maps are given by ▨, operations by ▯, and the output water water balance maps by ■. T_{min}, T_{max}, T_{ave} = Mean monthly minimum, maximum and average temperature, respectively; RH_{ave} = Mean monthly relative humidity; Rm = Monthly median rainfall; SVP = Monthly saturation vapour pressure deficit; VPD = Mean monthly atmospheric vapour pressure deficit; E = Mean monthly potential transpiration rates of *S. plumieri*. See text for further explanations of abbreviations and details of the listed equations.
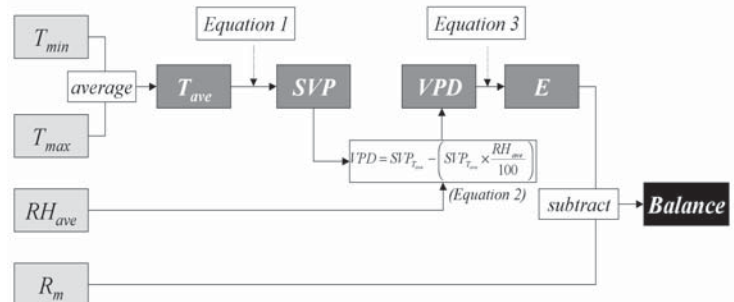
where the plant is absent. Our calculations of transpiration rates are probably good estimates of evapotranspiration for the dune system as evaporation from the surface of dune sand is negligible due to the insulating surface layer of dry sand (Hesp 1991). In some respects the canopy of *S. plumieri* approaches a hypothetical standard crop used by Stephenson (1998) to define actual evapotranspiration. This species has a low, well-ventilated canopy and probably has very low resistances to evaporative water loss (Peter & Ripley 2000). In addition, as already described, water loss from the surface of the dune sand is negligible. It should also be noted that we do not consider the buffering effect of soil water and the input of water from the dune aquifer water as this data is not available and difficult to model.

Distribution data

Locality records were collected using a hand-held Global Positioning System. Beaches between Cape Columbine on the west coast and the Mozambique border on the north-east coast were surveyed for presence or absence of *S. plumieri*. Continuous data were collected for much of the KwaZulu-Natal coast, north of the Tugela River, as well as the southeast coast between Port Alfred and East London. Photographs (R.A. Lubke & B.I. Peter pers. comm.) were used to confirm the presence of *S. plumieri* along inaccessible stretches of the east coast in the absence of formal records. Lists of presence and absence localities and voucher specimens are housed in the Schönland Herbarium, Grahamstown (GRA). Distribution data for *S. plumieri* obtained from most herbarium specimens housed in the Schönland Herbarium (GRA), Natal Herbarium (NH) as well as the National Herbarium, Pretoria (PRE) were insufficiently precise for use in this study. Only co-ordinates of localities recorded at one minute precision or better were used, due to the precision of the climatic maps used (one minute by one minute pixel size).

Monthly water balance

The values associated with presence and absence localities were extracted from each of the 12 monthly water balance maps using IDRISI. From these data sets, the mean water balance values for each month were calculated for 216 presence and 44 absence localities. A repeated measures ANOVA was performed on the water balances associated with presence and absence localities predicted for the 12 months. In the repeated measures ANOVA the sphericity assumption of the variance-covariance matrices is a necessary and sufficient condition for the univariate F-test to be valid (Johnson 1998). The sphericity assumption was tested using Mauchley's W-

criterion (Keselman & Keselman 1993). MANOVA procedures included Wilk's λ for multivariate comparisons of means and variance-covariance matrices. These were performed on the water balances predicted for the various months.

Temperature and water balance

To investigate the role that temperature may play in defining the distribution of *S. plumieri*, the South African coast was divided into four zones (east, south, southwest and west coasts) based on the following rationale. The east coast (Algoa Bay northeastwards) has substantial summer water surpluses (rain exceeds water use by the plants, Fig. 2) and *S. plumieri* is abundant. The south coast (Algoa Bay to Cape Agulhas) has year-round low positive water balance and the distribution of *S. plumieri* is patchy. The southwest coast (Cape Agulhas to Cape Columbine), where summer water deficits develop (rain does not balance the amount of water extracted by the plants), *S. plumieri* is absent. On the west coast (Cape Columbine northwards into Namibia) year-round water deficits occur and *S. plumieri* is absent. The extent of these zones approximate the regions proposed by Tinley (1985) and Lubke et al. (1997) which were based on climate, attributes of the physical nature of the coast, the different biomes along the coastline, species distributions and political boundaries. In each of these four sections ten localities were selected at approximately equal distances. The monthly values of water balance and T_{ave} associated with these localities were calculated to give a single value for each of the four sections of the coast.

Results

Distribution

S. plumieri is abundant along the entire east coast of South Africa and is found on almost all sandy beaches (Fig. 2F). Along the south coast (from Algoa Bay to Cape Agulhas) the distribution of *S. plumieri* becomes increasingly patchy proceeding westwards, with Arniston (near Cape Agulhas) being the western limit of its distribution. *S. plumieri* was confirmed to be present at 216 localities (based on 355 observations) along the east and south coasts and absent from a further 44 localities along the southwest and west coasts.

Annual water balance

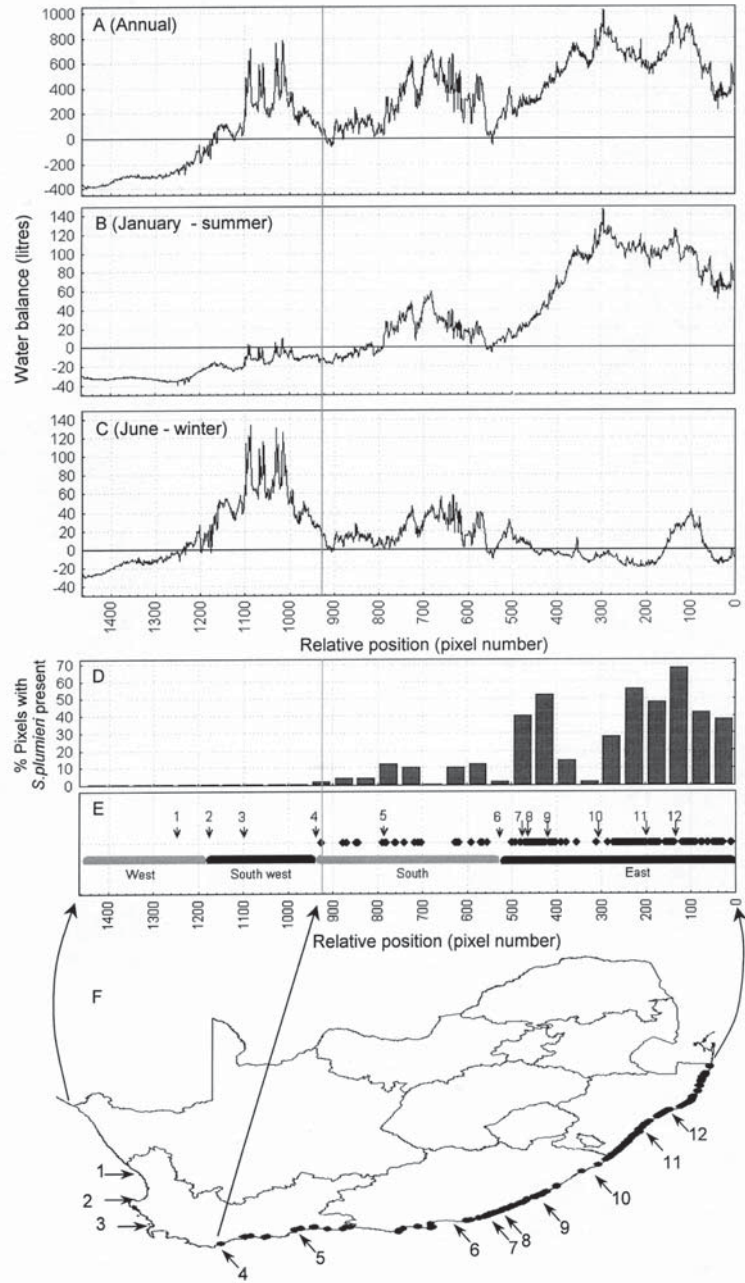Annual water balance values (the sum of 12 monthly

Fig. 2. Water balance of *S. plumieri* for (**A**) the entire year (sum of 12 months), (**B**) January and (**C**) June. The *x*-axis is the pixel number of all coastal pixels from one in the east at the Mozambique border to 1465 in the west at the Namibian border. (**D**) The coastline was divided into sections 50 pixels long and in each section the percentage of the pixels with *S. plumieri* recorded as present was determined. (**E**) All coastal pixels in which *S. plumieri* was recorded as present. Horizontal bars identify the sections of the coast refered to in the text. (**F**) Distribution of *S. plumieri* along the South African coast line. Numbers in (**E**) and (**F**) identify landmarks mentioned in the text:

1 = Lamberts Bay; 2 = Cape Columbine;
3 = Cape Town; 4 = Cape Agulhas;
5 = George; 6 = Algoa Bay;
7 = Port Alfred; 8 = Old Womans' River;
9 = East London; 10 = Port St Johns;
11 = Durban; 12 = Mtunzini.

Vertical line through (**A**) to (**E**) marks the westernmost limit of the distribution of *S. plumieri* at Arniston near Cape Agulhas and corresponds with pixel number = 925.

water balances) indicate that substantial water surpluses develop along the east coast and on much of the southern and southwest coasts, as far west as Cape Columbine (Fig. 2A). However, annual water surpluses in Algoa Bay and on the south coast (George to Cape Agulhas) were low. On the west coast, north of Cape Columbine, low rainfall coupled with high potential transpiration rates resulted in large annual water deficits.

The distribution of *S. plumieri* corresponded with annual water surpluses on the eastern and southern coasts. The absence of *S. plumieri* on the west coast corresponded with annual water deficits. However, annual water deficits could not explain the absence of *S. plumieri* on the southwest coast, which experiences high annual water surpluses due to high winter rainfall. It should be noted that none of the localities at which *S. plumieri* was present developed water deficits over the course of a year, although the water surpluses near the distribution limit of this species were low.

Monthly water balance

The variance-covariance matrices for the response variables (predicted water balance for the presence and absence localities) did not pass Mauchley's sphericity tests ($W < 0.0001$; $P < 0.0001$) and hence the univariate ANOVA procedure could only be considered reliable following a Greenhouse-Geisser adjustment (Greenhouse & Geisser 1959). The results of the ANOVA revealed that the predicted water balances differed significantly for presence and absence localities ($F = 93.36$ with 1 *df*; $P < 0.0001$) among months ($F = 6.77$ with a Greehouse-Geisser adjustment *df* = 1.3; $P = 0.005$) and for the interaction between the two ($F = 429.67$ with Greehouse-Geisser adjustment *df* = 1.3; $P < 0.0001$). MANOVA tests confirmed the univariate results (Wilk's $\lambda = 0.16$; $P < 0.0001$).

In the summer months (e.g. January, Figs. 2B, 3), water deficits developed along the southwestern and western parts of the coast from Cape Agulhas northwestwards along the arid west coast. *S. plumieri* was recorded as absent on these coasts (Fig. 2B, F). Localities at the limit of the distribution of *S. plumieri* also developed slight water deficits in some summer months. The distribution of *S. plumieri* along the east and south coasts is associated with summer water surpluses.

In winter (June, Figs. 2C, 3), the water surpluses occur predominantly in the winter rainfall region of the southwest coasts (Cape Agulhas to Cape Columbine). Surpluses also occurred on the KwaZulu-Natal east coast near Mtunzini. Along the southern coast water surpluses of varying magnitude developed in winter. It was only on the southwest coast (Cape Agulhas to Cape Columbine) that the potential water surpluses were high as a result of very high winter rainfall in this region (Schulze et al. 1997). *S. plumieri* does not extend into

the winter rainfall areas which experience summer drought (Fig. 2B, F).

Negative annual water balance (annual water deficit), therefore, does not explain the observed distribution of *S. plumieri*. The absence of *S. plumieri* (localities to the west of the vertical line in Fig. 2) appears to be correlated with summer water deficit (Fig. 2B, 3). The distribution only extends a short distance along the south coast (George to Cape Agulhas) where summer water balances were low and small summer water deficits apparently arise (Fig. 2B).

Localities where *S. plumieri* is present experience only four months of water deficit as opposed to seven months at localities where this species is absent (Fig. 3). Because the univariate and multivariate statistics are significant it is appropriate to compare the months using the *F*-test. March is the most predictive month ($F = 366.3$), while the spring and autumn months, when water balance at presence and absence localities is similar, are least predictive (e.g. September $F = 30.3$, Table 1). However, water balance at presence and absence localities is significantly different in all months.

Temperature

Mean monthly temperatures were compared to the water balance on four separate sections of the coast (Fig. 4). Along the east coast where *S. plumieri* is abundant, periods of water deficit correspond with periods of low temperature in winter. Along the south coast where *S. plumieri* is present (but with patchy distribution), low water surpluses occur throughout the year. By contrast, water deficits are synchronized with high summer temperatures on the southwest section of the coast where *S. plumieri* is absent. On the west coast,
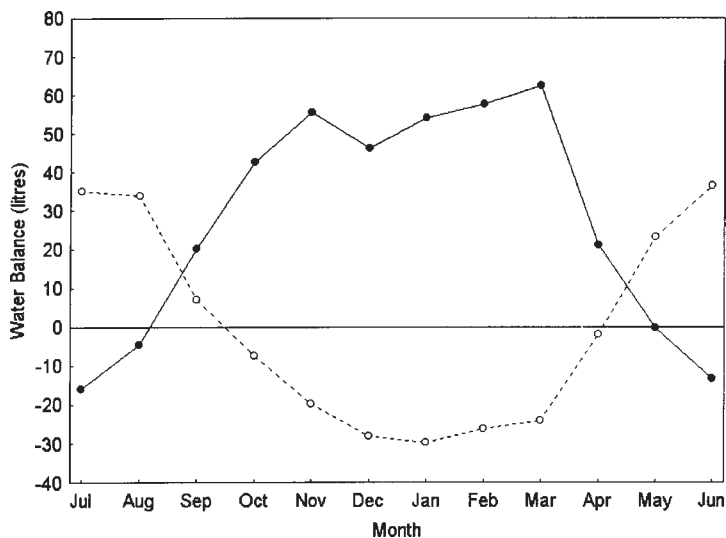

Fig. 3. Mean water balance values at sites where *Scaevola plumieri* is present (○; $n = 216$) and absent (●; $n = 44$) for 12 months from July to June.
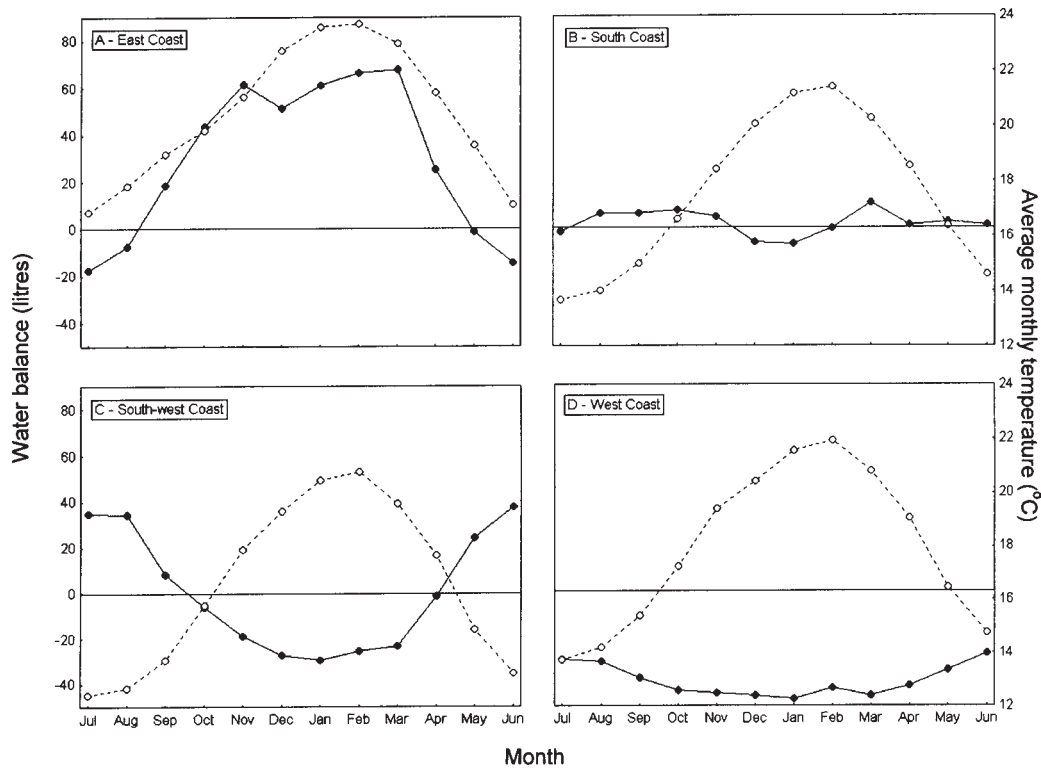
Fig. 4. Water balance (●) and mean temperature (○) for the east, south, southwest and west coasts. *Scaevola plumieri* is abundant on the east coast, present but with patchy distribution along the south coast and absent on the southwest and west coasts.

high water deficits develop and water balance rather than temperature is probably more important in limiting the plants' distribution on this coast.

S. plumieri is absent from the southwest coast, but due to the annual water surplus that this coast experiences it might be expected to support *S. plumieri*. However, as this coast experiences a mediterranean climate, water surpluses occur in winter when the growth and productivity of this species is low (or even negative). This section of the coast experiences long periods when temperature and water balance are unsynchronized (maximum water deficit and maximum temperature co-

occurring in January and February, Fig. 4C) and therefore appears to be unsuitable for *S. plumieri*.

Discussion

There is a strong correlation between localities with summer water deficit and the absence of *S. plumieri* (Fig. 2B). In the summer months high temperatures and moderate relative humidity translate into relatively high atmospheric *VPD*-values. As a result of the near-linear relationship of transpiration rates to *VPD* in *S. plumieri* (Peter & Ripley 2000), high summer *VPD*-values result in high rates of potential transpiration. Along the east and southeast coasts of South Africa these high rates of water use are balanced by the high rainfall resulting in positive water balance and positive soil water status. Along the southwest and west coasts, summer rainfall is extremely low, resulting in summer water deficits (Fig. 2B). *S. plumieri* is restricted to the east and southeast coasts of South Africa where summer water balances are positive. Elsewhere, along the southwest and west coasts, this species is replaced by various assemblages of pioneer species (Lubke et al. 1997).

In winter, lower temperature and *RH* result in lower

Table 1. Results of a MANOVA performed on the water balances associated with presence and absence localities predicted for the 12 months. Water balance at presence and absence localities is significantly different in all months.

Month	*F*-test	Month	*F*-test
January	234.8	July	297.3
February	311.7	August	203.8
March	366.3	September	30.3
April	57.9	October	219.8
May	79.6	November	284.5
June	273.4	December	234.0

VPD and lower potential transpiration rates. Along the southwest coast, these lower potential transpiration rates are coupled with very high rainfall resulting in high positive winter water balances. *S. plumieri* is not found along the southwest coast, which has very high winter surpluses resulting in positive annual water balances. The very low rainfall along the west coast explains the large water deficits in all seasons on this coast. There are no records of *S. plumieri* on the west coast.

Seasonal, not annual, water balance was most closely correlated with the observed distribution of *S. plumieri*. When considered in this manner, the data account for water availability at a time of the year that is energetically favourable for plant growth. The importance of considering water supply and energy have been highlighted by workers such as Stephenson (1990, 1998).

The fact that summer water deficit can be used to predict the absence of *S. plumieri*, particularly when considered in conjunction with ambient temperature and taking into account seasonal variation, suggests a causal link to aspects of plant function. Several aspects of plant function have seasonal variation and are likely to be strongly affected by water availability, which would explain why certain season's water budgets are better predictors of plant distribution than others. Published data show that the growth of *S. plumieri* is seasonal. Steinke & Lambert (1986), Pammenter (1983) and Ripley (unpubl.), working on plants at Durban, Mtunzini and Old Woman's River respectively, showed that leaf production is increased during the summer months. During the drier winter months, the rate of leaf abscission increases and in some months may exceed leaf appearance. Leaf longevity is also considerably higher in winter compared to summer. Pammenter (1983) recorded leaf production of up to 6.4 leaves per shoot per month in summer, decreasing to 2.4 leaves per shoot per month in winter at Mtunzini. Further south at Durban (slightly cooler and drier), Steinke & Lambert (1986) recorded leaf production rates of 3.8 and 1.8 leaves per shoot per month in summer and winter respectively. At the Old Woman's River study site in the southeast Ripley (unpubl.) recorded less distinct differences between summer and winter production. Steinke & Lambert (1986) recorded longevity of leaves in the region of 190 days in winter compared to 120 days in summer, while Harte & Pammenter (1983) noted values of 210 days and 140 days, suggesting that growth rates are depressed during winter periods and the plants retain their leaves for longer periods.

In addition to growth, net CO_2 assimilation is likely to have seasonal variation. Considerable evidence shows that the CO_2 assimilation of canopies due to mutual shading is determined more by intercepted photosynthetic photon flux density than by the light saturated assimilation rates (Hesketh 1980; Jarvis & Leverenz 1983). Photosynthetic productivity of *S. plumieri* is likely to be highest in the summer months as a result of higher summer levels of solar radiation and longer day length (Schulze et al. 1997). In addition, high photosynthetic rates have been correlated with the maintenance of high stomatal conductance (Körner 1995), which is only possible under conditions of favourable plant water status. As summer months represent physiologically active periods for this species positive water balance, and therefore positive soil and plant water status during this period, are likely to be more important than winter water balance. This may explain the correlation between the absence of the plants and water deficits in summer.

There is evidence that phenology of species may be phylogenetically fixed. Pierce & Cowling (1984), working on coastal subtropical thicket, suggest that only species with wide phenological flexibility have been able to extend their distribution into the non-seasonal rainfall areas along the south coast. This idea may apply to *S. plumieri* if its phenology is phylogenetically fixed to coincide with warm, wet periods. This species may not be flexible enough to adapt to growth in cool, wet winters of the summer drought areas of the southwest coast where the winter days are significantly shorter than those in summer.

The water balance values calculated here are likely to summarize the interaction of a number of climatic variables. Transpiration is essentially driven by potential evaporation which is, in turn, determined by temperature, relative humidity and, less directly, by solar radiation. As noted previously, our calculations of transpiration rates are probably good estimates of evapotranspiration for the dune system, as evaporation from the surface of dune sand is low due to the insulating surface layer of dry sand. Potential transpiration rates are then subtracted from rainfall, thus incorporating this important variable into the water balance. This approach therefore integrates a number of different environmental variables, which may play an important physiological role in limiting plant distribution. This is similar to the moisture index of Box (1981), which is calculated as mean annual precipitation divided by the estimated annual evapotranspiration rate (calculated from monthly mean air temperature) and "serves as the best single indicator of the dominant growth forms, general vegetation structure, and the degree of leaf xeromorphy" (Box 1981).

To date, the majority of studies investigating physiological explanations for plant distributions have been at the vegetation level. Mechanistic models predicting the distribution of individual species based on their physiology are rare. Bunce et al. (1979) is one of the few examples. This is because it is difficult to describe and

define the ecophysiological response of individual species to a variety of covarying climatic variables. Mechanistic models, such as that proposed by Woodward (1987) to predict the distribution of different vegetation types, draw on less specific physiological responses at the higher taxa or functional type level, and so are easier to implement. Correlative models provide an alternative to these mechanistic models and are generally simpler and less time consuming to build, although they usually provide fewer insights into the factors limiting the distribution of the target organism.

In this study we have suggested possible mechanisms to explain the observed distribution of *S. plumieri* on the South African coast. We have presented a model based on potential water use and phenology that successfully predicts the distribution of this plant. While this model is predictive, it is species specific as it relies on our knowledge of the ecophysiology of *S. plumieri*. The water balance data presented here examine the interactions of plant water use and water availability from rainfall without considering the supply of water held within the deeper sand layers and the dune aquifer. The fact that sand water status was not considered in this model is a weakness as the buffering effect of stored soil water would undoubtedly moderate the water balance values calculated. Although this model indirectly accounts for the effect of energy on plant distribution, as energy (light and temperature) is the driving force for transpiration, more direct measures may be required to elucidate underlying mechanisms.

The model of the potential distribution of *S. plumieri* and our understanding of factors that appear to limit its distribution provide an ideal case against which to assess the predictive power of more general correlative modelling techniques in the future.

References

Alpha, C.G., Drake, D.R. & Goldstein, G. 1996. Morphological and physiological responses of *Scaevola sericea* (Goodeniaceae) seedlings to salt spray and substrate salinity. *Am. J. Bot.* 83: 86-92.

Avis, A.M. 1992. *Coastal dune ecology and management in the Eastern Cape*. Ph.D. Thesis. Rhodes University, Grahamstown, SA.

Barker, N.P., Harman, K.T., Ripley, B.S. & Bond, J. 2002. The genetic diversity of Scaevola plumieri (Goodeniaceae), an indigenous dune coloniser, as revealed by Inter Simple Sequence Repeat (ISSR) Fingerprinting. *S. Afr. J. Bot.* 68: 532-541.

Beerling, D.J., Huntley, B. & Bailey, J.P. 1995. Climate and distribution of *Fallopia japonica*: use of an introduced species to test the predictive capacity of response surfaces. *J. Veg. Sci.* 6: 269-282.

Box, E.O. 1981. *Macroclimate and plant forms: an introduction to predictive modelling in phytogeography*. Tasks for vegetation science 1. Junk, The Hague, NL.

Bunce, J.A., Chabot, B.F. & Miller, L.N. 1979. Role of annual leaf carbon balance in the distribution of plant species along an elevational gradient. *Bot. Gaz.* 140: 288-294.

Busby, J.R. 1991. BIOCLIM – a bioclimatic analysis and prediction tool. In: Margules C.R., Austin M.P. (eds.) *Nature conservation: cost effective biological surveys and data analysis*. CSIRO, Melbourne, AU.

Carpenter, G., Gillison, A.N. & Winter, J. 1993. DOMAIN: a flexible modelling procedure for mapping potential distribution of plants and animals. *Biodivers. Conserv.* 2: 667-680.

Doing, H. 1985. Coastal fore-dune zonation and succession in various parts of the world. *Vegetatio* 61: 65-75.

Dyer, R.A. 1967. *The genera of Southern African flowering plants, volume 1, dicotyledons*. Department of Agriculture and Technical Services. Pretoria, SA.

Eastman, J.R. 1997. *IDIRISI for Windows version 2*. Clark Labs, Clark University, Worcester. WEB: http://www.clarklabs.org

Espejel, I. 1987. A phytogeographical analysis of coastal vegetation in the Yucatan Peninsula. *J. Biogeogr.* 14: 499-519.

Goff, J.A. & Gatch, S. 1946 Low-pressure properties of water from −160°F to 212°F. *Trans. Am. Soc. Heat. Vent. Engin.* 52: 95-121.

Greenhouse, S.W. & Geisser, S. 1959. On methods in the analysis of profile data. *Psychometrika* 24: 95-112.

Guisan, A. & Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology. *Ecol. Model.* 135: 147-186.

Guppy, H.B. 1917. *Plants, seeds, and currents in the West Indies and Azores*. Williams & Norgate, London, UK.

Harte, J.M. & Pammenter, N.W. 1983. Leaf nutrient content in relation to senescence in the coastal sand dune pioneer *Scaevola thunbergii* Eckl. & Zeyh. *S. Afr. J. Sci.* 79: 420-422.

Hesketh, J.D. 1980. Predicating canopy photosynthesis from gas exchange studies in controlled environments. In:

Hesketh, J.D. & Jones, J.W. (eds.) *Predicting photosynthesis for ecosystem models,* Vol I, pp. 37-50. CRC, Boca Raton, FL.

Hesp, P.A. 1991. Ecological processes and plant adaptations on coastal dunes. *J. Arid Environ.* 21: 165-191.

Jarvis, P.G. & Leverenz, J.W. 1983. Productivity of temperate, deciduous and evergreen forests. In: Lange, O.L., Nobel, P.S., Osmond, C.B. & Zeigler, H. (eds.) *Encyclopedia of plant physiology, New Series* 12D, pp. 233-280. Springer, Berlin, DE.

Jeffrey, C. 1979. On the nomenclature of the strand *Scaevola* species (Goodeniaceae). *Kew Bull.* 34(3): 537-545.

Johnson, D.E. 1998. *Applied multivariate methods for data analysis.* Brooks/Cole, Pacific Grove, CA.

Keselman, H.J., Keselman, J.C. 1993. Analysis of repeated measurements. In: Edwards, L.K. (ed.) Applied Analysis of Variance in Behavioral Science, pp 105-145. Marcel Dekker, New York, NY.

Körner, C.H. 1995. Leaf diffusive conductances in the major vegetation types of the globe. In: Schultze, E.-D. & Caldwell, M.M. (eds.) *Ecophysiology of photosynthesis,* pp. 463-490. Springer, Berlin, DE.

Lubke, R.A. & van Wijk, Y. 1998. Terrestrial plants and coastal vegetation. In: *Field guide to the Eastern and Southern Cape coasts.* In: Lubke R.A. & de Moor I. (eds.) University of Cape Town Press, Cape Town, ZA

Lubke, R.A., Avis, A.M., Steinke, T.D. & Boucher, C. 1997. Coastal vegetation. In: Cowling, R.A. (ed.) *Vegetation of Southern Africa,* pp. 300-321. Cambridge University Press, Cambridge, UK.

Pammenter, N.W. 1983. Some aspects of the ecophysiology of *Scaevola thunbergii,* a subtropical coastal dune pioneer. In: McLachlan, A. & Erasmus, T. (eds.) *Sandy beaches as ecosystems,* pp. 675-685. Junk, The Hague, NL.

Pammenter, N.W. 1985. Photosynthesis and transpiration of the subtropical coastal sand dune pioneer *Scaevola plumieri* under controlled conditions. *S. Afr. J. Bot.* 51: 421-424.

Panetta, F.D. & Mitchell, N.D. 1991. Homocline analysis and the prediction of weediness. *Weed Res.* 31: 273-284.

Peter, C.I. 2000. Water requirements and distribution of *Ammophila arenaria* and *Scaevola plumieri* on South African coastal dunes. M.Sc. Thesis, Rhodes University, Grahamstown, ZA.

Peter, C.I. & Ripley, B.S. 2000. An empirical formula for estimating the water use of *Scaevola plumieri*. *S. Afr. J.*

Sci. 96: 593-596.

Pierce, S.M. & Cowling, R.M. 1984. Phenology of fynbos, renosterveld and subtropical thicket in the south eastern Cape. *S. Afr. J. Bot.* 3: 1-16.

Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A. & Solomon, A.M. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. *J. Biogeogr.* 19: 117-134.

Richardson, D.M. & McMahon, J.P. 1992. A bioclimatic analysis of *Eucalyptus nitens* to identify potential planting regions in South Africa. *S. Afr. J. Sci.* 88: 380-387.

Ridley, H.N. 1930. *The dispersal of plants throughout the World.* Reeve, Kent, UK.

Robertson, M.P., Caithness, N. & Villet, M.H. 2001. A PCA-based modelling technique for predicting environmental suitability for organisms from presence records. *Divers. Distrib.* 7: 15-27.

Schulze, R.E., Kiker, G.A. & Kunz, R.P. 1993. Global climate change and agricultural productivity in southern Africa. *Global Environ. Change* 3: 330-349.

Schulze, R.E., Maharaj, M., Lynch, S.D., Howe, B.J. & Melville-Thomas, B. 1997. *South African atlas of agrohydrology and –climatology.* Report, TT82/96, Water Research Commission, Pretoria, SA.

Steinke, T.D. & Lambert, G. 1986. A preliminary study of the phenology of *Scaevola plumieri*. *S. Afr. J. Bot.* 52: 43-46.

Stephenson, N.L. 1990. Climatic control of vegetation distribution: the role of the water balance. *Am. Nat.* 135: 649-670.

Stephenson, N.L. 1998. Actual evapotranspiration and deficit: biological meaningful correlates of vegetation distribution across spatial scales. *J. Biogeogr.* 25: 855-870.

Sykes, M.T., Prentice, I.C. & Cramer, W. 1996. A bioclimatic model for the potential distributions of north European tree species under present and future climates. *J. Biogeogr.* 23: 203-233.

Tinley, K.L. 1985. *Coastal dunes of South Africa.* South African National Scientific Programmes, Report No. 109. Council for Scientific and Industrial Research, Pretoria, SA.

Woodward, F.I. 1987. *Climate and plant distribution.* Cambridge studies in ecology, Cambridge University Press, Cambridge, UK.

Woodward, F.I. & Williams, 1987. Climate and plant distribution at global and local scales. *Vegetatio* 69: 189-197.