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Spatial and Temporal Changes in South African Solar Ultraviolet-B Exposure: Implications for Threatened Taxa

Spatial and temporal changes in South African solar UV-B (280–315 nm) exposure were modeled and mapped at 2.5 km² resolution using ozone, relative humidity, cloud amount and elevation data. Computations indicated large natural gradients in UV-B exposure ranging from a 34.2% change over 14° of latitude to a 44.2% change over 16° of longitude. Modelling of future scenarios in annual UV-B exposure indicated small increases ranging from 2.5% in the year 2003 (best-case ozone depletion scenario) to 8.1% in the year 2051 (worst-case ozone-depletion scenario). Notable were substantial increases in intra-annual variability in UV-B radiation with ozone depletion. Exposure exhibits a 12% increase during late autumn (May) in the year 2003 and a 35% increase during this season in the year 2051. Taxonomic, life form and functional attributes were analyzed in 2146 threatened (rare, endangered, vulnerable) species representing 468 genera and 103 families, and their distributions compared with modeled spatial and temporal UV-B distribution patterns. The high fractions of evergreen and succulent life forms and geophytes, present among threatened taxa, indicate a high degree of physiological resilience to increased solar UV-B stress, though some life forms, e.g. trees, appear relatively less resistant. Conceivable reductions in per capita reproductive output and overall plant fitness were indicated in some plant functional types, e.g. herbaceous annuals, which may lead to altered patterns of species coexistence, floristic composition and diversity.

INTRODUCTION

It is widely accepted that the African environment is increasingly undergoing additional land-use pressures and desertification (1). The probable effects of climate change on the African biota and ecosystems have received far less attention. In particular, the impact of possible increased solar ultraviolet-B radiation as a consequence of accelerated depletion of the stratospheric ozone shield (2) has received little attention, especially at the regional scale.

Numerous experimental studies describing the effects of solar UV-B increases on terrestrial plants at various levels of organization (molecular, tissue, whole plant, community and more recently ecosystem level) have appeared over the last two decades (3, 4). These show that UV-B sensitivity differs with plant developmental stage, species, varieties and populations, and is also modified by microclimatic conditions in the plant's environment. A few studies, which have compared plant performance across natural solar UV-B gradients, indicate that species and ecotypes from high UV-B irradiance environments, e.g. montane and low latitude locations, are often less sensitive to elevated UV-B than those from low UV-B irradiance environments, though there are exceptions (5, 6). This has led to suggestions that genotypic differentiation may have developed among plants along these gradients. Various phenotypic acclimation mechanisms to high UV-B exposure displayed by

plants, such as altered branching, leaf size, shape and thickness, have been shown to differentially affect species canopy structure, light interception patterns, and stand photosynthesis. These alter species' competitive interactions, and may also impact on ecosystem structure and function (9).

Species that are distributed over extensive geographic areas are subjected to large spatial and seasonal variations in solar UV-B exposure (7), a function of the natural latitudinal gradient in thickness of stratospheric ozone layer, prevailing solar angles at different latitudes, elevation above sea level, cloud amount and form (6–8). Since natural variations in solar UV-B flux are large when compared with those anticipated from ozone depletion (2), only limited fractions of species populations with extensive geographical ranges would be subjected to UV-B exposures exceeding those encountered over natural distribution ranges with ozone depletion (Fig. 1). Conversely, species localized within restricted geographical areas or habitats or thinly scattered over a more extensive range due to habitat destruction or other environmental disturbance are potentially at greatest risk from ozone depletion because larger fractions of their populations would be subjected to increased UV-B exposure. In South Africa, conservation status ratings have been applied to 4149 species (19.2%) of the 21 661 species of South Africa (10, 11). Of these, 2146 species are included under the categories endangered, vulnerable and rare due to drastic reductions in numbers of their individuals and habitats, indeed to critical levels deemed to be in immediate danger of extinction in the endangered category (10). We examined the taxonomic, life form and functional attributes of these threatened taxa and compared their distributions to modeled spatial and temporal UV-B exposure patterns in order to assess their vulnerability to anticipated future increases in solar UV-B radiation.

TEMPORAL AND SPATIAL TRENDS IN SOLAR UV-B EXPOSURE

Changes in total column ozone at different latitudes (means over 16°E to 33°E longitude), computed from monthly ozone averages supplied by NASA for the 13-year 1979 to 1991 period, are shown in Figure 2A. Mean annual ozone depletion for all latitudes between 22°S to 35°S was only 2.8%. However, the intra-annual variability was greater, ranging from a 6 to 8% ozone depletion at all latitudes in late autumn (May) to a 2 to 4% ozone accumulation at high latitudes (34°S) during mid-winter (July). The latter reflected ozone build-up around the circumpolar vortex that forms in the Antarctic (12). Also a 2 to 4% ozone accumulation was apparent at lower latitudes (22°S to 23°S) during mid-spring (October).

Modeled changes in UV-B exposure for the 1979 to 1991 period are illustrated in Figure 2B. By the exposure we shall here mean the irradiance on a horizontal surface integrated over time (e.g., day, month or year), and spectrally weighted as described below. Calculations were performed with the aid of a computer-based empirical model (13), modified for large-scale computation (14), which was integrated with Geographic Information Systems (GIS). The calculations included monthly averages

of total column ozone, and relative humidity and cloud amount at 1400 SAST (15), as well as digital elevation data at 2.5 km² resolution (1.6 km x 1.6 km grid). Ultraviolet attenuation by cloud amount was described solely by a simple linear function (16), applicable at temporal scales of a month or larger (17), and shown to agree with both UV-B (18) and UV-A (19) measurements at Penang in Malaysia. Spectral irradiances, computed hourly for the 15th day of each month, were weighted with the alfalfa action spectrum for intact DNA pyrimidine base dimerization (20), normalized at 290 nm, and integrated over wavelength and time to give total daily biologically effective UV-B exposure (kJ m⁻² d⁻¹). If normalization would have been for 300 nm instead, as commonly used, the exposure values would have been about 75% higher. Computed UV-B exposure, like total column ozone, showed large intra-annual variability, ranging from a 4 to 5% increase at all latitudes in late autumn (May), to virtually no increase (0 to 1%) during mid-winter (July), and a 2 to 3% reduction during mid-spring (October).

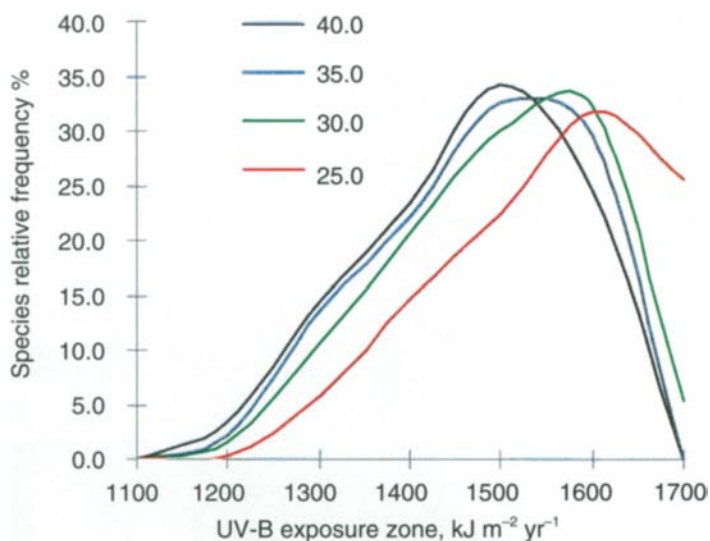
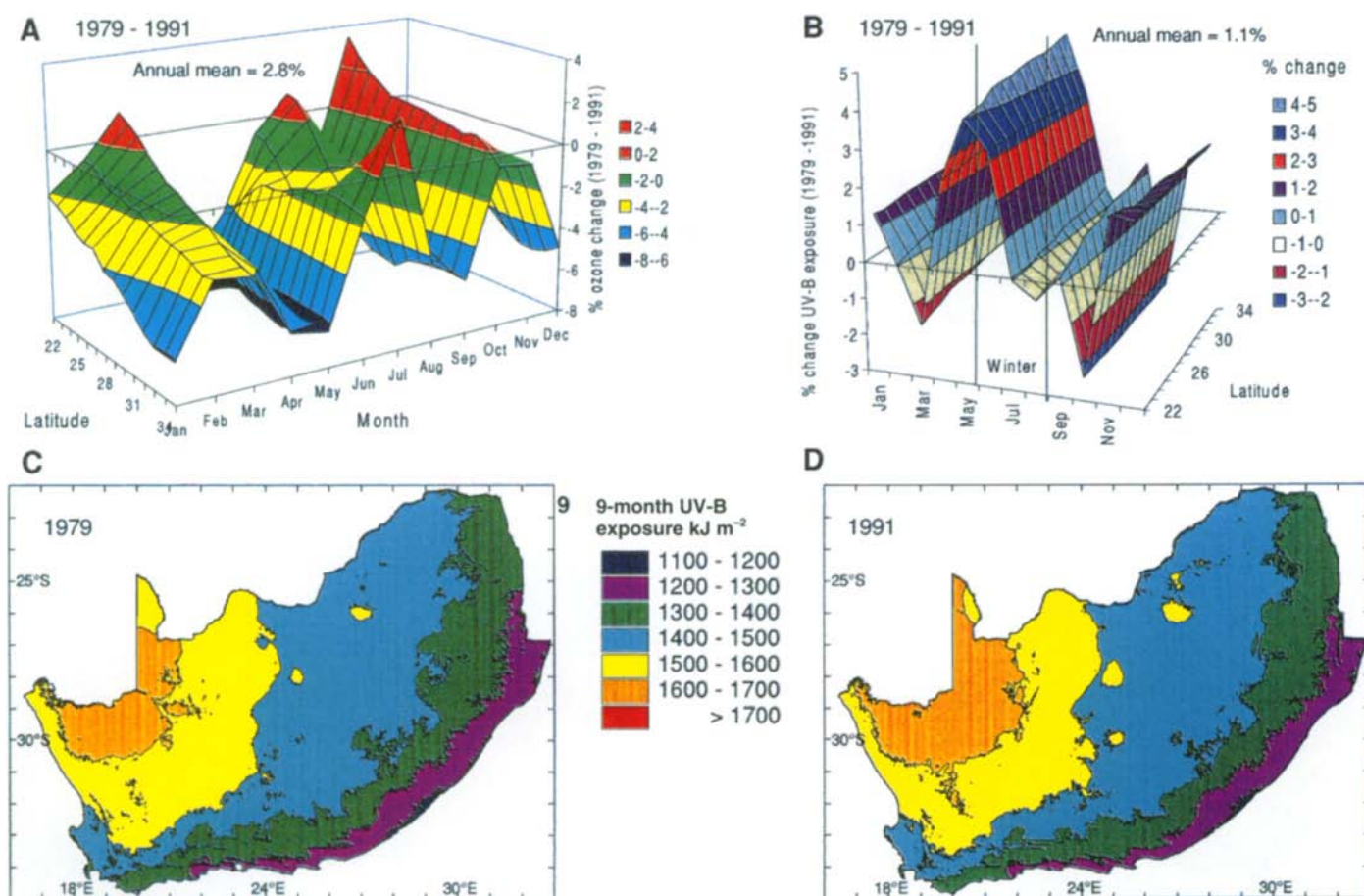


Figure 1. Computed shifts in species frequency distributions across 7 designated UV-B exposure zones due to spatially altered UV-B distribution patterns for the period 1979 to 2051. Computations based on field records of a sample of 500 species positively correlated with high UV-B environments extracted from a Canonical Correspondence Analysis of 4791 species against 17 environmental variables. Areas between lines beneath points of intersection indicate fractions of populations subjected to UV-B levels exceeding those encountered over the natural distribution range with increasing ozone depletion (12.8% in year 2003 and 32.6% in year 2051).

Figure 2 A. Recorded monthly changes in total column ozone (averaged over 16°E to 33°E longitude) for the 13-year period 1979 to 1991. B. Modeled intra-annual changes in biologically weighted UV-B exposure over this period. C. Modeled spatial UV-B exposure distribution patterns in South Africa for 1979. D. Those for 1991.



Mean annual increase in UV-B exposure for all latitudes was only 1.1%.

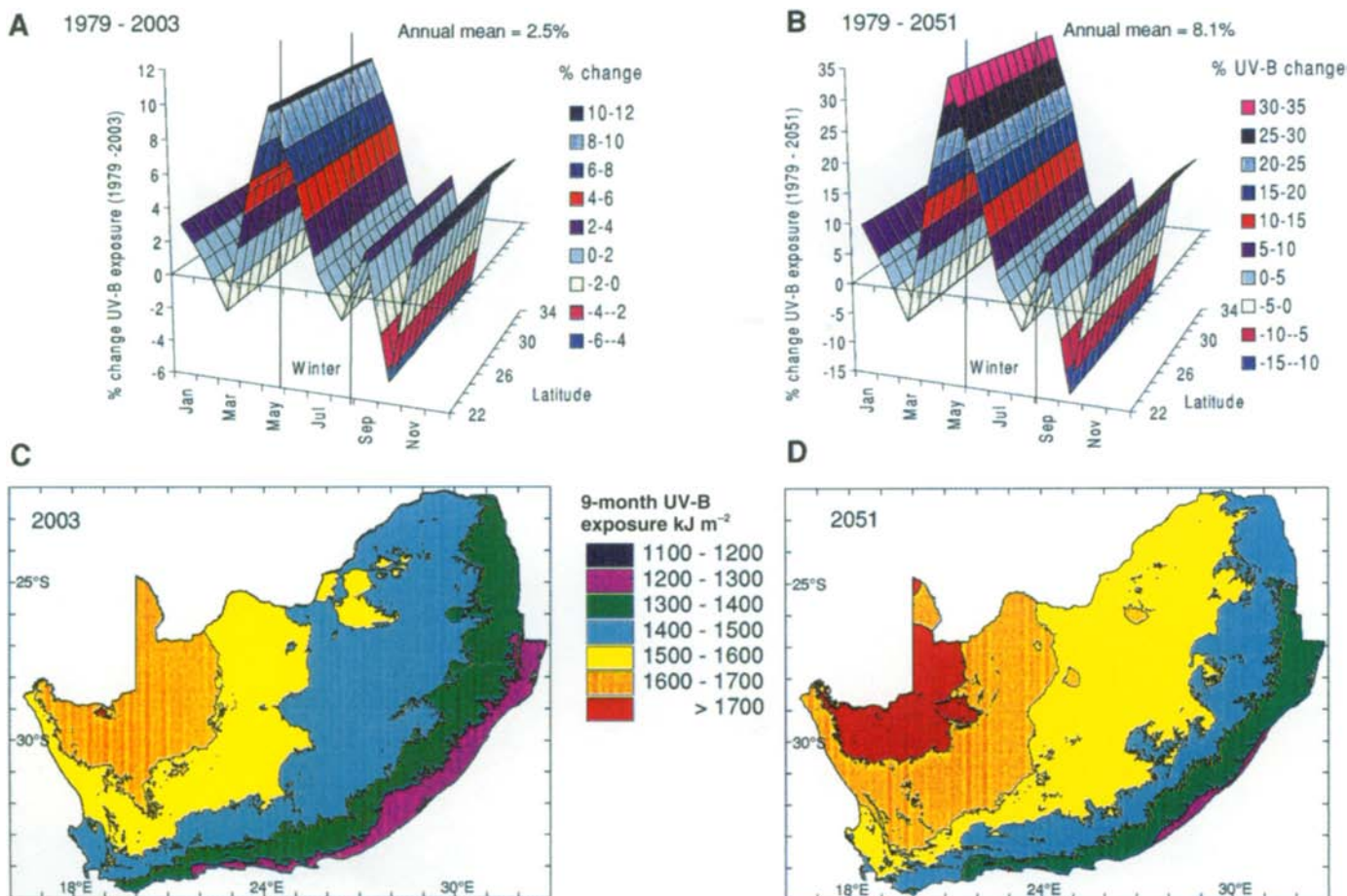
Spatial UV-B distributions (exposure integrated over a 9-month spring to autumn growing period) are mapped at 2.5 km² resolution for the years 1979 and 1991 (Figs 2C and D). Spatial gradients in UV-B were large, ranging from a 34.2% exposure change over the 14° gradient in latitude to a 44.2% change over the 16° gradient in longitude. The former reflected increasing

solar elevations and reduced total column ozone thickness with decreasing latitude, and the latter mainly decreasing summer cloud amount from high summer rainfall areas in the eastern and southeastern regions of South Africa to arid-winter rainfall areas in the southwestern and northwestern regions of the country. A comparison of spatial changes in UV-B over the 1979 to 1991 period showed that areas experiencing UV-B exposures in excess of 1600 kJ m⁻² expanded from 91 449 km² (7.2% of the

Table 1. Taxonomic, life form and functional attributes of threatened (rare, endangered, vulnerable) South African taxa. Evg = evergreen, Geo = geophyte, Suc = succulent.

Life form	No. species	Family: 20 largest	No. species	Genus (life form): 20 largest	No. species
Geophytes	624	Iridaceae	307	<i>Erica</i> L. (Evg)	98
Large shrubs	587	Fabaceae	203	<i>Gladiolus</i> L. (Geo)	59
Succulents	386	Proteaceae	164	<i>Leucadendron</i> R. Br. (Evg)	42
Small shrubs	194	Aizoaceae	133	<i>Encephalartos</i> Lehm. (Evg)	40
Herbs	120	Asclepiadaceae	126	<i>Aloe</i> L. (Suc)	40
Trees	77	Asphodelaceae	121	<i>Euphorbia</i> L. (Suc)	40
Sedges/Restioids	48	Ericaceae	105	<i>Haworthia</i> Duval (Suc)	38
Gymnosperms	42	Orchidaceae	101	<i>Kniphofia</i> Moench (Suc)	35
Graminoids	35	Asteraceae	94	<i>Agathosma</i> Willd. (Evg)	35
-C ₃	85.7%	Rutaceae	77	<i>Disa</i> Berg. (Geo)	34
-C ₄	14.3%	Amoryllidaceae	68	<i>Psoralea</i> L. (Evg)	31
Pteridophytes	14	Hyacinthaceae	60	<i>Moraea</i> L. (Geo)	30
Climbers	11	Euphorbiaceae	44	<i>Otholobium</i> C.H. Stirtion (Evg)	30
Parasites	4	Restionaceae	44	<i>Romulea</i> Marrati (Geo)	29
Hydrophytes	2	Crassulaceae	41	<i>Serruria</i> Salisb. ex Knight (Evg)	29
Epiphytes	2	Zamiaceae	40	<i>Aspalathus</i> L. (Evg)	28
Total species	2146	Eriospermaceae	35	<i>Geissorhiza</i> Ker. (Geo)	26
Total genera	468	Poaceae	35	<i>Protea</i> R. Br. (Evg)	26
Total families	103	Scrophulariaceae	20	<i>Conophytum</i> N.E. Br. (Suc)	25
		Potulacaceae	16	<i>Lachenalia</i> Jacq. f. (Geo)	24

Figure 3 A. Extrapolated intra-annual changes in biologically weighted UV-B exposure over the period 1979 to 2003. **B.** Those extrapolated over the period 1979 to 2051. **C.** Extrapolated spatial UV-B distribution patterns in 2003. **D.** Those modeled for 2051.

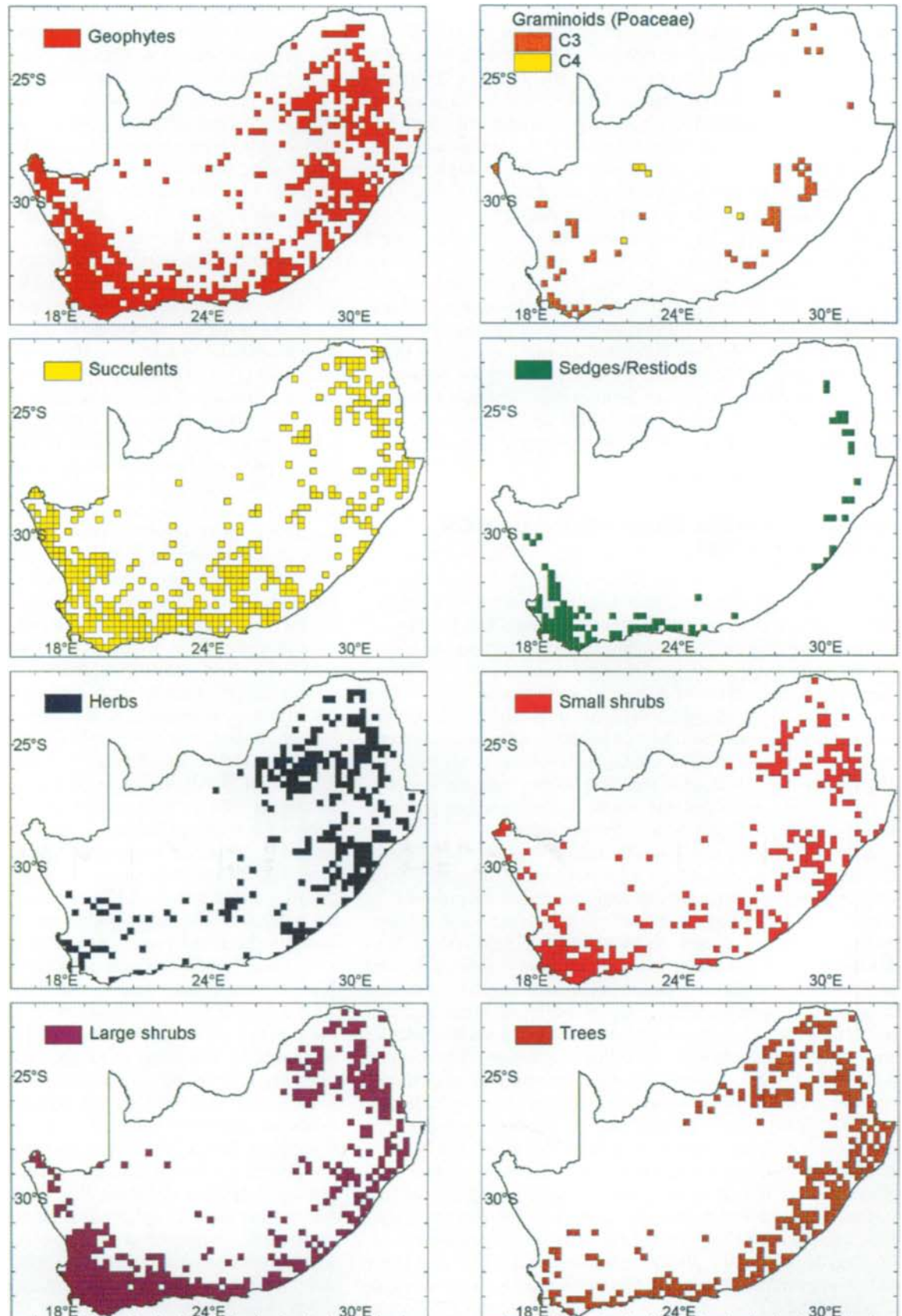


area of South Africa) in 1979 to 144 827km² (11.4% of South Africa) in 1991.

Potential future changes in UV-B exposure, extrapolated from modeled trends over the 1979 to 1991 period, were based on two ozone depletion scenarios. The first scenario (ozone depletion averaged over a whole year 5.4%), represented by the year 2003, was designated “best-case scenario”. It conformed with expected peaking of chlorine levels in the stratosphere towards the

end of this century (2). The second less realistic scenario (ozone depletion averaged over a whole year 14.9%) represented by the year 2051, was designated the “worst-case scenario”. It presumed continued ozone depletion into the next century due to incomplete adherence to the Montreal Protocol and its amendments. Computations indicated relatively small increases in annual UV-B exposure (2.5% for the year 2003 and 8.1% for the year 2051) but substantially increased intra-annual (Figs 3A and B). For a

Figure 4. Herbarium-based distribution records for threatened (rare, endangered, vulnerable) South African taxa grouped according to life form.



worst-case ozone depletion scenario (year 2051), the predicted 30 to 35% increase in UV-B exposure during late autumn (May) was of similar magnitude (34.2% increase) as occurs with a 14° reduction in latitude. Areas experiencing UV-B exposure in excess of 1600 kJ m⁻² showed an expansion from 188 362 km² (14.9% of South Africa) in 2003, to as much as 386 933 km² (30.5% of South Africa) in 2051.

ATTRIBUTES AND DISTRIBUTIONS OF THREATENED TAXA

Taxonomic, life form and functional attributes of 2146 threatened South African taxa are summarized in Table 1. Notable is the preponderance of geophytes, of the families Iridaceae, Orchidaceae and Amaryllidaceae, large (> 1 m in height) shrub species of the families Fabaceae, Proteaceae and Ericaceae, and succulents of the families Aizoaceae, Asclepiadaceae and Asphodelaceae. Among graminoids (Poaceae), a high fraction of species (85.7%) possess the C₃ photosynthetic pathway. The sedge/restioid group was represented mostly by aphyllous, evergreen members of the Restionaceae. Of the 20 largest genera including threatened taxa, nine contained exclusively evergreen species, six comprised geophyte species and five contained succulent species (Table 1). Herbarium-based distribution records (11) for threatened taxa, grouped according to life form, are mapped in Figure 4. Notable is that all life forms occur in areas of both low to intermediate UV-B exposure in southern, eastern and northeastern regions of South Africa, with geophytes and succulents, and to a lesser extent small and large shrubs, also extending into areas of high UV-B exposure in arid northwestern regions.

IMPACT OF FUTURE INCREASES IN UV-B ON THREATENED TAXA

Long-term UV-B predictions are exceedingly difficult and uncertain, and only appropriate in a statistical sense of averages, variabilities, and broad geographical patterns. The predictions presented contain only extrapolated trends regarding the ozone layer, but do not include possible long-term changes in clouds, tropospheric pollutants and changes in surface albedo. Also, they exclude potential changes in ecosystem size and composition due to anticipated future changes in other environmental variables, notably atmospheric CO₂, temperature, rainfall amount and seasonality (1). Despite the complexities referred to above, several broad generalizations can be made regarding potential UV-B impacts on South African threatened taxa.

Available data suggest that succulent, evergreen and geophyte life forms, which comprise a high fraction of threatened taxa, possess physiological attributes conferring a high degree of UV-B resilience. Regarding succulents it is known that many thermotolerant organisms possess an inherent or induced resistance to oxidative stress caused by UV-B (21). This co-tolerance, and sometimes co-sensitivity, to oxidative and thermal conditions suggests that hyperthermia is also an oxidative stress, and that plants may have common mechanisms that respond to oxidative stresses (22), possibly through cellular induction of heat shock proteins by UV-B radiation (23). Also, xeromorphic adaptations, such as thick leaf cuticles, surface waxes and dense trichomes (24), which are thought to have evolved in plants in response to water stress (25), are known to be beneficial in alleviating UV-B stress. In fact, leaf surface reflectance and scattering of UV-B can exceed 40% in species with pubescent or glaucous leaf surfaces (26). Leaf trichomes also contain UV-B-absorbing phenolic compounds (27–29), which alter leaf optical properties (30) limiting damage to the photosynthetic apparatus (31) and DNA (32). However, the presence of these trichomes is sometimes age-dependent, and more prevalent in young leaves still developing

internal UV-B-absorbing capabilities (33).

Other studies have reported that enhanced UV-B radiation alleviates the effects of summer drought (34). The proposed mechanism was improved foliar water status caused by UV-B-induced changes in foliar surface properties, namely thicker cuticles (35). Indeed, increased cuticular thickness and concentrations of epicuticular UV-B-absorbing compounds during summer have been reported in two mediterranean-climate sclerophylls *Nerium oleander* L. and *Cistus creticus* L. (36, 37). Also, generally poor transmission of incident UV-B radiation (<10% to 25%) occurs through the epidermis of many evergreen species (38, 39), and many South African evergreens are known to possess exceptionally high levels of polyphenolics in their leaves (40). Polyphenolic derivatives of the phenylpropanoid pathway (41) have been implicated in several mechanisms leading to UV-B protection and adaptation (42). High foliar anthocyanin levels have also been reported in South African succulents, particularly during early developmental stages and during dry summer periods (43). These are thought to provide protection against photo-inhibition by excess visible radiation (43), and may also play a role in UV-B protection (42).

Regarding geophytes, many South African species contain high foliar alkaloid levels (44), which also have UV-B screening properties. In fact, a negative correlation has been demonstrated between the percentage of alkaloid bearing plants in floras and latitude, with tropical floras from environments of naturally high UV-B irradiance having proportionately nearly twice as many species of alkaloid-bearing plants as temperate floras (45). Graminoids (Poaceae) in general are relatively resistant to UV-B (46), and this is also true of African savanna grass species (47, 48). However, one study concluded that plants with the C₄ photosynthetic pathway were less affected, in terms of plant height and biomass accumulation, by UV-B than those with the C₃ pathway (49), which are present in substantially higher numbers among threatened graminoid species (Table 1).

Despite the UV-B resilient physiological and biochemical features present in some plant functional types, there exists an ostensibly widespread effect of elevated UV-B on pollen quality. Several studies have demonstrated frequent UV-B-induced inhibition of pollen germination and/or tube growth in taxa representing diverse families, e.g. Poaceae, Commelinaceae, Scrophulariaceae, Geraniaceae, Papaveraceae, Capparaceae, Solanaceae, Brassicaceae (50–54). In a recent study of binucleate and trinucleate pollen of 34 taxa representing 15 families exposed to elevated UV-B, pollen tube growth inhibition occurred in more than 50% of the taxa examined, although significant reductions in pollen germination were observed in only 5 of these taxa (55). Increased frequencies of seed abortion occur where either UV-B-irradiated pollen (56), or pollen sampled from plants growing under enhanced UV-B conditions (54) has been used for pollination. Reduced pollen germination and tube growth have also been observed in several South African taxa exposed to elevated UV-B, and also associated with reduced seed production, though discrepancies did occur (57).

Of particular relevance to UV-B effects on pollen viability and vigor, is that photo-reactivating radiation does not undo all UV-B-induced DNA damage in longer-lived pollens, which are considerably dehydrated (58). Since dark repair is several orders of magnitude less rapid than photoreactivation repair (59), there exists an increased potential for mutagenesis during DNA replication (60) in offspring of progenitors exposed to elevated UV-B, and a likelihood of carryover of UV-B induced DNA damage in pollen of progenitors to offspring. In one South African herbaceous ephemeral, *Dimorphotheca sinuata* DC. (Asteraceae), progressive alterations to the physiology, growth, development and fecundity of offspring were observed with cumulative generations of exposure of progenitors to elevated UV-B, which indicated conceivable genetic inheritance of UV-

B damage (61). These findings were supported by evidence of a simple linear exposure-response relationship between the number of enhanced UV-B exposure iterations in seed parentage of offspring of *D. sinuata* and their leaf fluctuating asymmetry, an indirect measure of developmental instability indicating genetic damage (62). This carryover of UV-B damage to offspring (61), the widespread effect of UV-B on pollen quality (55) and evidence of reduced seed production (54, 57) under elevated UV-B, all point to changes in per capita reproductive output and overall plant fitness, at least in some plant taxonomic groups. Such effects could conceivably lead to altered patterns of species coexistence, floristic composition and diversity.

Aspects of floral architecture and flowering phenology may moderate UV-B effects on pollen quality and reproductive output in some plant functional types. Less susceptible life forms include late-spring flowering geophytes, particularly those of the Iridaceae. Indeed, reductions in pollen tube growth were observed only in one Iridaceae species (*Gladiolus carneus* Delaroché), but this was not associated with any significant change in seed production (57). Similar discrepancies between pollen quality and seed production have also been reported. In *Brassica rapa* Aaa. RCB, for example, an observed decline in viable pollen production under elevated UV-B did not cause significant changes in seed yield, although there was an increased incidence of seed abortion (54). Nevertheless, UV-B effects on pollen may be more severe in some summer flowering geophytes of the Amaryllidaceae and Iridaceae. Some of these geophytes grow vegetatively during winter and early spring and flower in a leafless condition only during autumn at the end of the dry summer season (63). Indeed, large increases in UV-B exposure during May when ozone depletion occurs could exacerbate effects on pollen quality in this guild and other taxa, which flower during this season. Examples include some shrub species of the genus *Barleria* L. in the family Acanthaceae, three species of which are categorized as rare and vulnerable (10). Clearly, the timing of life phases of plants, such as flowering, entering and breaking of dormancy, in relation to periods of maximum UV-B increase would conceivably be of great importance. Also, evidence of accelerated deterioration of dispersed seeds exposed to UV-B radiation (64), could potentially exacerbate any deleterious UV-B-induced effects on per capita reproductive output of these guilds.

Succulent life forms seem less susceptible to reproductive inhibition by UV-B, since most flower, predominantly, in late winter and early-spring (65), many have short flowering periods, e.g. day-flowering succulents of open habitats (66), and some even flower only at night (67). Also, delayed release of seeds from dead inflorescences in some succulents (e.g. Mesembryanthemaceae) to periods when sufficient moisture is available for germination (68, 69) provides an additional means for protection of seeds from the damaging effects of UV-B.

There are few data on UV-B effects on other life-form categories, though forest trees from diverse geographical regions do appear relatively sensitive to elevated UV-B. In the non-threatened African sub-tropical savanna tree species *Acacia tortilis* (Forsk.) Hayne, for example, reduced photosynthesis and a tendency to decreased biomass accumulation were observed in saplings after 190-day exposure to elevated UV-B (48). In a separate study of another nonthreatened African savanna tree species, *Acacia karroo* Hayne, photosynthesis and biomass accumulation were not significantly affected after 120-day UV-B exposure, though there was a significant reduction in stomatal conductance (47). Among tropical tree species, exclusion of ambient solar UV-B radiation caused increased growth, suggesting that even minor ozone depletion in the tropics may have biological implications (70).

In mid-temperate tree species, significant reductions in biomass were observed in loblolly pine seedlings, derived from

several different geographical areas, after one year's elevated UV-B exposure, with severalfold greater biomass reductions observed in one variety after three years elevated UV-B exposure (71). Reduced leaf mass and length of conifer needles, and leaf area of broad-leaved tree species, have also been observed under elevated UV-B. However, these effects were not always accompanied by sizeable reductions in photosynthesis due partly to leaf epidermal thickening, which may prevent leaf cellular wall extension, and UV-B penetration into older foliage (70–72).

It would appear that only those tree species occupying the upper vegetation stratum are likely to be sensitive to growth and reproductive inhibition by elevated UV-B. Surveys of UV-B radiation in forests have shown that geometric mean UV-B transmittance is only 1 to 2% of incident radiation under closed canopies and 8 to 17% of incident radiation under disturbed canopies (73). Since the structure and composition of the outer canopy have a strong influence on the vegetation below, reported UV-B effects on leaf size and shape in forest tree species (70–72) could conceivably affect light interception patterns with implications for forest composition and succession. A suggested scenario for ecological change in southeastern United States forests is an improved competitive advantage of the hardwood weedy *Liquidambar styraciflua* L., which suffers no change in biomass and some increase in leaf area under elevated UV-B, against *Pinus taeda* L., an important lumber species (73). Noteworthy, also are the reported large fluctuations in UV-B:PAR (photosynthetically active radiation) ratios, known to be important mitigating factors in plant responses to UV-B (74), in forest canopy space (73). Indeed, high UV-B:PAR ratios observed in partially shaded areas such as forest gap edges and other broken sites, which admit much diffuse UV-B radiation but relatively less direct solar radiation, could induce biological responses even in the absence of extreme fluxes (75), leading to a loss of species diversity.

Despite recent signs of a break in the ozone depletion trend (76, 77), the ozone layer is still at risk (77–79). The effects of ozone depletion would have been dramatically worse without the protective measures taken under the Montreal Protocol (80). The present paper shows the perils to the flora of South Africa that would ensue, should the international agreements for protection of the ozone shield not be complied with.

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