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Structure and Alpha Biodiversity of Major Plant Communities in South Africa, a Close Biogeographical Relation with Australia

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Abstract

During the short season of annual shoot growth, Foliage Projective Covers (FPCs) in both overstorey and understorey strata, coupled with leaf attributes (Leaf Specific Weight, Leaf Area), are determined by aerodynamic fluxes flowing over and through the plant community. These parameters determined the Evaporative Coefficient — the monthly ratio of actual to potential evapotranspiration per mm of available soil moisture. Maximal FPC is produced in habitats supplied with optimal soil moisture during this short season of shoot growth.

Vertical growth of foliage shoots — the number of leaves per shoot and internode lengths — is determined in relation with available soil water and soil nutrients (especially phosphorus and nitrogen ions) during this seasonal growth. Ambient temperature is similarly concerned.

The Leaf Area Index (area of all leaves per hectare) determines the interception of solar radiation — and hence net photosynthesis per hectare per annum. This energy-fixation by overstorey foliage determines the yearly growth of the producer, consumer and decomposer sections of the ecosystem. In turn, the biodiversity (number of species per hectare) of producers and resident consumers is determined.

Wherever optimal soil water occurred in median-nutrient soils in the coastal subtropical region, closed-forests/scrubs developed containing 131 ± 11 species compared with 80-90 species per hectare in nearby open-forests.

Wherever optimal soil water occurred in nutrient-poor soils in the warm temperate region, closed-heathland (± tall proteoid shrubs) vegetation developed containing 90-135 species per hectare, compared with about 60 species per hectare in nearby open-heathlands.

Keywords: Evaporative coefficient, Foliage projective cover, Alpha biodiversity, Open-communities, Closed-communities, Arid to humid climates

1. Introduction

The study of community-physiological processes was promoted internationally during the International Biological Program (Specht 1967). During the 1970s, David Goodall, then Director of the IBP Desert Biome Centre in Logan, Utah, U.S.A., was invited to compile a 30 volume series on *Ecosystems of the World* for Elsevier Scientific Publishing Company, Amsterdam (Goodall 1977-2006). Ray Specht was co-opted to compile the volume on *Heathlands and Related Shrublands.* Vol. 9A. *Descriptive Studies.* (Specht 1979a) and Vol. 9B. *Analytical Studies* (Specht 1981a) that develop on nutrient-poor soils throughout the world. Articles on '*The sclerophyllous (heath) vegetation of Australia'* (Specht 1979b), '*Heathlands of Western Australia'* (George *et al.* 1979, 1988), *'The vertebrate fauna of Australian heathlands* (Kikkawa *et al.* 1979*)*, *'Seasonal growth and flowering rhythms: Australian heathlands'* (Specht *et al.* 1981), *'Dark Island heathland, South Australia: Faunal rhythms'* (Edmonds & Specht, M. 1981), *'South African heathlands'* (Kruger 1979), *'Aspects of vertebrate life in fynbos, South Africa'* (Bigalke 1979), '*African mountain heathlands'* (Killick 1978, 1979), *'Seasonal growth and flowering rhythms: South African heathlands* (Kruger 1981) were included. *The Role of Nutrients in Mediterranean-type Ecosystems* was expanded in a Stellenbosch meeting of MEDECOS (Kruger *et al.* 1983).

The plant communities that develop on median-nutrient soils in southern Australia and South Africa were explored in *Ecosystems of the World.* Vol. 11. *Mediterranean-Type Shrublands* (di Castri *et al.* 1981). Articles on *'South African Mediterranean Shrublands'* (Boucher & Moll 1981), '*Mallee ecosystems in Southern Australia'* (Specht 1981b), *'Bird communities of the Australian mallee'* (Schodde 1981) and *'Structure, pattern and diversity of a mallee community in New South Wales'* (Whittaker *et al.* 1979) contrasted these nutrient-richer plant communities with the nutrient-poor heathlands of South Africa and Australia.

Detailed information on the climate, eco-morphological characteristics, foliar nutrients, species richness, vertebrates and soil/litter invertebrates in '*Mediterranean-type Ecosystems'* of the world was collated in '*A Data Source Book'* (Specht 1988a).

Information on South African ecosystems north of the Capensis Region was collated in *Ecosystems of the World*. Vol. 8B. *Natural Grasslands* (Coupland 1993) and Vol. 12B. *Hot Deserts and Arid Shrublands* (Evanari *et al*. 1986).

The compilation of the data for the Mediterranean-type climate of Capensis Region (Specht 1988a) was extended throughout South Africa by the authors of this paper.

1.1 Biogeographical Relationship of South Africa with Australia

The broad patterns of the evolution of vascular plants on the southern continents of Gondwanaland were traced in *'Comparative evolution of Mediterranean-type ecosystems: A southern perspective'* (Deacon 1983), *'Patterns of Gondwana plant colonisation and diversification'* (Anderson *et al.* 1999) and in *'Southern (Austral) Ecosystems'* (Weston & Hill 2013). Angiosperms appeared in the palynological records during the Mid-Cretaceous, about 100 million years ago. 'The Proteaceae originated in northern Gondwana in Late Cenomanian times and radiated into southern high latitudes by the Turonian. There the family underwent substantial differentiation during the Santonian-Maastrichian' — the Late Cretaceous, over 65 million years ago (Dettmann 1999).

Both the Australasian and African Tectonic Plates separated from Antarctica after the Cretaceous, about 65 million years ago (Smith & Briden 1977) when the climate at the southern part of each continent, at latitude 60°S, was then subtropical (Specht *et al.* 1992). Under this subtropical climate, the seasonal shoot growth of the overstorey occurred when mean monthly temperatures ranged from 15°C to 25°C with a peak at 20°C (Specht & Rayson 1957; Specht & Brouwer 1975; Hegarty 1990; Specht & Specht 1999). As both the African and Australasian Tectonic Plates drifted northward from Antarctica — the Australasian Plate at an average rate of 66 mm per year (Wellman & McDougall 1974) — the cold Southern Ocean current that had been formed induced cooler weather on the southern part of each Plate — a Mediterranean-type climate with a wet winter-spring alternating with a dry summer season resulted. Today in Australia, elements of the original Gondwanan flora of the south merge with the tropical flora of the north in the subtropical region of south-eastern Queensland and north-eastern New South Wales (Burbidge 1960; Johnson & Briggs 1981). Examples of the heathland vegetation (± overstorey trees) on nutrient-poor soils, grassland vegetation (± overstorey trees) on median-nutrient soils and closed-forest vegetation in well-watered habitats occur from the tropical north to the temperate south of the continent (Specht 1958a, 1958b, 1981d; Specht & Specht 1999).

The close biogeographical relationships between South Africa and Australia are studied in this article:

- The nutrient-poor heathland vegetation, on quartzite/sandstone outcrops, as well as on the remnant Gondwanan lateritic soils, with two genera of Cyperaceae and three genera of Restionaceae common with Australia (Table 1 after Kruger 1979);

Table 1. Generic composition of major families in fynbos/heathland vegetation on nutrient-poor soils in Cape Province, South Africa (Sites 1-10 in Appendix III, Kruger 1979, pp. 58-78).

Overstorey — Proteaceae: *Leucadendron* (Sites 1, 2, 3, 4, 8. 10); *Mimetes* (Site 3); *Protea* (Sites 1, 2. 3, 4, 5, 8, 10)

Tall shrublands of *Leucospermum cuneiforme* and tall closed-scrub of *Protea neriifolia* occur along drainage lines near ridge crests (Kruger 1979, p. 47).

Understorey — Ericaceae: *Aniserica* (Site 4); *Blaeria* (Sites 1, 4, 5); *Eremia* (Site 1); *Erica* (Sites 1, 2, 3, 4, 5, 7, 10); *Sympieza* (Site 3);

Cyperaceae: *Chrysothrix* (Sites 3, 4, 5); *Epischoenus* (Site 6); *Ficinia* (Sites 1, 3, 4, 7, 8, 10); *Kobresia* (Site 7); **Scirpus* (Site 8); **Tetraria* (Sites 1, 2, 3, 4, 5, 10);

Restionaceae: *Chondropetalum* (Sites 3, 4, 6, 10); *Elegia* (Sites 3, 4, 6, 10); *Hypodiscus* (Sites 1, 3, 4, 5, 10); **Hypolaena* (Site 6); **Leptocarpus* (Sites 2, 3, 4); **Restio* (Sites 1, 2, 3, 4, 5, 6, 7, 9, 10); *Staberoha* (Sites 4, 5); *Thamnochortus* (Sites 2, 3, 4, 10); *Willdenowia* (Sites 4, 5, 8)

Genera of Poaceae on marginal, median-nutrient soils — +*Aira* (Site 2); *Alloteropsis* (Site 7); +*Andropogon* (Site 7); +*Anthoxanthum* (Site 1); *Cymbopogon* (Sites 2, 9); +*Ehrharta* (Sites 1, 4, 5, 6, 8, 9); **Eragrostis* (Sites 2, 7, 8); **Festuca* (Site 4); *Helictotrichon* (Site 2); *Lasiochloa* (Site 9); *Merxmuellera* (Sites 1, 3, 4, 5, 9); *Pentaschistis* (Sites 2, 3, 4, 5, 6, 7, 8); *Plagiochloa* (Site 2); *Pseudopentameris* (Site 3); **Themeda* (Site 7)

* Genera recorded in both South Africa and southern Australia (Jessop & Toelken 1986).

\+ Genera introduced into southern Australia (Jessop & Toelken 1986).

- The median-nutrient savanna vegetation, with 15 C4 grass genera common, including the kangaroo-grass, *Themeda triandra*, and five genera of C3 grasses (Table 2 after Clifford & Simon 1981; Gibbs Russell *et al.* 1990; Simon & Alfonso 2011);

Table 2. Genera of Poaceae recorded in the savannas and grasslands in the Austral Domain of the Sudano-Zambesian Region of South Africa (Gibbs Russell *et al.* 1990), as well as in Australia (Clifford & Simon 1981; Simon & Alfonso 2011)

C4-photosynthetic grass genera: +*Andropogon, Aristida, Cenchrus, Cymbopogon, Digitaria, Eragrostis, Enneapogon, Elionurus,* +*Ehrharta, Heteropogon, Hyparrhenia, Imperata, Panicum, Setaria, Sporobolus, Themeda, Tragus* (Clifford & Simon 1981; Simon & Alfonso 2011).

The South African C4 grass genera — *Monocymbium, Pogonarthria, Rendlia, Stipagrostis, Trachypogon* and *Tristachya* —are not found in Australia.

C3-photosynthetic grass genera in cooler highland and alpine habitats: *Festuca, Microchloa, Oplismenus, Poa* and *Merxmuellera* (allied to *Danthonia* in Australia)

\+ Genera introduced into southern Australia (Clifford & Simon 1981; Simon & Alfonso 2011).

- The subtropical closed-forest (rainforest) vegetation of eastern South Africa and eastern Australia, with 35 genera common with Australia (Table 3 after Moll & White 1978).

Table 3. Generic composition of the closed-forest vegetation in the Indian Ocean Coastal Belt of South Africa (Moll & White 1978)

Canopy trees — *Albizia* (Mimosaceae), *Brachylaena* (Asteraceae), *Cassipourea* (Rhizophoraceae), **Celtis* (Ulmaceae), *Chaetachme* (Ulmaceae), *Chrysophyllum* (Sapotaceae), *Combretum* (Combretaceae), **Croton* (Euphorbiaceae), **Drypetes* (Euphorbiaceae), **Ficus* (Moraceae), **Millettia* (Fabaceae), *Mimusops* (Sapotaceae), **Strychnos* (Loganiaceae), *Trichilia* (Meliaceae), *Vepris* (Rutaceae).

Canopy trees (infrequent) — *Cavacoa* (Euphorbiaceae), *Cola* (Sterculiaceae), **Homalium* (Flacourtiaceae), *Nuxia* (Buddlejaceae), **Phyllanthus* (Phyllanthaceae), **Podocarpus* (Podocarpaceae), *Scolopia* (Flacourtiaceae), **Syzygium* (Myrtaceae).

Subcanopy trees (common) — *Bequaertiodendron* (Sapotaceae), **Canthium* (Rubiaceae),

**Clausena* (Rutaceae), *Dracaena* (Dracaenaceae), **Drypetes* (Euphorbiaceae), **Erythroxylum* (Erythroxylaceae), **Eugenia* (Myrtaceae), *Memecylon* (Melastomaceae), **Pavetta* (Rubiaceae), *Peddiea* (Thymelaeaceae), *Teclea* (Rutaceae), *Tricalysia* (Rubiaceae).

Subcanopy trees (less common) — *Allophyllus* (Sapindaceae), *Anastrabe* (Scrophulariaceae), *Baphia* (Leguminosae), *Buxus* (Buxaceae), **Cryptocarya* (Lauraceae), **Diospyros* (Ebenaceae), **Gardenia* (Rubiaceae), *Ochna* (Ochnaceae), *Oxyanthus* (Rubiaceae), *Pancovia* (Rosaceae), *Rawsonia* (Flacourtiaceae), *Rothmannia* (Rubiaceae), *Xylotheca* (Flacourtiaceae).

Small trees and woody shrubs at edge — *Antidesma* (Euphorbiaceae), **Clerodendrum* (Lamiaceae), *Combretum* (Combretaceae), *Dichrostachys* (Leguminosae), *Fagara* (Rutaceae), **Grewia* (Tiliaceae), *Heteropyxis* (Malvaceae), *Hippobromus* (Sapindaceae), *Kraussia* (Asteraceae), **Maytenus* (Celastraceae), *Rhus* (Anacardiaceae).

Sub-woody plants (2-3 m) at edge — *Clutia* (Euphorbiaceae), **Euphorbia* (Euphorbiaceae), *Euryops* (Asteraceae), **Hibiscus* (Malvaceae), **Leonotis* (Lamiaceae), *Lippia* (Verbenaceae), **Polygala* (Polygalaceae), *Pseudarthria* (Fabaceae), **Solanum* (Solanaceae), *Syncolostemon* (Lamiaceae).

Lianes and climbers — **Acacia* (Mimosaceae), *Acridocarpus* (Malpighiaceae), *Buddleja* (Buddlejaceae), **Canthium* (Rubiaceae), **Capparis* (Capparaceae), **Cissus* (Vitaceae), *Combretum* (Combretaceae), *Cnestis* (Connaraceae), *Dalbergia* (Fabaceae), **Diospyros* (Ebenaceae), *Embelia* (Myrsinaceae), *Entada* (Mimosaceae), *Monanthotaxis* (Annonaceae), *Quisqualis* (Combretaceae), *Oncinotis* (Apocynaceae), *Putterlickia* (Celastraceae), *Rhoicissus* (Vitaceae), *Scutia* (Rhamnaceae), **Secamone* (Asclepiadaceae), *Urera* (Urticaceae), *Uvaria* (Annonaceae).

* Genera recorded in both South Africa and south-eastern Queensland (Stanley & Ross 1983, 1986); genera Chrysophyllum —> Amorphophyllum; Gardenia —> Randia and Uvaria —> Fitzalania in south-east Queensland.

The structure and species richness of plant communities in South Africa in the biogeographical regions (Figure 1) — Capensis (Taylor 1978; Kruger 1979; Specht & Moll 1983; Specht *et al.* 1983); the Austral Domain of the Sudano-Zambesian Region (Werger & Coetzee 1978); in the closed-forests of the Indian Ocean Coastal Belt (Moll & White 1978) — are examined in relation to the values predicted by the Australian investigations on community-physiology.

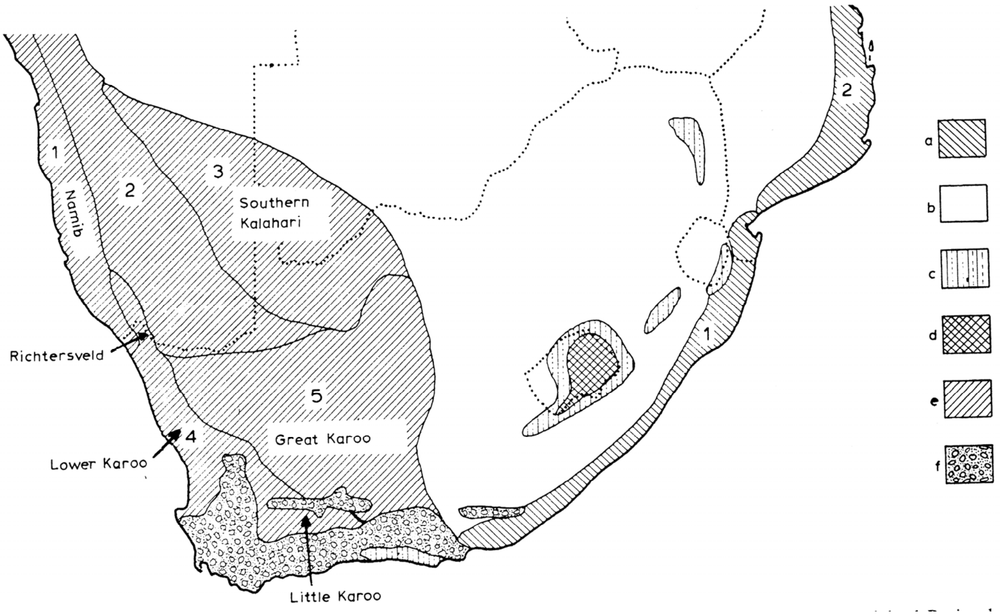

Figure 1. Biogeographical regions in southern Africa (Werger 1986)

a = Indian Ocean Coastal Belt; a1 = Tongaland-Pondoland Regional Mosaic; a2 = Zanzibar-Inhambane Regional Mosaic; b = Zambesian Domain, Sudano-Zambezian Region; c = Afromontane Region; d = Austral Domain, Afro-Alpine Region; e = Karoo-Namib Region; e1 = Namib Domain; e2 = Namaqualand Domain; e3 = Southern Kalahari Subdomain; e4 = Western Cape Domain; e5 = Karoo Domain; f = Capensis (after Werger 1978a).

The inserted names denote geographical regions.

2. Methods

Evaporative Coefficient of each Meteorological Station: The community-physiological constant — the Evaporative Coefficient (*k*) — of each meteorological site was computed by optimising the monthly rate of usage of soil water so that some water (albeit minimal) is available for evapotranspiration from the evergreen plant community during the driest season of the year (Specht 1972a, 1972b, 1981c; Specht & Specht 1999).

For every macroclimate, in spite of seasonal and yearly fluctuations in rainfall, the monthly moisture index (M.I.), the ratio of actual to potential evapotranspiration (*Ea/Ep),* is correlated with available soil water (W mm) by the Evaporative Coefficient (*k*) — defined by analysis of long-term studies on soil moisture of representative plant communities from the arid to the humid climatic zone (Specht 1957a, 1957b; Martin & Specht 1962; Carrodus & Specht 1965; Specht & Jones 1971; Specht 1972a) as

$$\text{M.I.} = (Ea/Ep) \text{ equivalent to } (Ea/Eo) = kW = k(P\text{-}R\text{-}D\text{-}Sext) \qquad (1)$$

Where k is the Evaporative Coefficient (a community-physiological constant), Ea is actual evapotranspiration (mm), Ep is potential evapotranspiration (mm), Eo is pan evaporation (mm), which was estimated using mean maximum temperature and vapour pressure

(Fitzpatrick 1963), *P* is monthly precipitation (mm), *R* is monthly runoff (mm), *D* is monthly drainage (mm) and *Sext* is extractable soil water (mm at the beginning of the month) — between Permanent Wilting Percentage and Field Capacity.

All values of *k* assess the monthly ratio of actual to potential evapotranspiration per mm of soil water available during each month. The perhumid climatic zone is defined where $k >$ 0.75 X 10^{-2}; the humid climatic zone where $k = 0.75 - 0.55 \times 10^{-2}$; the subhumid climatic zone where $k = 0.55 - 0.45 \times 10^{-2}$; the semiarid climatic zone where $k = 0.45 - 0.35 \times 10^{-2}$; the arid climatic zone where $k < 0.35 \times 10^{-2}$ (Figure 2).

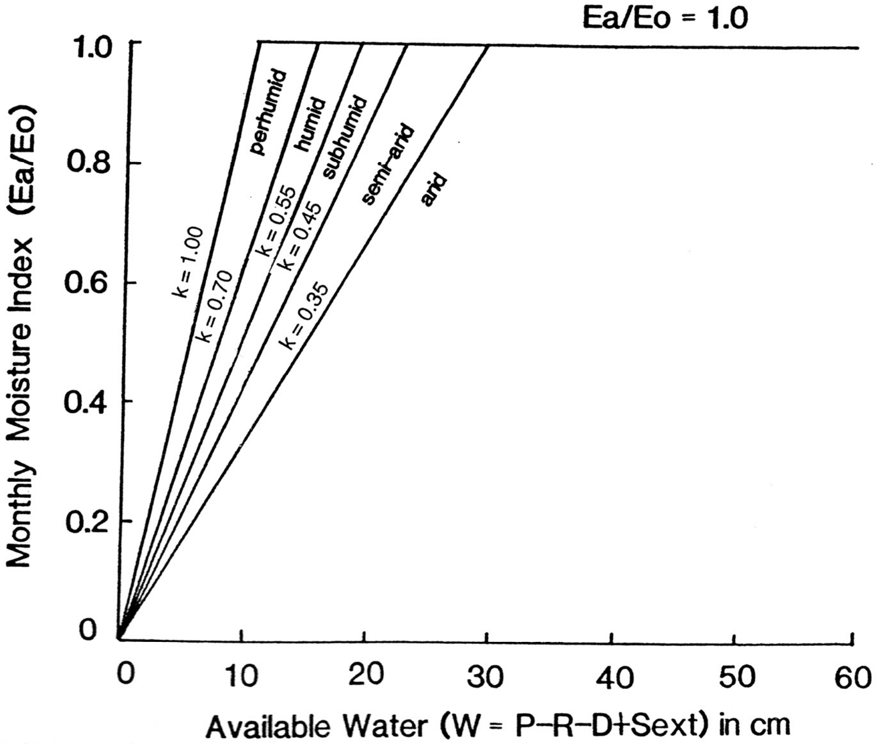

Figure 2. Relationship between Monthly Moisture Index of actual to potential evapotranspiration (*Ea/Eo*) and Available Soil Water (*W*) in perhumid to arid climatic zones. (Specht 1972a)

Range of Evaporative Coefficients (k) in climatic zones — Arid Zone ($k < 0.35 \times 10^{-2}$), Semi-arid Zone ($k = 0.35\text{-}0.45 \times 10^{-2}$), Subhumid Zone ($k = 0.45\text{-}0.55 \times 10^{-2}$), Humid Zone ($k = 0.55\text{-}0.75 \times 10^{-2}$), Perhumid Zone ($k > 0.75 \times 10^{-2}$).

Where available soil water (*W*) is sufficient (or more) for optimal evapotranspiration (*Ep*) during the short period of annual foliage growth, the linear relationship between the Moisture Index (M.I.) and available soil water (*W*) asymptotes to unity (Figure 2). On soils of median-nutrient to nutrient-rich fertility, a closed-forest (rainforest) or a closed-scrub develops, markedly in contrast to the open-structured plant communities that develop in seasonally-droughted climates; on nutrient-poor soils, a closed-heathland (± tall Proteaceae) develops.

Seasonal shoot growth and leaf fall: Seasonal shoot growth is measured monthly on tagged shoots of representative overstorey and understorey species in a plant community. Monthly samples of foliage shoots harvested from the canopy of tall overstorey species will reveal the number of new leaves produced, also the number of leaves retained from the previous season of growth. Monthly leaf fall is measured in random litter trays.

Leaf Area and Leaf Specific Weight (dry weight of leaf per unit leaf area) is measured on leaves of foliage shoots harvested at maturity.

Foliage Projective Cover: The horizontal coverage of foliage in a plant community is measured by cross-wire sighting tubes at 50cm intervals along randomly-located 50m line transects (Specht 1970). The overstorey stratum of trees and tall shrubs (over 2m in height) is recorded using upward sighting tubes; the understorey stratum of low shrubs and ground stratum (< 2m in height) is recorded using downward sighting tubes.

Satellite imagery of the intensity of red and infrared wavelengths reflected from the vegetation in each pixel will enable the Foliage Projective Cover to be assessed by the *Normalised Difference Vegetation Index* (NDVI) (Tucker 1979). The NDVI has been used to assess the amount of tree-clearing throughout Queensland from 1988 to 2010 (Queensland Department of Science, Information Technology, Innovation and the Arts 2012).

$$\text{NDVI} = (\text{infrared} - \text{red}) / (\text{infrared} + \text{red}) \quad (2)$$

Alpha Biodiversity (species richness – N, number of species per unit area): The biodiversity of vascular plants in the plant community was recorded in random quadrats of increasing area (*A*) — the Species-Area Curve (Jaccard 1928, Hopkins 1955; Whittaker 1972, 1977).

$$N = a \, \text{Log}_{10} A + b \quad (3)$$

Increasing quadrat-size of 1 m^2, 100 m^2, 500 m^2 and 1000 m^2 was adopted for the 'Species Richness' section, coordinated by Walt Westman in the *'Mediterranean-type Ecosystems. A Data Source Book'* (Specht 1988a). As an even larger quadrat size of one hectare (10,000 m^2) ensured maximal assessment of biodiversity in Australian open-structured plant communities (Specht 2012), species richness per hectare was estimated by extrapolating the data from smaller quadrats, using Equation (3).

Smaller 'survey plots' of 25-50 m^2 (termed *relevé* by Braun-Blanquet 1932; Long 1974) had been used to assess biodiversity in South African vegetation (Werger 1978b). The total number of species recorded in the random relevés in each plant community provided an estimate of the species richness per hectare.

Species richness of disjunct stands of closed-rainforests: As the growth of foliage at the edges of isolated stands of closed-rainforest is abraded by prevailing winds, the species-area-curve of these stands reaches a maximum at about 100 hectares (Specht, A. 1988; Specht 2007) —far larger than the species-area-curves of open-structured plant communities that asymptote at about a hectare in area or less (Jaccard 1928; Hopkins 1955; Whittaker 1972, 1977; Specht *et al.* 1990; Specht & Specht 1999; Specht & Specht 2010; Specht & Tyler 2010; Specht 2011).

3. Results

Evaporative Coefficient (k): The Evaporative Coefficient — the relationship between the monthly Moisture Index (the ratio of actual/potential evapotranspiration) and available soil water (Equation 1) — was computed for 102 climatic stations throughout South Africa where long-term meteorological data had been recorded. The dominant and diagnostic plant species that are recorded in Acocks' Veld Types (1953, 1975) are tabulated in Table 4, together with the calculated values of the Evaporative Coefficients and estimated Foliage Projective Covers and Species Richness (number of species of plants per hectare).

Table 4. Dominant plant species in Acocks' Veld Types (1953, 1975) in South Africa, with the Evaporative Coefficients (k) and estimated Foliage Projective Covers (FPC %) and species richness (SR, number of species per hectare) of each Veld Type.

Range of Evaporative Coefficients (k) in climatic zones — Arid Zone ($k < 0.35 \times 10^{-2}$), Semi-arid Zone ($k = 0.35\text{-}0.45 \times 10^{-2}$), Subhumid Zone ($k = 0.45\text{-}0.55 \times 10^{-2}$), Humid Zone ($k = 0.55\text{-}0.75 \times 10^{-2}$), Perhumid Zone ($k > 0.75 \times 10^{-2}$).

Acocks' Veld Type	**Dominant plant species**	**Diagnostic species**	**Evaporative Coefficient ($k \times 10^{-2}$)**	**FPC % (estimated)**	**SR (estimated)**
Tropical Arid Zone					
Orange River Broken Veld	Trees and large shrubs: Mimosaceae (*Acacia*), Anacardiaceae (*Searsia*). Small shrubs: Asteraceae (*Chrysocoma*, *Eriocephalus*, *Euryops*), & understorey: Poaceae (*Aristida*, *Digitaria*, *Cenchrus*)	*Aloe dichotoma* (Asphodelaceae) & *Euphorbia avasmontana* (Euphorbiaceae)	0.22 (5)*	(14=22=36)	(6+13=19)
Subtropical Arid Zone					
Kalahari Thornveld	Trees: Mimosaceae (*Acacia*), Asteraceae (*Tarchonanthus*). Shrubs: Mimosaceae (*Dichrostachys*), Malvaceae (*Grewia*). Understorey: Poaceae (*Stipagrostis, Aristida, Eragrostis, Tragus, Pogonarthria*), Sterculiaceae (*Hermannia*)	*Acacia erioloba* and *A. haematoxylon* (Mimosaceae)	0.30 (5)	(22+28=50)	(4+25=29)
Karoo					
- Arid Karoo	Chenopodiaceae (*Salsola*), Asteraceae (*Pentzia*, *Eriocephalus*, *Pteronia*), Bignoniaceae (*Rhigozum*) & Poaceae (*Stipagrostis, Enneapogon*) and many annuals in many families and genera (Aizoaceae, Iridaceae, Asteraceae, Fabaceae)	*Salsola aphylla* (Chenopodiaceae) in alluvium & *Rhigozum trichotomum* (Bignoniaceae) and in calcareous country *Lycium* spp. (Solanaceae), *Salsola* spp. & *Stipagrostis* spp. (Poaceae)	0.22 (2)	(14+22=36)	(6+13=19)
Central Upper	Shrubs: Asteraceae (such as	On mountains	0.26 (2)	(18+25=43)	(3+23=26)

Karoo	*Eriocephalus, Pentzia, Pteronia , Felicia, Rosenia*), Aizoaceae (*Plinthus*, *Tetragonia*) Rubiaceae (*Nenax*) & Poaceae (*Eragrostis*, *Aristida*, *Sporobolus*, *Panicum*)	*Merxmuelleri* (Poaceae) & *Searsia* (Anacardiaceae), on flats *Eriocephalus* (Asteraceae) & *Eberlanzia* (Aizoaceae)			
False Upper Karoo	Shrubs: Asteraceae (*Chrysocoma*, *Pentzia*), Poaceae (*Aristida*, *Eragrostis*, *Themeda*) & Iridaceae (*Homeria*)	On hills *Searsia erosa* (Anacardiaceae) & *Tetrachne* (Poaceae)	0.30 (6)	(22+28=50)	(4+25=29)
Noorsveld	Shrubs: Bignoniaceae (*Rhigozum*), Malvaceae (*Grewia*), Celastraceae (*Gymnosporia*) & Poaceae (*Eragrostis*, *Aristida*, *Cenchrus*)	*Euphorbia coerulescens* (Euphorbiaceae)	0.33 (1)	(25+29=54)	(5+27=32)
Subtropical Semi-arid Zone					
Bankenveld	Poaceae (*Eragrostis*, *Digitaria*, *Setaria*, *Heteropogon*)	*Acacia caffra* (Mimosaceae)	0.39 (3)	(30+33=63)	(6+32=38)
Cymbopogon – *Themeda* Veld	Poaceae (*Themeda*, *Eragrostis*, *Microchloa*,*Aristida*, *Cymbopogon*), Oxalidaceae (*Oxalis*) & Asteraceae (*Gazania*, *Osteospermum*, *Helichrysum*) & on hillsides Mimosaceae (*Acacia*), Malvaceae (*Grewia*)	*Cymbopogon plurinodis* & *Themeda triandra* (Poaceae)	0.39 (3)	(30+33=63)	(6+32=38)
Ngongoni Veld	Poaceae (*Aristida*, *Themeda*, *Monocymbium*, *Trachypogon*, *Tristachya*) and many forb spp. Forest with Myrsinaceae (*Rapanea*), Lauraceae (*Cryptocarya*), Myrtaceae (*Syzygium*)	*Aristida junciformis* grassland (Poaceae) with rain forest in ravines and on cool slopes	0.44 (1)	(36+36=72)	(8+36=44)
Valley Bushveld	Trees and large shrubs: Euphorbiaceae (*Euphorbia*), Mimosaceae (*Acacia*), smaller shrubs Rubiaceae (*Coddia*), Asphodelaceae (*Aloe*), Oleaceae (*Jasminum*) , Acanthaceae (many genera & spp.), Poaceae (*Panicum*, *Sporobolus*)	*Acacia* spp. (Mimosaceae) *Euphorbia* spp. (Euphorbiaceae) and spp. of Acanthaceae	0.39 (1)	(30+33=63)	(6+32=38)
Subtropical Subhumid Zone					
Coastal Forest	Forest trees: Fabaceae (*Millettia*, *Erythrina*), Anacardiaceae (*Protorhus*), Asteraceae (*Brachylaena*), Strelitziaceae (*Strelitzia*). Shrubs and climbers Annonaceae (*Uvaria*), Fabaceae (*Dalbergia*), Rubiaceae (*Tricalysia*, *Isoglossa*). Understorey Poaceae (*Oplismenus*)	Many spp. (see opposite for genera) and in between *Acacia* spp. and grasses	0.49 (3)	(41+39=80)	(10+40=50)
Natal Mist-belt	Trees: Podocarpaceae (*Podocarpus*), Myrsinaceae	*Podocarpus* (Podocarpaceae),	0.57 (1)	(49+43=92)	(14+49=63)

	(*Rapanea*), Lauraceae (*Cryptocarya*), Ulmaceae (*Celtis*)	*Xymalos* (Monimiaceae)			
Sourveld Highland Sourveld	Poaceae (*Themeda, Trachypogon, Tristachya, Monocymbium, Rendlia*) and many forbs in the Asteraceae, Fabaceae, Rubiaceae, Iridaceae, Orchidaceae, etc.	Many grasses and low forbs all to ~1 m.	0.54 (2)	(46+42=88)	(12+46=58)
Sourveld Piet Retief Sourveld	Poaceae (*Tristachya*, *Themeda, Rendlia*, *Eragrostis*, *Andropogon*), Asteraceae (*Berkheya*)	Grassland with scrub on rocky slopes with *Leucosidea* (Rosaceae) and *Scolopia* (Salicaceae) and some scattered *Protea roupelliae* (Proteaceae)	0.56 (2)	(47+42=89)	(13+48=61)
Thornveld	Mimosaceae (*Acacia*, *Dichrostachys*) & Poaceae (*Themeda*, *Diheteropogon*, *Imperata*, *Digitaria*)	*Acacia* and grasses			
False Thornveld	Poaceae (*Sporobolus, Digitaria, Eragrostis*, *Cymbopogon*, *Themeda*). Shrubs are Celastraceae (*Gymnosporia*), Boraginaceae (*Ehretia*), Apocynaceae (*Carissa*)	*Acacia karoo* (Mimosaceae) dominated with mixed grasses	0.48 (1)	(39+39=78)	(10+40=50)
Zululand Thornveld	Poaceae (*Stipagrostis*, *Ehrharta, Diheteropogon*, *Aristida*, *Themeda*), Cyperaceae (*Ficinia*), Asteraceae (*Metalasia*)	*Acacia* and Asteraceae and *Imperata cylindrica* (Poaceae)	0.46 (1)	(38+37=75)	(8+38=46)
Valley Bushveld	Mimosaceae (*Acacia*), Anacardiaceae (Searsia), Oleaceae (*Olea*), Celastraceae (*Cassine*), Sapotaceae (*Sideroxylon*)	*Acacia* and broad-leaved small trees	0.48 (5)	(39+39=78)	(10+40=50)
WarmTemperate Arid Zone					
Fynbos (Heathland) variants	Proteaceae, Ericaceae, Restionaceae		0.31 (2)	(23+29=51)	(2+41=43)
Namaqualand Broken Veld	Aizoaceae (*Galenia*, *Ruschia*, *Eberlanzia*, *Tetragonia*), Euphorbiaceae (*Euphorbia*), Asteraceae (*Pteronia*), Crassulaceae (*Crassula*)	*Aloe dichotoma* and many spp. of dwarf succulents in the Aizoaceae (no *E. avasmontana*)	0.22 (3)	(14+22=36)	(3+21=24)
Renosterbosveld - Coastal	Asteraceae (*Elytropappus, Eriocephalus*, *Helichrysum*, *Athanasia*), Scrophulariaceae (*Selago*) Fabaceae (*Aspalathus*) Polygalaceae (*Muraltia*), Crassulaceae (*Tylecodon*)	*Elytropappus rhinocerotis* sometimes with *Olea europaea*, *Gymnosporia* on rocky outcrops and heuweltjies	0.24 (1)	(16+24=40)	(2+33=35)
Renosterbosveld - Mountain	Asteraceae (*Elytropappus*, *Relhania*, *Eriocephalus*, *Euryops, Pteronia*), Poaceae (*Merxmuellera*), Aizoaceae (*Galenia*)	*Elytropappus rhinocerotis* – seemingly monospecific from afar	0.30 (3)	(22+28=50)	(2+39=41)
Succulent Karoo	Aizoaceae (*Ruschia, Drosanthemum, Lampranthus, Galenia, Sphalmanthus*)	Many small succulent spp. in the Aizoaceae and Asteraceae – some	0.30 (4)	(22+28=50)	(2+39=41)

	Euphorbiaceae (*Euphorbia*), Crassulaceae (*Tylecodon*, *Crassula*), Geraniaceae (*Pelargonium*)	Crassulaceae too.			
WarmTemperate Semi-arid Zone					
Alexandria Forest	Celastraceae (*Cassine*, *Maytenus*), Asteraceae (*Brachylaena*), Anacardiaceae (*Searsia*), Ebenaceae (*Diospyros*, *Euclea*)		0.37 (1)	(29+31=60)	(3+43=46)
Fynbos (variants)	Proteaceae, Asteraceae, Restionaceae		0.41 (2)	(33+34=67)	(3+45=48)
Themeda – *Festuca* Alpine Veld	Poaceae (*Elionurus*, *Heteropogon*, *Eragrostis*, *Festuca*, *Merxmuelleri*, *Poa*), Buddlejaceae (*Buddleja*), Rosaceae (*Leucosidea*)		0.43 (2)	(34+35=69)	(3+46=49)
WarmTemperate Subhumid Zone					
Alexandria Forest	Ochnaceae (*Ochna*), Icacinaceae (*Apodytes*), Fabaceae (*Erythrina*), Podocarpaceae (*Podocarpus*), Sapotaceae (*Sideroxylon*)		0.37 (1)	(29+31=60)	(3+43=46)
Fynbos (variants)	Proteaceae, Ericaceae, Restionaceae		0.41 (2)	(33+34=67)	(3+45=48)
Cymbopogon – *Themeda* Veld	Poaceae (*Cymbopogon, Themeda*)		0.43 (2)	(34+35=69)	(3+46=49)
WarmTemperate Humid Zone					
Fynbos (variants)	Proteaceae, Ericaceae, Restionaceae		0.57 (1)	(49+43=92)	(4+49=53)
Closed-fynbos	Ericaceae with many Asteraceae (*Athanasia* & others)		0.71/0.98 (1)	(89+68=157)	~ 70 spp.
Coastal Renosterbosveld	Asteraceae (*Elytropappus, Eriocephalus*, *Helichrysum*, *Athanasia*), Scrophulariaceae (*Selago*), Fabaceae (*Aspalathus*), Polygalaceae (*Muraltia*) and Poaceae (*Themeda*, *Hyparrhenia*) with Mimosaceae in ravines (*Acacia*)	*Elytropappus rhinocerotis* Before European settlement — Tall shrubs: *Olea europaea* subsp. *africana* (Oleaceae), *Sideroxylon inerme* (Sapotaceae), *Euclea undulata* (Ebenaceae). Poaceae (*Themeda triandra. Eragrostis curvula*) (Boucher & Moll 1981)	0.57 (1)	(49+43=92)	(4+49=53)
Knysna Forest	Oleaceae (*Olea*), Lauraceae (*Ocotea*), Podocarpaceae (*Podocarpus*), Apocynaceae (Gonioma), Hamamelidaceae (*Trichocladus*)		0.61/0.98 (1)	(89+68=157)	~71 spp.
North East Sandy Highveld	Poaceae (*Tristachya*, *Trachypogon*, *Themeda*, *Heteropogon*,		0.56 (1)	(47+42=89)	(4+48=52)

	Eragrostis), Asteraceae (*Helichrysum*, *Dicoma*)				

* Number of Meteorological Stations in brackets

Values of the Evaporative Coefficient range from over 0.5 x 10^{-2} in humid pockets and highlands around the southern and eastern coast but decrease rapidly inland to semi-arid and arid climates where the Evaporative Coefficient declines to less than 0.2 x 10^{-2} (Figure 3)

Maximum soil water storage during the wettest month of the year was estimated for each meteorological station. As most of the soils in the region are shallow, the extra soil moisture is lost as drainage. In localities where rainfall is high, this excess water drains down gullies and may pond in basins where sub-soil moisture may still be high during the summer season of foliage shoot growth; a closed-structured plant community then results.

The subtropical region was defined with mean annual temperatures between 20-30°C (with summer rainfall). In southern South Africa, the warm temperate region (with winter-spring rainfall and a dry summer season) has mean annual temperatures between 10-20°C in a Mediterranean-type climate (Figure 3).

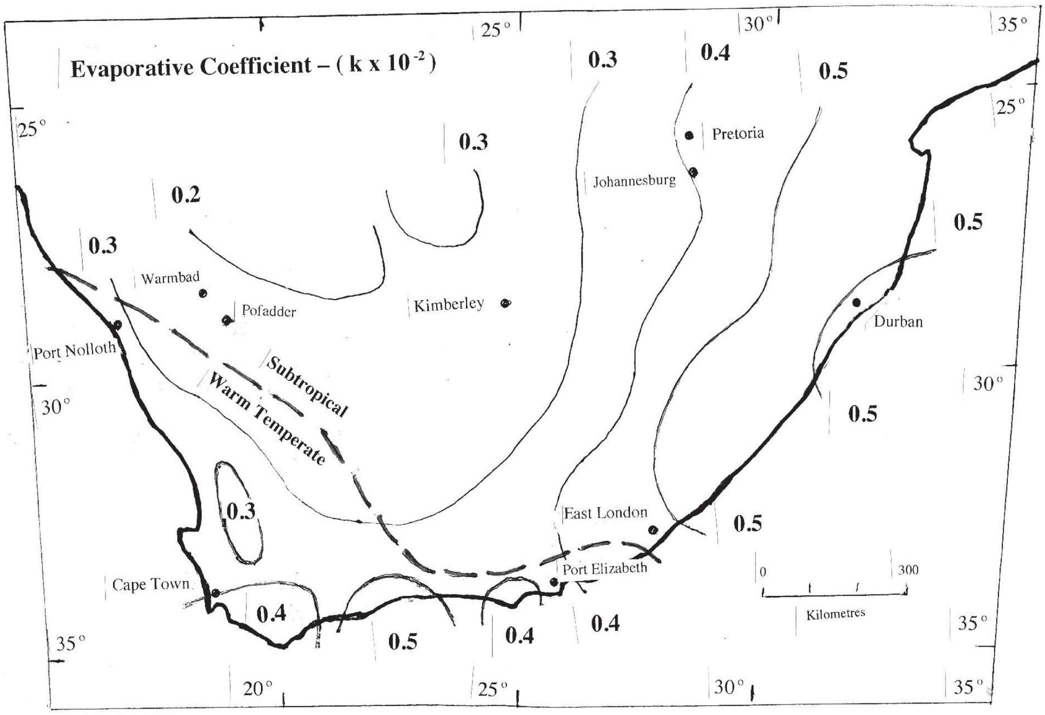

Figure 3. Isolines of the Evaporative Coefficient (k, monthly ratio of actual to potential evapotranspiration per mm available soil water) of meteorological sites in South Africa

Range of Evaporative Coefficients (k) in climatic zones — Arid Zone (k < 0.35 x 10^{-2}), Semi-arid Zone (k = 0.35-0.45 x 10^{-2}), Subhumid Zone (k = 0.45-0.55 x 10^{-2}), Humid Zone (k = 0.55-0.75 x 10^{-2}), Perhumid Zone (k > 0.75 x 10^{-2}).

Seasonal shoot growth and leaf fall: The seasonal foliage shoot growth of Proteaceae in the overstorey of Cape Fynbos Heathland vegetation growing on nutrient-poor soils in the

Capensis Region of South Africa occurs during late spring through summer — the driest season of the year (Figure 4); shoot growth in Ericaceae and Restionaceae in the understorey occurs during late winter through spring. On moderately leached soils, the original overstorey survivors of the Renosterveld (Boucher & Moll 1981; Bergh *et al.* 2014) — tall shrubs such as *Olea europaea* subsp. *africana* (Oleaceae), *Sideroxylon inerme* (Sapotaceae), *Euclea undulata* (Ebenaceae) — also show foliage growth during summer, followed by leaf fall (Figure 4, after Specht *et al.* 1983). *Elytropappus rhinocerotis* (Asteraceae)— an understorey survivor of the *Olea-Sideroxylon* overstorey of the Renosterveld — develops new foliage shoots during the wettest season of the year (Figure 4).

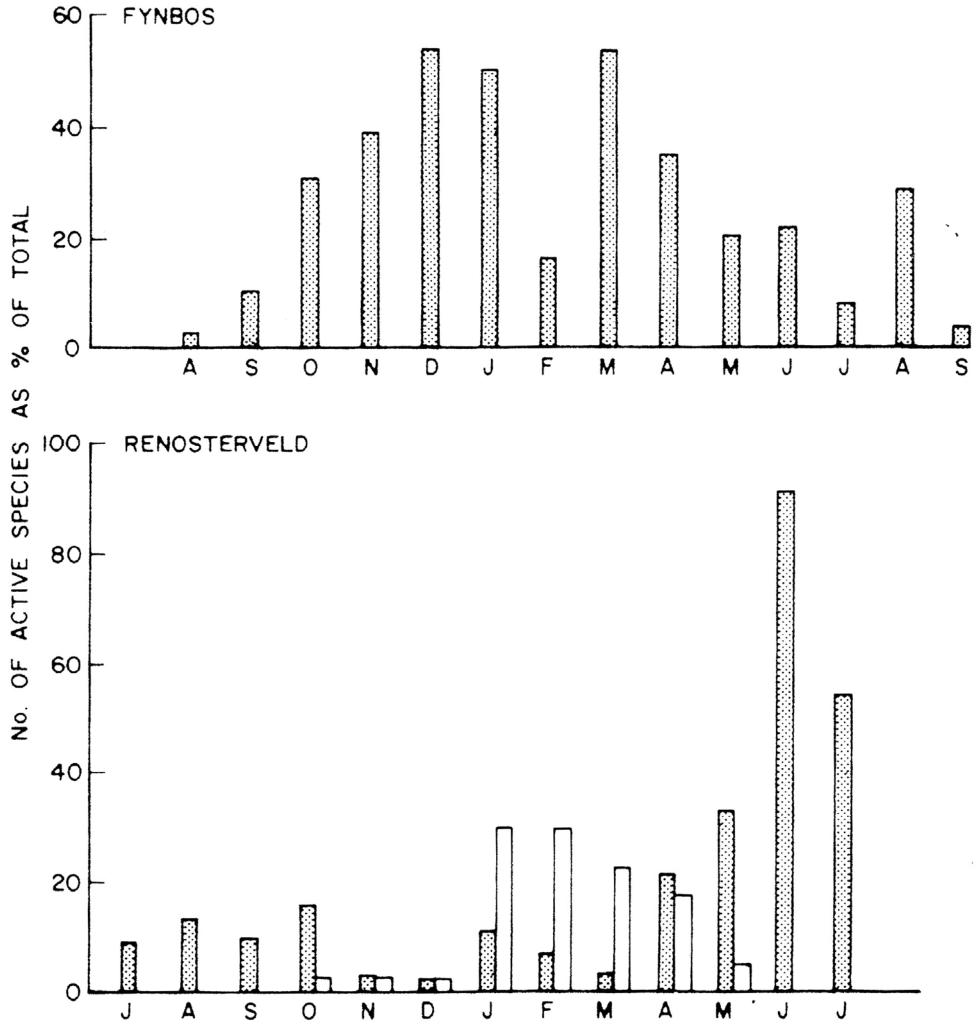

Figure 4. Seasonal shoot growth and leaf fall in Coastal Fynbos (heathland) on strongly leached soils and in remnant stands of Rhenosterveld on moderately leached soils in the Mediterranean-type climate region of South Africa (Specht *et al.* 1983)

Main study plants in Coastal Fynbos: *Leucospermum parile* (overstorey); *Thamnochortus punctatus* (understorey).

Main study plants in Rhenosterveld: *Olea europaea* subsp. *africana* and *Sideroxylon inerme* (in remnant overstorey); *Elytropappus rhinocerotis* (understorey).

Shaded bars: percentage of species growing; open bars: percentage of overstorey species losing leaves in Rhenosterveld.

A savanna understorey of C3 and C4 grasses dominates the vegetation on median-nutrient soils in humid and sub-humid climates throughout much of South Africa. In the Mediterranean-type climate of southern Africa, C3 grasses grow during spring into early summer, whereas C4 *Themeda triandra* has a growth rhythm in late spring through summer — surviving on soil moisture stored during the wet winter-spring seasons. C3 grass genera also grow in Afro-alpine habitats wherever temperatures are too low for C4 grasses (Figure 5).

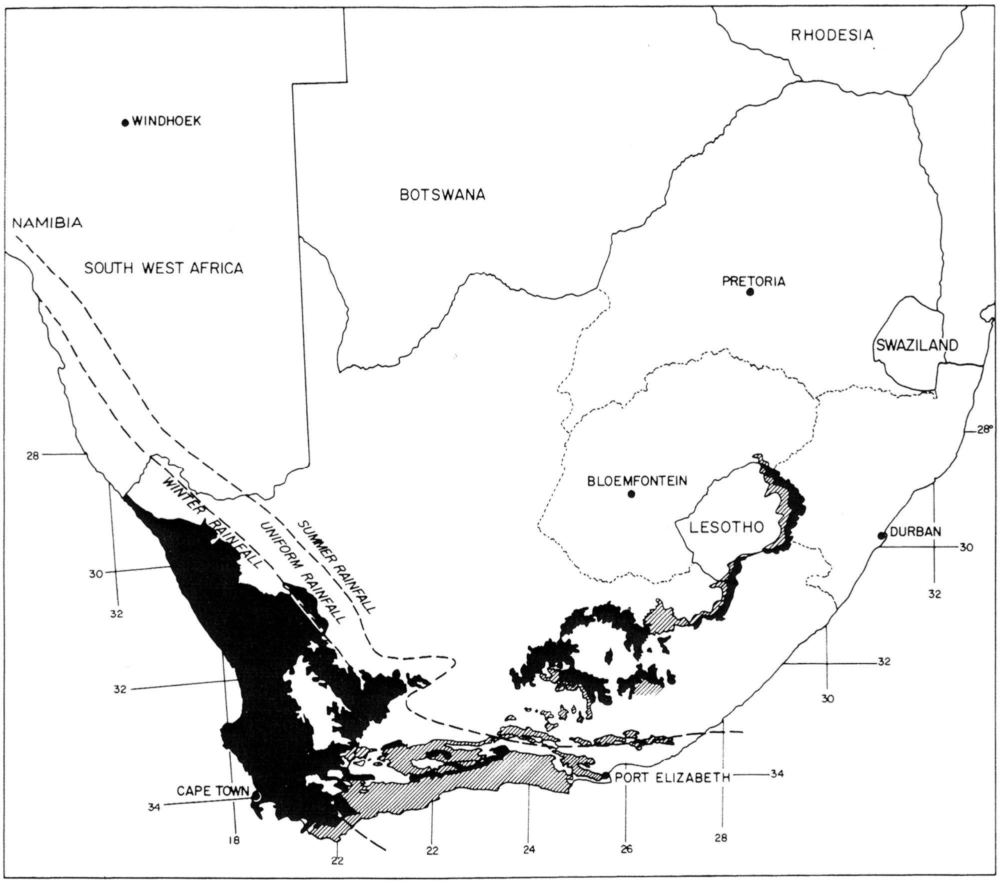

Figure 5. The distribution of C3 and C4 grasses in southern Africa and their relation to the three rainfall zones (Werger 1986, Figure 8.27, after Vogel *et al.* 1978)

Unshaded area has more than 90% of the grass cover of the C4 type; *black area* has more than 90% of the grass cover of the C3 type; *hatched area* has intermediate amounts of cover of C3 and C4 grasses.

Foliage Projective Cover: The Foliage Projective Covers (FPCs) of overstorey and understorey strata in South African plant communities appear to be similar to those recorded in Australia — correlated with the community-physiological constant, the Evaporative Coefficient (k) of the meteorological site (Figure 6). Plant communities in the arid climatic zone ($k < 0.35 \times 10^{-2}$) have an overstorey FPC of about 30% with an understorey FPC less than 30% — total FPC less than 60%. As the climate improves from the arid through the semi-arid and the subhumid climatic zones to the humid climatic zone (k = between 0.55 and 0.75×10^{-2}), both overstorey FPCs and understorey FPCs increase to about 60% — total FPC over 120%.

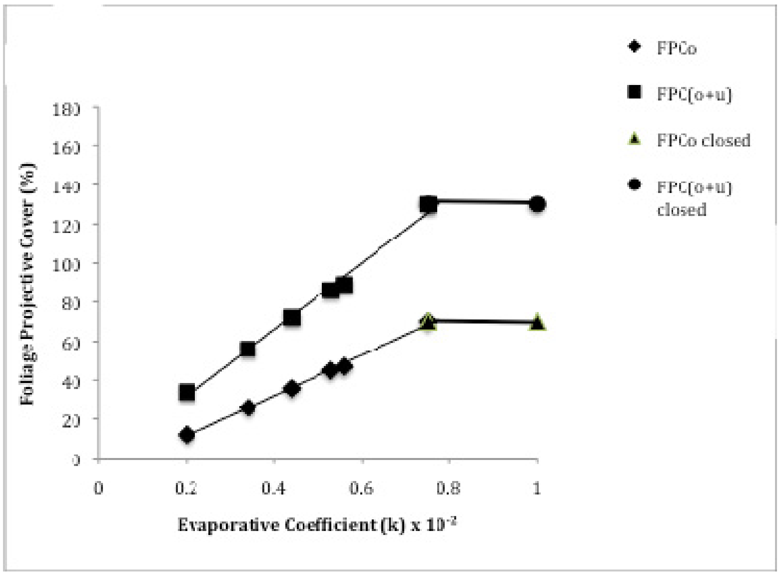

Figure 6. Foliage Projective Covers (FPCs) of the overstorey (o) stratum and the sum of FPCs recorded in both overstorey (o) and understorey (u) strata, FPC(o+u), in South African plant communities in relation to the Evaporative Coefficient (k). FPC reaches a maximum in plant communities that have optimal soil water during the season of foliage growth — FPCo closed and FPC(o+u) closed

FPC (overstorey) = 104.1 k – 9.6 $r^2 = 0.99$

FPC (over + understorey) = 171.2 k – 2.6 $r^2 = 0.99$

Range of Evaporative Coefficients (k) in climatic zones — Arid Zone ($k < 0.35 \times 10^{-2}$), Semi-arid Zone ($k = 0.35\text{-}0.45 \times 10^{-2}$), Subhumid Zone ($k = 0.45\text{-}0.55 \times 10^{-2}$), Humid Zone ($k = 0.55\text{-}0.75 \times 10^{-2}$), Perhumid Zone ($k > 0.75 \times 10^{-2}$).

In perhumid climates (with the Evaporative Coefficient over 0.75×10^{-2}) and in well-watered habitats within drier climates where available soil water is optimal during the season of foliage shoot growth, a closed-forest or closed-scrub, with Foliage Projective Covers markedly different from the adjacent open-structured plant communities, develops on median-nutrient soils (Figure 6). On nutrient-poor soils, a closed-heathland (± tall Proteaceae) develops.

After fire in fynbos (heathland) vegetation in the south-west Cape, the Total FPC is reduced to zero. As the proteoid component of the fynbos rapidly regenerates, the understorey restioid understorey declines — with Total FPC reaching a plateau of 50-60% in equilibrium with the Evaporative Coefficient of the area (Figure 7a and 7b).

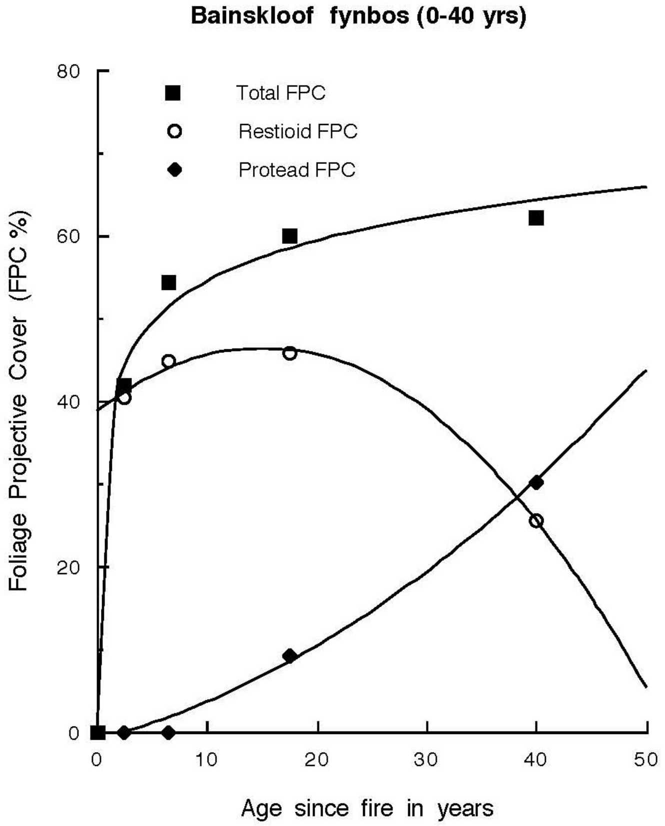

Figure 7a. Foliage Projective Covers (FPC) of Proteoid and Restioid components in four stands of fynbos — aged 2, 6, 18 and 40 years post-fire — at Bainskloof (33 ° 36'S, 19° 06'E).

Total FPC = 16.46 Log (year) + 38.01

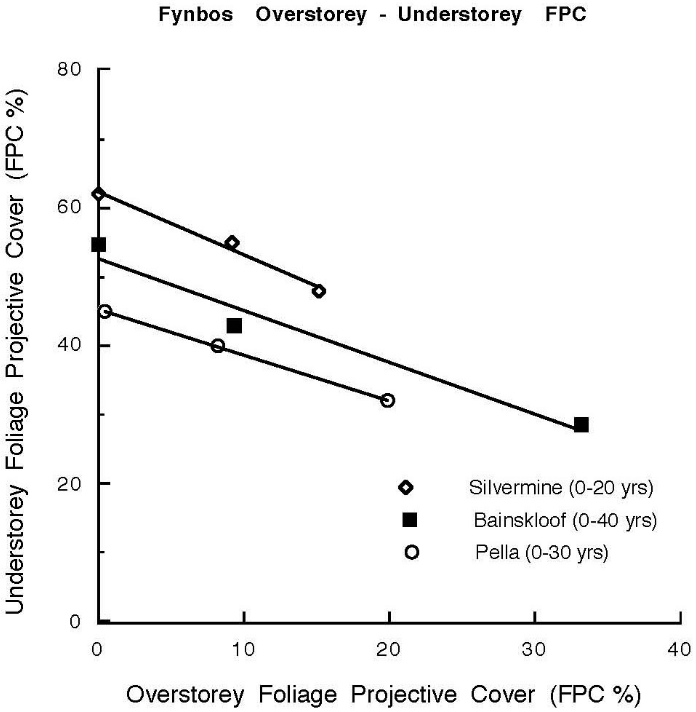

Figure 7b. The relationship of understorey Foliage Projective Cover (FPCo) to overstorey Foliage Projective Cover (FPCu) during post-fire successions in fynbos vegetation at Silvermine (34 ° 05’S, 18° 25’E), Bainskloof (33 ° 36’S, 19° 06’E) and Pella (33 ° 31’S, 18° 32’E)

Silvermine — FPCu = - 0.908 FPCo + 62.38
Bainskloof — FPCu = - 0.751 FPCo + 52.66
Pella — FPCu = - 0.671 FPCo + 45.40

Alpha Biodiversity (species richness – number of species per unit area): Table 5 lists the species richness (number of species per 1000 m^2 and per hectare) recorded in plant communities in the warm temperate Capensis Region of South Africa. As the fynbos (heathland) vegetation on the nutrient-poor quartzitic/sandstone ranges (Figure 8) was the focus of these studies (Bond 1983, 1988; Cowling 1988), only a few observations were made on the remnant vegetation on median-nutrient soils surviving at the fringes of these outcrops. Species richness (per hectare) of these lowland sites appears to increase linearly from about 30 spp. in the arid climatic zone ($k < 0.35 \times 10^{-2}$) to about 80 spp. in the humid climatic zone ($k = 0.55\text{-}0.75 \times 10^{-2}$) (Figure 9).

Table 5. Species richness (number of species per hectare) of plant communities in the Capensis Region of South Africa (Bond 1983, 1988; Cowling 1988).

Plant community	Species richness (per 1000 m^2)	Species richness (per hectare)	Evaporative Coefficient ($k \times 10^{-2}$) ..
Swartberg Mts (33° 22’S, 21 ° 55’E) – Bond 1988			0.35

Tall open proteoid shrubland – With heath understorey	67	83	
Tall open proteoid shrubland – With restioid heath understorey	46	61	
Low closed *Erica* heath	90	118	
Low open heathland – arid fynbos	59	73	
Arid fynbos – renosterveld transition	49	62	
Renosterveld	28	31	
Succulent karoo	36	47	
Baviaanskloof Mts (33° 30’S, 24° 15’E) – Bond 1988			0.35
Tall closed proteoid shrubland – With heath understorey	77	90	
Tall open proteoid shrubland – With heath understorey	64	93	
Tall proteoid shrubland – With grassy heath understorey	75	98	
Low grassy heathland	65	80	
Karroid shrubland	49	60	
Valley bushveld (Short, spinescent thicket)	79	100	
Outeniqua Mts (33° 45’S, 21° 50’E) – Bond 1988			0.45
Closed proteoid shrubland – heath understorey	55	65	
Tall open proteoid shrubland – heath understorey	65	75	
Low open heathland – arid fynbos	60	80	
Tall open shrubland (*Protea nitida*) – heath understorey (waboomveld)	104	135	
Tsitsikama Mts (33° 50’S, 23° 03’E) – Bond 1988			0.45
Tall open shrubland – heath understorey	45	53	
Tall open shrubland – grassy heath understorey	69	82	
George (35° 57’S, 22° *28’E*) – Bond 1988			
Moist forest	52	66	0.57
Bontebok N.P., Swellendam (34° 10’S, 20° 30’E) (Cowling 1988)			0.35
South Coast renosterveld	60	72	
Burtkraal (near Grahamstown) (33° 20’S, 26° 30’E) (Cowling 1988)			0.49
South Coast renosterveld	95	115	
Elandsberg Mts (33° 45’S, 25° 00’E) (Cowling 1988)			0.38
Mountain fynbos (proteoid – restioid)	41	57	
Knysna Afro-montane forest (*Rapanea – Canthium*)	53	71	
Gamtoos (33° 50’S, 25° 00’E) – Cowling 1988			0.38
Kaffarian succulent thicket (*Sideroxylon – Euphorbia*)	61	84	
Kaffarian succulent thicket (*Euclea – Brachylaena*)	98	150	
Humansdorp (34° 07’S, 24° 47’E) – Cowling 1988			0.38
Grassy fynbos – *Protea-Clutia*	87	125	
Grassy fynbos – *Thamnochortus-Tristachya*	74	100	
Grassy fynbos – *Thamnochortus-Erica*	45	55	
South Coast dune fynbos – *Restio-Maytenus*	55	75	
South Coast dune fynbos – *Restio-Agathosma*	60	88	
South Coast renosterveld – *Eltyropappus*, etc.	93	140	

Kaffarian thicket – *Pterocelastrus-Gonioma*	71	103	
Kaffarian thicket – *Cassine-Cussonia*	37	47	
Cape Town (Signal Hill) (33 ° 57’S, 18 ° 30’E) (Cowling 1988)			0.32
West Coast Strandveld	99	118	
Koeberg (33 ° 46’S, 18 ° 28’E) – Cowling 1988			0.35
West Coast Strandveld – *Putterlickia-Rhus*	35	46	
Tygerberg (33 ° 50’S, 18 ° 30’E) – Cowling 1988			0.35
West Coast Strandveld – *Elytropappus-Aristida*	103	135	

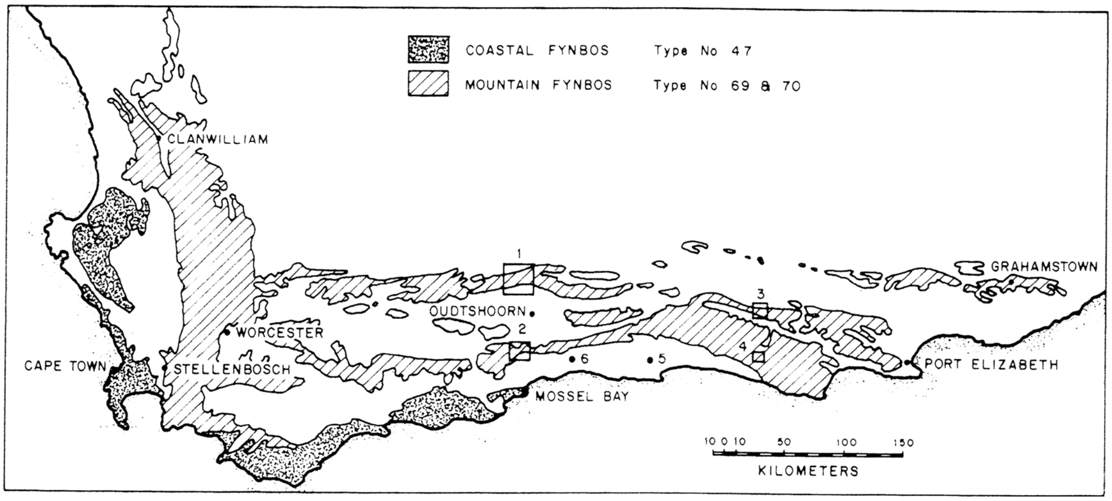

Figure 8. The study areas in the fynbos (heathland) biome in the southern Cape Province of South Africa (Bond 1983)

1. Swartberg; 2. Outeniquas; 3. Baviaanskloof; 4. Tsitsikamma; 5. Fynbos ‘island’ (Dirk se Eiland); 6. Moist forest.

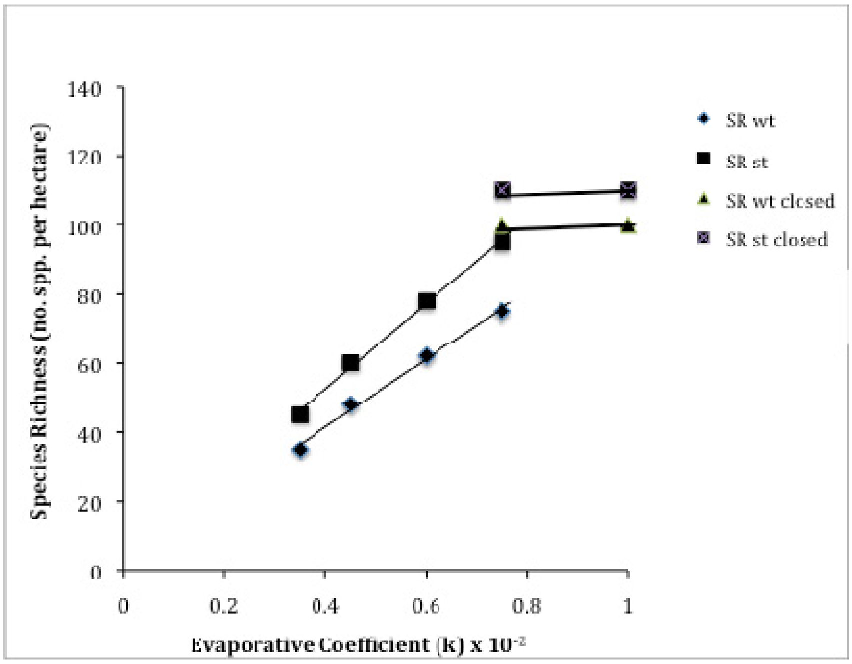

Figure 9. Species richness (SR, number of vascular plant species per hectare) of plant communities in the warm temperate (SR wt) and subtropical (SR st) regions of South Africa in relation to the Evaporative Coefficient (k). A sharp increase in species richness is found in plant communities that have optimal soil water during the season of foliage growth — SR wt closed and SR st closed

$$\text{SR (Warm Temp.)} = 95.2\,k + 6.1 \qquad r^2 = 0.95$$

$$\text{SR (Subtropical)} = 125.6\,k + 2.2 \qquad r^2 = 0.99$$

Range of Evaporative Coefficients (k) in climatic zones — Arid Zone (k < 0.35 x 10-2), Semi-arid Zone (k = 0.35-0.45 x 10-2), Subhumid Zone (k = 0.45-0.55 x 10-2), Humid Zone (k = 0.55-0.75 x 10-2), Perhumid Zone (k > 0.75 x 10-2).

The species richness (per hectare) of vegetation on median-nutrient soils in the subtropical climate, north of the warm temperate Capensis Region of South Africa, was estimated by the total number of species that had been recorded on random relevé 'survey plots' (only 25-50 m^2 in area) in the Karoo-Namib Region (Table 6) and in the Austral Domain of the Sudano-Zambesian Region (Table 7) — values confirmed in recent species richness studies in stations along the BIOTA transects in southern Africa (Table 8). The higher ambient temperatures experienced during the short shoot-growth rhythm in this subtropical climate will produce more leaves per vertical foliage shoot, thus higher net photosynthesis per annum and higher species richness (Figure 9).

Table 6. Species richness (number of species per 'plot' of 25-50m^2) of plant communities in the Karoo - Namib Region of South Africa (Werger 1978b) and Welwitschia Plain, Namibia (Moisel & Moll 1981)

Plant community	Species richness (spp. per 25-50m^2)	Species richness (spp. per hectare)	Evaporative Coefficient (k x 10^{-2})
Central Namib (Robinson 1977)			
Acacia erioloba community - in washes	3	10	
Faidherbia albida community - in rivers	2	8	
Augrabies Falls N.P. (Werger & Coetzee 1977)			
Schotia afra community – on river sides	14	30	
Southern Kalahari (Leistner & Werger 1973)			
Stipagrostis amabilis + *Acacia* spp.	10	22	0.20
Northern Cape Province (Dept Agricultural Technical Services)			
Western Mtn Karoo – *Elytropappus rhinocerotis*	25	55	0.35
Succulent Karoo – *Stipagrostis zeyheri*	20	45	0.35
Succulent Karoo – *Chaetobromus dregeanus*	32	75	
Succulent Karoo *Tetragonia–Stipagrostis*	5	12	0.10
Bushmanland - *Stipagrostis brevifolia* - sand flat	2	8	
Karoo Domain (Werger 1973)			
Zizipho – Rhigozetum obovati	20	45	
Melhania rehmannii – Hermannietum spinosae	9	20	0.22
Monoechmatetum incani	12	28	0.22
Nestlero humilis – Pteronietum sordidae	10	22	0.22
Eriocephalo – Eberlanzietum	15	33	0.22
Namibia (Moisel & Moll 1981) (22° 45'S, 15° 01'E)			
Community 1 on marble & dolerite soils	9 per 500m^2	15	0.10
Community 2 on granite & gravel soils	10 per 800m^2	16	0.10
Community 3 on fine sand	8 per 600m^2	14	0.10

Table 7. Species richness (number of species per ‘plot’ of 25-50m^2) of plant communities in the Austral Domain of the Sudano-Zambezian Region of South Africa (Werger & Coetzee 1978)

Plant community	Species richness (spp. per 25-50m^2)	Species richness (spp. per hectare)	Evaporative Coefficient (k x 10^{-2})
Broad–orthophyll Plains Bushveld (Myre 1971)			
Andropogono gayani – Corchoretum junodii	(6 + 21)* =27	60	0.45
Microphyllous Thorny Plains Bushveld (Myre1971)			
Themedo – Turbinetum oblongatae (subassoc. typicum on dark clayey soils)	(3 + 11) = 14	38	
Themedo – Turbinetum oblongatae (subassoc. albizietosum, on more sandy soils)	(6 + 20) = 26	60	0.45

* Total number of species recorded = (overstorey species + understorey species)

Table 8. Species richness (number of species per 100 m^2, 1000 m^2 and 1 hectare) of vascular plants along the BIOTA transects in southern Africa (Schmeidel *et al.* 2010).

Plant community	Species richness			See also Table No.
	(spp. per 100 m^2)	(spp. per 1000 m^2)	(spp. per hectare)	
Subtropical – Subhumid Zone				
Woodland Savanna	21	42	60	Table 7
Thornbush Savanna	28	48	63	Table 7
Subtropical – Arid Zone				
Nama Karoo	12	20	35	Table 6
Namib Desert	2	3	4	Table 6
Warm temperate – Northern Cape				
Succulent Karoo	29	57	80	Table 6
Warm temperate – Humid Zone				
Fynbos - closed	53	91	121	Table 5

In habitats that are well supplied with soil water during the season of foliage shoot growth, Foliage Projective Cover (FPC) abruptly changes to maximum to produce a closed-structured community (Figure 6) — species richness values of the closed-communities increase greatly (Figure 9). Coastal rainforests develop in the well-watered, nutrient-rich sites along the subtropical, eastern coast (Moll & White 1978) while Afro-montane rainforests occur in similar well-watered habitats in the Drakensberg Range (White 1978). However, the lower temperatures in the Drakensberg reduce vertical shoot growth compared with the temperatures experienced along the coast, thus reducing net photosynthesis per year and species richness of the rainforest stands — (70 ± 14) species-composition in Afro-montane Rainforests, compared with (131 ± 11) species-composition in Coastal Rainforests (Table 9). As solar radiation is less in the warm temperate Capensis Region (latitude 33-35°S) than in the subtropical Indian Ocean Coastal Belt (latitude 25-32°S) (Specht *et al.* 1992), annual foliage shoot growth is reduced (Specht, A. & Specht 1993, 1994), thus resulting in less annual net photosynthesis and species richness — 71 spp. in the Knysna rainforest, decreasing to 47 spp. in the rainforest stand near Kirstenbosch (Table 9).

Table 9. Species richness (number of species recorded) in closed-forests (over 100 hectares in area) in the Indian Ocean Coastal Belt (Cooper & Swart 1992), the Dwesa Forest Reserve (Moll 1974) and the Capensis Region (Bond 1983, 1988; Campbell & Moll 1977; McKenzie *et al.* 1990)

Closed-forest community	Species richness
Indian Ocean Coastal Belt **Afromontane rainforests** (Cooper & Swart 1992)	
31° 01'S 29° 20'E	~ 95 spp.
31° 28'S 28° 36'E	~ 75 spp.
31° 26'S 28° 46'E	~ 70 spp.
30° 09'S 29° 47'E	~ 80 spp.
30° 22'S 29° 26'E	~ 60 spp.
30° 51'S 29° 26'E	~ 50 spp.
30° 03'S 29° 30'E	~ 60 spp.
Indian Ocean Coastal Belt **Coastal rainforests** (Cooper & Swart 1992)	
31° 49'S 29° 17'E	~ 123 spp.
31° 32'S 29° 39'E	~ 140 spp.
31° 32'S 29° 39'E	~ 130 spp.
32° 27'S 28° 36'E	~ 150 spp.
32° 37'S 29° 23'E	~ 130 spp.
31° 37'S 29° 34'E	~ 130 spp.
31° 35'S 29° 34'E	~ 110 spp.
31° 27'S 29° 42'E	~ 125 spp.
31° 27'S 29° 45'E	~ 125 spp.
31° 30'S 29° 41'E	~ 130 spp.
Dwessa Forest Reserve, **Transkei** (Moll 1974)	
32° 10'S 28° 57'E	~ 150 spp.
Capensis Region **Afromontane rainforests**	
George (35° 57'S 22° 28'E) (Bond 1983, 1988)	~ 66 spp. per hectare

Knysna (33 ° 45'S 25 ° 00'E) (Cowling 1988)	~ 71 spp. per hectare
Kirstenbosch (33 ° 59'S 18 ° 26'E) (Campbell & Moll 1977)	~ 47 spp. per hectare
Capensis Region **Coastal rainforests**	
Platbos, near Hermanus (34 ° 25'S 19 ° 15'E) (McKenzie *et al.* 1990)	~ 32 spp. per hectare

Species richness (per hectare) in well-watered sites in the nutrient-poor fynbos stands and proteoid thickets on the infertile quartzitic/sandstone ranges in the Capensis Region (Table 5) also show much higher values (90-135 spp.) than in fynbos on habitats droughted during the season of foliage growth (circa 60 spp.).

Cyclic salt in sea-winds: Wind speeds that are produced by the Roaring Forties are exceedingly high across the southern shores of South Africa (Table 10). Even in southern Australia, these strong winds blow inland high levels of sodium chloride in the atmosphere (Isbell *et al.* 1983) that appear to limit the growth of the C4 grasses such as *Themeda triandra* — that needs minute traces of sodium for the C4 dicarboxylic photosynthetic pathway (Brownell & Crossland 1972). The input of cyclic salt in the strong winds of south-western Cape Province appear to have inhibited the growth of C4 grasses, except in sheltered pockets on nutrient-rich soils (Figure 5); further east across Cape Province where the winds are slower, an admixture of C3 and C4 grasses survive (Figure 5). As in Australia, the C4 grass, *Themeda triandra*, is widespread in subtropical South Africa, where cyclic salt is low; it even forms a 'lawn-type' savanna on the coast south of Port St Johns — similar to such communities on headlands in eastern Australia.

Table 10. Mean wind speed (km hr-1) and pan evaporation (mm per annum) data recorded at climate stations within the Mediterranean-type climatic regions of South Africa and Australia (Specht & Moll 1983; Specht & Specht 1999).

Climate station	Mean wind speed (km hr^{-1})			Pan evaporation (mm per annum)
	January	July	Year	
Cape Town, South Africa	22.4	15.4	17.4	2049
Port Elizabeth, South Africa	19.5	13.8	17.1	1920
Perth, Western Australia	17.5	14.2	15.8	1480
Adelaide, South Australia	12.6	11.6	12.2	1206
Melbourne, Victoria	13.5	13.0	12.7	1205

4. Discussion

The subtropical phenology — with foliage shoot growth between 15-25°C with a peak at 20°C — of plants in the heathlands (± trees/tall shrubs) persists today in the warm temperate, Mediterranean-type climate of each continent (Specht & Rayson 1957; Specht *et al.* 1981, 1983, 1992; Kruger 1981). Foliage growth in overstorey trees and tall shrubs — with internodes well ventilated between leaves — occurs during late spring through summer, when soil water is minimal. Foliage leaves in dicotyledonous understorey plants, on the other hand, are more closely packed than in the overstorey and trap solar energy momentarily so that foliage growth occurs earlier in spring (Specht & Yates 1990, Specht *et al.* 1991a). Even greater amounts of solar energy are trapped in dense clumps of Cyperaceae or Restionaceae, thus enabling new shoots to be formed even during winter (Specht *et al*. 1983, 1991a).

The late spring through summer phenology is also found in the overstorey trees (*Olea europaea* spp. *africana, Sideroxylon inerme*, *Euclea undulata*, etc.) that formerly dominated the Renosterveld on median-nutrient soils of the Cape (Boucher & Moll 1981). The Asteraceae (*Elytropappus rhinocerotis*, etc.) that now survive on remnant areas possess densely packed leaves that trap solar energy to enable foliage growth during the wetter seasons of the Mediterranean-type climate (Figure 4, after Specht *et al.* 1983).

> The foliage growth rhythm of the overstorey during the dry Mediterranean climate appears to be assisted by the conservation of orthophosphates — released from litter-decomposition during the wet winter-spring — in polyphosphate granules in rootlets and associated rhizosphere organisms; this polyphosphate is hydrolysed back to orthophosphate when shoot growth begins in late spring-summer (Specht & Groves 1966; Jeffrey 1964, 1967, 1968; Ashford *et al.* 1975; Coleman & Specht 1981; Specht *et al.* 1983).

The C4-photosynthetic (Hatch & Slack 1966) Gondwanan grass, *Themeda triandra*, that flourishes on nutrient-rich soils in south-eastern Australia wherever the input of sodium chloride in sea-spray is low (Isbell *et al.* 1983), also retain a subtropical growth rhythm in these Mediterranean-type climates — producing new foliage during late spring through summer when available soil moisture is lowest (Groves 1965; Stuwe & Parsons 1977; Specht *et al.* 1983). Exotic C3 plants with a warm temperate growth rhythm are thus able to invade the median-nutrient savannas where soil moisture is highest during spring (Davies & Sim 1931; Davies *et al.* 1934; Tiver & Crocker 1951; Specht & Clifford 1991; Moore 1993; Specht 2000). Even the heathy communities on nutrient-poor soils may be invaded by warm temperate exotic C3 species when the soil is enriched by ash after fire (Specht *et al*. 1958) — especially if phosphate-pollution has occurred (Specht 1963; Heddle & Specht 1975; Ozanne & Specht 1981).

Subtropical grasslands (± trees) — composed of many C4-photosynthetic Gondwanan genera that are common in South Africa and Australia (Table 2) — retain their seasonal growth rhythm between 15-25°C with a peak at 20°C, often growing during the driest months of the year (Specht *et al.* 1991b; Specht & Specht 1999). The photosynthetic pathway of all these C4 grasses need minute traces of sodium, blown far inland in sea-spray from the eastern coastlines (Brownell & Crossland 1972) — possibly recycled in the saliva of grazing animals (McNaughton 1985).

> The leaves of C4-grasses survive quite long periods of drought — even though appearing dry. As the water potential of the soil is slowly reduced, both water potential and net photosynthesis of the leaves decrease (Doley & Trivett 1974). The organelles in these desiccation-tolerant leaves are rapidly restored to normal on the application of water (Mittelheuser 1977).

During the short period of foliage shoot growth, aerodynamic fluxes (frictional, thermal, evaporative) in the atmosphere as it flows over and through the plant community (Marshall 1971) influence the lateral growth of each plant within the plant community — determining the Foliage Projective Covers (FPCs) of the overstorey (o) and understorey (u) strata (Specht & Morgan 1981; Specht 1983; Specht & Specht 1999). The sum, Σ(FPCo + FPCu), is a constant in space and time at each meteorological station.

At the same time as the Foliage Projective Covers of overstorey and understorey strata are determined in the plant community, the foliage attributes (Leaf Area, Leaf Specific Weight) of each newly-formed leaf, with their physiological-biochemical attributes, are determined — Foliar N:P Ratio (Specht & Rundel 1990; Specht & Specht 2010; Stock & Verboom 2012); stomatal resistance (Carbon Isotope Ratio, Farquhar & Sharkey 1982; Farquhar & Richards 1984; Schultze *et al.* 1998); Chlorophyll a/b Ratio (Gracia in Stewart *et al.* 1990); Nitrate Reductase Activity (Stewart *et al.* 1990).

The Foliage Projective Covers and leaf attributes in the overstorey and understorey strata determine the monthly evapotranspiration (per hectare) from the plant community. The monthly ratio of actual to potential evapotranspiration (Ea/Ep) per mm available soil water is a community-physiological constant — termed the Evaporative Coefficient (k) — in plant communities in the Arid to the Humid Climatic Zones that experience seasonal drought. In sites where available soil water is optimal during the season of foliage growth, the Σ(FPCo + FPCu) asymptotes to maximum — a closed rainforest or closed scrub is formed on median-nutrient soils, a closed heathland (± taller Proteaceae species) is formed on nutrient-poor soils (Figure 9). As available soil water under these closed plant communities fluctuates throughout the year, the net photosynthesis (and other physiological-biochemical processes, including monthly evapo-transpiration per hectare) of the Foliage Projective Cover (overstorey + understorey) of the vegetation varies accordingly (Doley *et al.* 1987; Mitchell *et al.* 2008; Lambers *et al.* 2012).

The amount of both available soil water and soil nutrients during this short period of foliage growth influences vertical foliage growth — the number of leaves and internode length — but not their foliage attributes (Leaf Area, Leaf Specific Weight) or Σ(FPCo + FPCu). Ambient temperature experienced during the short period of foliage growth also influence vertical foliage growth in the overstorey — in the gradient from temperate to tropical climates (Specht *et al.* 1992; Specht & Specht 1999). Foliage attributes within the plant community are also influenced by the gradient in ambient temperature around developing foliage shoots in the strata from overstorey to ground layer (Specht & Yates 1990; Specht *et* *al*. 1991a).

The combination of Foliage Projective Covers and number of leaves — and their foliage attributes — produced on vertical foliage shoots determine the Leaf Area Index (area of all leaves per hectare) in the plant community. The potential of the plant community to fix solar energy as net photosynthate each year is correlated with the Alpha Biodiversity (number of species per hectare) of plants in each plant community (Specht & Specht 1989a, 1989b, 1989c; Specht, A. & Specht 1993, 1994, 2001, 2011). The species richness of resident consumers (small mammals, birds, snakes, lizards and amphibia) — that depend on the energy fixed by the producers — is also correlated (Braithwaite *et al.* 1985; Specht, A. 1988; Specht 1994, 2012; Specht & Specht 1999; Specht & Tyler 2010).

Species richness of disjunct stands of closed-forests: As the growth of foliage at the edges of isolated stands of closed-rainforest is abraded by prevailing winds, the species-area-curve of these stands reaches a maximum at about 100 hectares (Specht, A. 1988; Specht 2007) — far larger than the species-area-curves of open-structured plant communities that asymptote at about a hectare in area or less (Specht *et al.* 1990; Specht & Specht 1999; Specht 2012; Specht & Tyler 2010). As annual solar radiation decreases with latitude, the species richness of closed-forests (rainforests) decreases as net photosynthesis per annum decreases in both eastern Australia and eastern South Africa.

Species richness of closed-heathlands and proteoid thickets (kwongan): On nutrient-poor lateritic soils in southwest Western Australia, a closed-heathland (with species richness 107.7 ± 12.1 spp. per hectare, n = 11) may develop on lateritic soils (Havel 1975) or a tall sclerophyllous shrubland, termed *kwongan* (with species richness 109.3 ± 13.9 spp. per hectare, n = 8) may develop on the northern Swan Coastal Plain (Heddle 1980) — with much higher species richness than in open-heathlands (59.8 ± 4.5 spp. per hectare, n = 9) on sites experiencing seasonal drought (George *et al*. 1979, 1988; Bell & Watson 1988). Similarly, closed-heathlands and proteoid thickets, with species richness of 90-135 species per hectare develop in well-watered sites on the infertile quartzite/sandstone ranges in the Capensis Region — much greater than in adjacent stands of open-heathland with species richness about 60 species per hectare.

5. Conclusions

The community-physiological processes that determine the structure, growth and biodiversity in Australian plant communities also apply to the Gondwanan vegetation of South Africa — heathlands (both open- and closed-structured), subtropical grasslands (± trees) and closed-forests (rainforests) that have developed in the arid to the humid zones in warm temperate and subtropical climates.

These community-physiological processes will continue to operate to modify the structure, growth and biodiversity of these ecosystems during environmental impacts such as nutrient pollution, invasion of exotic species, overgrazing and climate change (Specht 1988b; Specht & Specht 1995, 1999; Specht *et al.* 1974, 1995).

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