Macrothink Institute™

Journal of Environment and Ecology
ISSN 2157-6092
2015, Vol. 6, No. 1

Structure and Alpha Biodiversity of Major Plant Communities in Chile, a Distant Gondwanan Relation of Australia

Raymond L. Specht (Corresponding author)

Emeritus Professor of Botany, The University of Queensland, Brisbane, Queensland 4072, Australia

Email: r.specht@uqconnect.net

Gloria Montenegro

Departamento de Ciencias Vegetales, Pontificia Universidad Católica de Chile, P.O. Box 306, Santiago-22, Chile

Email: gmonten@puc.cl

Mary E. Dettmann

Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia

Email: mary.dettmann@qm.qld.gov.au

Received: May 2, 2015 Accepted: May 19, 2015 Published: May 8, 2015

doi:10.5296/jee.v6i1.7780 URL: http://dx.doi.org/10.5296/jee.v6i1.7780

Abstract

The structure, growth and biodiversity of Chilean vegetation are explored from the arid north, through the Mediterranean-climate zone of Central Chile to the evergreen and semi-deciduous *Nothofagus* vegetation in the south and into the treeless wet-heath vegetation of the Magellanic islands. The northern Desert Zone has four to six genera of plants that have been recorded in Australia, while the southern vegetation reveals many relationships with the cool temperate vegetation of Australia with which Chile was conjoined in the Gondwanan assembly during the Late Mesozoic. As the physico-chemical processes that determine the structure, growth and biodiversity of plant communities on median-nutrient soils are similar in the temperate climates of Chile and Australia, similar values of Foliage Projective Cover, Leaf Area, Leaf Specific Weight and Alpha Biodiversity result.

Keywords: production processes; seasonal growth; vegetation structure; leaf attributes; biodiversity; Biome Studies; biogeography

1. Introduction

1.1 The International Biological Program on Mediterranean-Type Ecosystems

In 1964, a program under the title *'The Biological Basis of Productivity and Human Welfare'* was launched by the International Council of Scientific Unions (ICSU) to initiate the International Biological Program (IBP) — an integrated study of terrestrial, freshwater and marine ecosystems of the world. Its objective was "to promote a world-wide study of organic production on the land, in freshwater and in the seas, and of human adaptability to changing conditions."

Six sections of IBP were organized: —

- Productivity of Terrestrial Communities (Section PT).
- Production Processes in Terrestrial Communities (Section PP).
- Subsection — Photosynthesis.
- Subsection — Nitrogen Metabolism.
- Subsection — Community Physiology.
- Conservation of Terrestrial Communities (Section CT).
- Productivity of Freshwater Communities (Section PF).
- Productivity of Marine Communities (Section PM).
- Human Adaptability (Section HA).

As Specht had pioneered research on the Productivity, Production Processes and Conservation of Terrestrial Plant Communities (and associated consumers and decomposers) in southern Australia, he was invited to serve on the International Planning Committees for each of these three Sections PT, PP and CT.

Post-fire biomass productivity — Dark Island heathland (Specht *et al*. 1958).

Community-physiological processes — Phosphorus nutrition of heathland communities (Specht 1963; Heddle & Specht 1975); phosphorus nutrition of heathland species (Specht & Groves 1966; Jeffrey 1964, 1967, 1968); water-balance studies in heathland communities (Specht 1957a, 1957b).

Conservation of Australian plant communities — (Specht & Cleland 1961, 1963).

These research studies undertaken as part of the International Biological Program in Australia have been pursued into the 21st Century: —

Community-physiological processes (Specht & Morgan 1981, Specht 1983; Specht & Rundel 1990; Specht & Yates 1990; Specht *et al.* 1990, 1991; Specht & Specht 1989a, 1989b, 1989c, 1999);

Conservation (Specht *et al.* 1974, 1995).

As it had proven difficult to co-ordinate the six IBP Sections, the United States decided to integrate the research projects under **Biome Studies** of major ecosystems in their domain. A co-ordinated program on the Mediterranean-climate Biome in California was formulated by

Prof. Hal Mooney of Stanford University who then sought an international research study between scientists on the chaparral of California and the matorral of Chile. Prof. Francesco di Castri readily organised the first international symposium on **Mediterranean-climate Biomes (MEDECOS)** in Valdivia, Chile, in March 1971 and invited Specht to present an article on the Australian ecosystem research (Specht 1973).

Co-ordinated research into Mediterranean-climate ecosystems was fostered worldwide, with participating nations organising MEDECOS symposiums on the major environmental threats to the survival of these ecosystems (Specht 2011).

Mediterranean-climate conferences were held in:

- Valdivia, Chile (August 1971) on '*Mediterranean-Type Ecosystems. Origin and Structure*' (Di Castri & Mooney 1973)
- Palo Alto, California (August 1975) on '*Environmental Consequences of Fire in Mediterranean Ecosystems*' (Mooney & Conrad 1977)
- Stellenbosch, South Africa (September 1980) on the '*Role of Nutrients in Mediterranean-type Ecosystems*' (Kruger *et al.* 1983)
- San Diego, California (June 1981) on '*Dynamics and Management of Mediterranean-Type Ecosystems*' (Conrad & Oechel 1982)
- Montpellier, France (May 1983) on '*Bioclimatologie Méditerranéenne*' (Long & Pons 1984)
- Perth, Western Australia (August 1984) on '*Resilience in Mediterranean-type Ecosystems*' (Dell *et al.* 1986)
- Sesimbra, Portugal (October 1985) — '*Plant Response to Stress*' (Tenhunen *et al.* 1987)
- Barcelona and Zaragoza in Spain (October 1985) — (Carles Gracia & Heime Terradas unpubl.);
- Woods Hole, Mass., U.S.A. (October 1986) — '*Patterns and Processes in Biotic Impoverishment*' (Woodell 1990)
- Montpellier, France (August 1987) on '*Time Scales of Biological Responses to Water Constraints*' (Roy *et al.* 1995)
- Thessaloniki, Greece (August 1988) — (Margarita Arianoutsou unpubl.);
- Alicante and Barcelona, Spain (1990) — (Carles Gracia unpubl.);
- Israel (1990) — Memorial Volume 39 of *Israel Journal of Botany* on death of Professor Michael Evanari, Botany Department, University of Jerusalem (*Israel Journal of Botany* Vol. 39, 1990: Specht *et al.* 1990)
- Aix-en-Provence, France (1991) — Festschrift Volume 16 for Professor Pierre

Quézel. (*Ecologia Mediterranea* Vol. 16, 1991; Specht *et al.* 1991)

- Crete, Greece (September 1991) on *'Plant-Animal Interactions in Mediterranean-type Ecosystems'* (Arianoutsou & Groves 1994)
- Reñaca near Santiago, Chile (October 1994) on *'Landscape Degradation in Mediterranean-Type Ecosystems'* (Montenegro 1994)
- San Diego, California (1997) — (Walt Oechel unpubl.)
- Stellenbosch, South Africa (2000) — (William Bond, Richard Cowling & Glaudin Kruger unpubl.);
- Greece (2004) — (Margarita Arianoutsou & Costas Thanos unpubl.);
- Perth, Western Australia (2007) — (Kingsley Dixon unpubl.)

Chilean scientists under Prof. Francesco di Castri were inspired by the community-physiological research on the structure, growth and biodiversity of heathland in the Mediterranean-type climate of southern Australia (Specht 1957a, 1957b, 1963; Specht & Rayson 1957; Specht *et al.* 1958) and began similar studies on the matorral in Central Chile.

- Biomass, phenology and growth (Kummerow *et al.* 1981)
- Ecomorphological characters (Montenegro 1988)
- Plant growth forms of Chilean matorral (Orshan *et al.* 1985)
- Anatomy of species in the Central Zone of Chile (Montenegro 1984)
- Seasonal cambial activity of Chilean shrubs (Avila *et al.* 1975)
- Herbaceous vegetation in the Chilean matorral (Montenegro *et al.* 1978)
- Growth dynamics of Chilean matorral shrubs (Montenegro *et al.* 1976, 1979, 1982, 1983)
- Species richness of plant communities in the Mediterranean-climate of Chile (Montenegro & Teillier 1988)
- Water economy of representative evergreen sclerophyll and drought deciduous shrubs of Chile (Mooney & Kummerow 1971)
- Effect of fertilizers on fine root density and shoot growth in the Chilean matorral (Kummerow *et al.* 1982)

Under the auspices of the International Society for Mediterranean Ecosystems (ICSU-ISOMED), initiated in 1984 by the Ecological Director of UNESCO, Dr Francesco di Castri, scientists from all Mediterranean-climate countries cooperated to produce *"A Data Source Book for Mediterranean-Type Ecosystems*" (Specht 1988).

A thirty volume series on **Ecosystems of the World** was initiated by Elsevier Scientific Publishers in 1975 with David W. Goodall as General Editor (Goodall 1975-2005). Five volumes summarised the vegetation of Chile — Desert Region (Rauh 1985); Matorral Zone in the Mediterranean-type climate (Rundel 1981, 1988); the temperate broad-leaved evergreen forests (Veblen *et al.* 1983); the temperate deciduous forests (Schmaltz 1991); the southern oceanic wet-heaths (Moore 1979).

This article analyses the community-physiological data that were assembled by scientists, not only on vegetation in the Mediterranean-climate Central Zone of Chile, but from the arid north to the Antarctic south of the country.

2. Palaeo-biogeographical Gondwanan Relationship of Chile with Australia (by Mary E. Dettmann)

Phytogeographical relationships between Australia and southern South America are closest among perhumid communities, as was first noted by Hooker (1847) who suggested that Antarctica must have been an important source and/or gateway for elements now restricted to southern perhumid forests. Confirmation of Hooker's thesis is to be found in the fossil record of southern South America, Antarctica and Australasia. Similarity/dissimilarity patterns of lineages represented in the fossil record and cladistic biogeography confirm shared Gondwanan rainforest history (Weston & Hill 2013; Kooyman *et al.* 2014).

The genesis of these communities dates to the Late Mesozoic when Africa, India, Australia, Antarctica and South America were conjoined in the Gondwana assembly. Here, at the close of the Jurassic, the vegetation spanned two broad floristic regions under a warmer climatic regime and a lower equator to pole temperature gradient than exists today (e.g. Frakes 1979; Hallam 1984). In the low-mid latitudinal northern areas (northern South America and Africa), the extinct conifer family, Cheirolepidaceae, was important in the climax vegetation, whereas in mid-high latitudinal southern Gondwanan regions (Antarctica, Australasia southernmost South America, and India) the vegetation comprised a series of cheirolepidacean/podocarp/araucarian forests (Dettmann 1989, 1992). Intermingling of the forests of these two broad floristic regions occurred during the Late Jurassic – Early Cretaceous as India rifted from the west coast of Australia and Antarctica and South America from Africa to form respectively the proto- Indian and South Atlantic Oceans. With widening of these oceans the north-south climatic gradient moderated, and the region encompassing southern South America, Antarctica, Australasia and India supported podocarp/araucarian forests and woodlands in a range of terrestrial habitats. However, there was marked east-west regionalism in the vegetation as evidenced by the fossil record with diverse araucarians and cycads in the southern South America - Antarctic Peninsula region whereas in southern Australia diverse podocarps occurred with ginkgoaleans (Dettmann 1992). The regionalism may have been influenced by climatic as well as edaphic and topographic factors resulting from tectonic disturbances. Moreover, in the high latitudinal regions the forests had a more open canopy and more widely spaced trees than the forests in lower latitudes (Specht *et al.* 1992).

Angiosperms migrated into the southern Gondwanan region during the Barremian-Aptian, possibly from a northern Gondwanan source. Early angiosperms were of the ANITA clade (of APG II 2003) and by the Aptian-Albian basal eudicots were also represented. As India rifted and commenced its fast drift north, floral exchange lessened and ceased between India and the Antarctic-Australasian-southern South American assembly by the close of the Early Cretaceous. However, exchange continued between northern South America and regions south with the southern South America-Antarctica Peninsula area forming an important evolution and exchange centre during the Late Cretaceous and early Paleogene. During that period the Cheirolepidaceae were of decreasing importance in the podocarp/araucarian forests that instead contained increasingly diverse podocarps, araucarians, and angiosperms. The progenitors of some of the angiosperm elements migrated from northern Gondwana, possibly via shorelines of the rift systems, whilst others evolved and diversified in the region. Amongst the former were members of the Winteraceae, Proteaceae, Myrtaceae, Sapindaceae, Ericaceae and Gunneraceae, all of which have earlier known first appearances in northern Gondwana and/or Laurasia. Taxa represented only at Cretaceous high southern latitudes of southern South America, Antarctica, and Australasia include *Nothofagus, Lagarostrobos, Dacrycarpus*, *Dacrydium,* and *Agathis/Wollemia*. The latest Cretaceous-earliest Paleogene vegetation at a site on Seymour Island (Antarctic Peninsula) is interpreted to represent lowland cool-warm temperate rainforest, with higher elevation araucarian forests and subalpine ericaceous heathland growing under humid conditions with temperatures of 10 - 15°C in lowland areas and of -5–8°C in subalpine regions. Although without an exact modern equivalent the vegetation is considered closest to that of the Andes in southern Chile and Argentina (Bowman *et al.* 2014). Further north, in southern Argentina, well preserved fossils occur in Paleocene and early Eocene sediments of Gondwanan elements; these include araucarian (*Agathis, Araucaria* sect.*Eutacta),* podocarp *(Dacrycarpus, Acmopyle, Retrophyllum),* and cupressoid (*Papuacedrus)* taxa together with the angiosperms *Eucalyptus, Gymnostoma*, *Akania*, and *Ripogonum* that today are restricted to Australasia and regions north (Gandolfo *et al.*2011; Wilf *et al.* 2013; Carpenter *et al.* 2013). Thus, by the early Eocene there was strong similarity between mesic floras of southern South America and southern Australia (Kooyman *et al.* 2014).

With establishment of the circumpolar current and the transition from greenhouse to icehouse conditions at the close of the Eocene together with tectonic displacements and landscape disturbances in southern South America there was considerable lineage filtering amongst elements of the mesic communities (Acosta *et al.* 2014). Meanwhile Antarctica lost its rainforest vegetation due to icehouse conditions, whilst in Australia the rainforest taxa survived in newly emerging mesic highlands during its period of fast drift northward and increasing seasonality. A comparison of modern and fossil distributions of plant lineages represented in the Australian and southern South America flora through time confirms decreasing similarity from the Late Cretaceous-early Paleogene flora through to the Neogene and present day (Kooyman *et al.* 2014).

From the Neogene through to the present day, floral exchange between southern South America and Australia has ceased or been limited to long distance dispersal (Thomas *et al.* 2014 and references therein). The latter mechanism has been attributed to the presence in New Caledonia and other areas of the southwest Pacific of many of the Gondwanan taxa, ancient lineages of which were shared by Australia and southern South America (e.g.

Sanmartin and Ronquist 2004; Sauquet *et al.* 2009). However, attention needs to be accorded to increases in knowledge of the break-up history and subsequent tectonic, displacement and land/sea modification events that are interpreted to have occurred in the southern Pacific and fringing areas (e.g. Lisker & Läufer 2013).

3. Major Plant Communities in Chile (adapted from Gajardo 1994) (by Gloria Montenegro)

3.1 The Desertic Zone Extends from Copiapó to the Extreme Northern Part of Chile.

The city of Arica is characterized by a few species of endemic Cactaceae in the coastal region such as *Eulychnia aricensis* and *Opuntia echinacea*, with a winter annual herbaceous strata on soils protected in ravines or by the coastal fog. Inland in some areas the only trees are *Prosopis tamarugo* and *Prosopis alba* in the area called Pampa del Tamarugal on soils with shallow and saline water. Representative shrubs of this dry region are *Tessaria absinthiodes, Euphorbia tarapacana, Atriplex atacamensis, Acantholippia trifida, Baccharis juncea, Baccharis petiolata, Atriplex deserticola.* Toward the Andes Mountains, a belt of the columnar cactus *Browningia candelaris* appears up from 1500 to 2700 meters above sea level in front of Arica and Iquique with another belt on the slopes of San Pedro de Atacama of *Echinopsis atacamensis*.

At high altitude in the Tropical Zone with precipitation in summer, a pre-Andean band occurs in front of the interior desert with mid-height shrubs of *Tessaria* and *Baccharis* and perennial grasses of the genus *Cortaderia*. Above 3000 metres, the vegetation is the Andean steppe of '*pajonal*' with dominance of dense perennial grasses such as species of the genera *Stipa* and *Festuca* . The *'Llaretal'* is a plant community formed by species of the genera *Azorella* and *Laretia*, resinous and woody cushion plants intensively used by the local people as source of fuel.

3.2 Major Plant Communities Along the Mediterranean Zone of Chile

3.2.1 Mediterranean Arid corresponding politically to the IV Region of Chile:

1. Coastal Matorral with sclerophyllous shrubs on the slopes of the Coastal Range with seasonal herbaceous strata flowering in spring.

Dominant Species: Tree stratum - *Adesmia microphylla, Lobelia polyphylla, Porlieria chilensis:* Mid-height stratum - *Cassia coquimbensis, Fuchsia lycioides, Bahia ambrosioides, Proustia cuneifolia, Puya chilensis.* Found from north of La Serena to Ovalle by the coast.

2. Steppe Matorral toward the inland represented by a xeric vegetation present in valleys and on Andean slopes far from marine influence. Dominant Species: Mid-height stratum - *Flourencia thurifera, Heliotropium stenophyllum, Bridgesia incisifolia, Gutierrezia resinosa, Atriplex* spp., *Lithraea caustica, Colliguaja odorífera.* Found from La Serena to Illapel.

3. Steppe Matorral-Forest corresponds to a shrubby vegetation that develops small forests protected in ravines and on southern-faced slopes where trees can reach high densities. Dominant Species: Tree stratum - *Azara celastrina, Schinus latifolius, Lithraea caustica,*

Cryptocarya alba, Kageneckia oblong: Mid-height stratum - *Baccharis concava, Escallonia revoluta*. Found from Ovalle up to the north of Los Vilos by the coast.

4. Steppe matorral- shrubby a well developed plant community similar in species to the Sclerophyllous Evergreen Matorral from the Semiarid Region but with lower shrubs of chamaephyte life forms.

Dominant Species: Tree stratum - *Peumus boldus, Quillaja saponaria, Cryptocarya alba, Schinus latifolius:* Mid-height stratum - *Lithraea caustica, Baccharis concava, Eupatorium salvia*. The most representative area is near Los Vilos.

3.2.2 Mediterranean Semiarid corresponding politically to the V Región of Chile

1. Sclerophyllous Foothill Andean Matorral, a community with high plant diversity located in the transition to the true Matorral highly impacted by human density. Dominant Species: Tree stratum - *Kageneckia angustifolia, Quillaja saponaria, Schinus montanus*: Mid-height stratum - *Colliguaja integerrima, Escallonia myrtoidea, Maytenus boaria,* Distributed from the north of the city of Los Andes to the south of Rancagua.

2. Coastal Matorral with abundance of sub-shrubs and succulents on coastal slopes. Dominant Species: Tree stratum - *Peumus boldus, Adesmia microphylla, Schinus latifolius:* Mid-height stratum - *Podanthus mitiqui, Colliguaja odorifera, Eupatorium salvia, Flourencia thurifera, Lithraea caustica, Baccharis* spp., *Echinopsis chilensis, Puya chilensis*. Distributed near Valparaiso, Quintero, Cachagua, Zapallar and Papudo.

3. Sclerophyllous Evergreen Forest, well developed trees with sclerophyllous leaves abundant in ravines and on mesic southern facing slopes of the Coastal Range. In some areas abundance of resprouts due to the harvesting for charcoal and fire-wood. Dominant Species: Tree stratum - *Beilschmiedia miersii, Crinodendron patagua, Cryptocarya alba, Peumus boldus, Schinus latifolius, Drimys winteri, Aextoxicon punctatum, Persea lingue, Quillaja saponaria:* Mid-height stratum - *Myrceugenia obtusa, Luma chequen, Maytenus boaria, Aristotelia chilensis, Azara celastrina, Jubaea chilensis, Escallonia revoluta*. Geographically distributed from the south of La Ligua to the south of Pichilemu.

4. *Nothofagus* Forest appears on higher elevation of the sclerophyllous forest with *Nothofagus obliqua* as the dominant species coexisting in some areas with Tree stratum - *Nothofagus glauca, Aristotelia chilensis, Azara integrifolia, Cryptocarya alba, Kageneckia oblonga, Lomatia hirsuta:* Mid-height stratum - *Ribes pinctatum, Berberis actinacantha, Escallonia pulverulenta*.

3.2.3 Mediterranean Subhumid and Humid Region corresponding politically to the VIII and IX Region of Chile.

1. Montane Sclerophyllous Forest located at the foothill of the Andes Mountain developed on less severe environmental conditions than the Sclerophyllous Forest of the semiarid region. Dominant Species: Tree stratum - *Nothofagus glauca, Cryptocarya alba, Kageneckia oblong*a, *Persea lingue, Peumus boldus:* Mid-height stratum - *Aristotelia chilensis, Azara integrifolia, Lomatia hirsuta, Ribes punctatum, Berberis actinacantha, Escallonia pulverulenta, Luma*

apiculata, Aextoxicon punctatum, Myrceugenia obtusa, Escallonia pulverulenta. Dominant surrounding Chillan and Maule.

2. Montane *Nothofagus* Forest on the Andean slopes from Linares to the south of Chillan dominated by *Nothofagus obliqua, Nothofagus glauca*, shedding leaves during winter and with a few pure formations of *Austrocedrus chilensis.* On the coast and on southern facing slopes from Constitucion to the north of Concepcion dominated by the so-called '*Mauline Forest*' with species such as *Nothofagus glauca, Nothofagus obliqua, Azara petiolaris, Aristotelia chilensis, Lithraea caustica, Ribes punctatum, Cryptocarya alba, Escallonia pulverulenta, Peumus boldus.* Toward the south this forest changes gradually to a Forest dominated by the genus *Nothofagus* but with now more mesic evergreen species from Temuco up to Villarrica. Dominant Species: Tree stratum - *Nothofagus obliqua, Nothofagus dombeyi, Podocarpus saligna, Laurelia sempervirens, Aextoxicon punctatum:* Mid-height stratum - *Gevuina avellana, Lomatia hirsuta, Amomyrtus luma, Azara lanceolata,*

3. Mixed Forest of *Nothofagus* and *Araucaria*

Dominated by trees of *Araucaria araucana* with species of *Nothofagus* — *Nothofagus pumilio, Nothofagus antarctica, Nothofagus dombeyi* — on volcanic soils of Andean slopes. Occurs from Los Angeles to the southern region of Villarrica.

4. Valdivian Forest

Valdivian Forest is a dominant community in the southern part of the country from Villarrica to Chiloe. Evergreen forest found on slopes of both Cordillera Coastal and Andean, with great plant diversity in growth forms and cover. Dominant species: Tree stratum - *Aextoxicon punctatum, Eucryphia cordifolia, Laurelia philippiana, Laurelia sempervirens, Podocarpus saligna, Nothofagus dombeyi:* Mid-height stratum - *Gevuina avellana, Luma apiculata, Myrceugenia planipes, Amomyrtus luma, Lomatia ferruginea, Lomatia hirsuta, Gevuina avellana.*

3.3 The Austral Region

The Austral Region with a high oceanic influence extends from the southern limit of the Mediterranean region down to Patagonia, Tierra del Fuego, Isla Navarino and Cabo de Hornos. The northern area of this region, with Mediterranean influence, begins near Temuco down to Chiloe with dominance of the Valdivian or Temperate Forest. In the continental area of Chiloe, remnants of *Fitzroya cupressoides* still remain. Toward the south of the region, the vegetation on the slopes of the Andean mountain is still the Valdivian type forest but with more dominance of Coniferous species, *Pilgerodendron uviferum,* with a dense vegetation of Ericaceae, Cyperaceae, Juncaceae and ferns. The dominant species are *Nothofagus pumilio, Ribes cucullatum, Gevuina avellana, Podocarpus nubigena, Pernettya mucronata Nothofagus betuloides, Chusquea macrostachya* and *Berberis microphylla.*

The degradation of the forest gives way to the Magellanean steppe or Patagonian Steppe in the region of Chile Chico near the Lake General Carrera with dominance of perennial Poaceae and low sclerophyllous shrubs. Dominant species *are Baccharis patagonica, Gunnera magellanica,* *Festuca pallescens, Acaena splendens, Mullinum spinosum*.

4. Chilean Genera, also Native in Australia (by Ray Specht)

Desert Zone: — *Acacia* (Mimosaceae); *Atriplex* (Chenopodiaceae), *Euphorbia* (Euphorbiaceae), *Stipa* (Poaceae)

Mediterranean Arid Region: — *Atriplex* (Chenopodiaceae), *Cassia* (Caesalpiniaceae), *Cryptocarya* (Lauraceae), *Heliotropium* (Boraginaceae), *Lobelia* Campanulaceae), *Muehlenbeckia* (Polygonaceae)

Mediterranean Semi-arid Region: — *Beilschmiedia* (Lauraceae), *Cryptocarya* (Lauraceae), *Drimys* (Winteraceae), *Lomatia* (Proteaceae), *Maytenus* (Celastaceae), *Nothofagus* (Nothofagaceae)

Mediterranean Subhumid to Humid Region: — *Araucaria* (Araucariaceae), *Cryptocarya* (Lauraceae), *Eucryphia* (Cunoniaceae), *Lomatia* (Proteaceae), *Nothofagus* (Nothofagaceae), *Podocarpus* (Podocarpaceae)

Austral Zone: — *Acaena* (Rosaceae), *Apium* (Apiaceae), *Blechnum* (Blechnaceae), *Carex* (Cyperaceae), Drimys (Winteraceae), *Gaultheria* (Ericaceae), *Gunnera* (Gunneraceae), *Nothofagus* (Nothofagaceae), *Sphagnum* (Sphagnaceae)

Fungi (*Cyttaria* sp. Basidiomycetes)

'A peculiar vegetable product of this region (Southern Chile) is a small globular fungus growing on the bark of the beech; it is a staple article of food among the Fuegians.' (Information from Google)

Prof. Des Herbert (1935) recorded this genus (*Cyttaria septentrionalis*) on *Nothofagus moorei* near Binna Burra in Lamington National Park.

5. Structure and biodiversity of Chilean Vegetation (by Ray Specht)

The research on the processes that determine the structure, growth and biodiversity in heathlands on nutrient-poor soils in the Mediterranean-type climate of South Australia inspired scientists to develop similar studies on the matorral vegetation on richer soils in the Mediterranean Zone of Central Chile.

5.1 Methods

5.1.1 Emberger Pluviothermic Quotient (Q) of Emberger (1955): The classification of Mediterranean-climate regions

$$Q = 2000P / M^2 - m^2 \qquad (1)$$

Where 'P' is the annual precipitation, 'M' is the mean maximum temperature of the hottest month and 'm' is the mean minimum temperature of the coldest month.

5.1.2 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, 1981).

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

$$\text{M.I.} = (Ea/Ep) \text{ equivalent to } (Ea/Eo) = kW = k(P\text{-}R\text{-}D\text{-}Sext) \quad (2)$$

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), 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 $k > 0.75 \times 10^{-2}$; 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 $k < 0.35 \times 10^{-2}$.

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 1). 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.

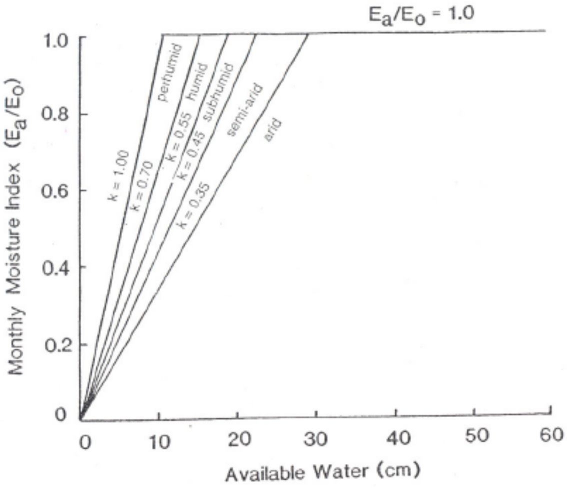

Figure 1. The effect of increasing complexity of foliage profile of evergreen plant communities on the Evaporative Coefficient (k), the slope of the linear relationship between the monthly Moisture Index

(Ea/Eo) and Available Water (Specht 1972a. 1981c, 1981f, Specht & Specht 1999). The Moisture Index asymptotes to 1.0 when monthly Available Water is optimal.

5.1.3 Seasonal shoot growth and *leaf fall*: Seasonal shoot growth is measured monthly on tagged shoots of representative 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.

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

5.1.5 Sclerophyll Index of Loveless (1961):

$$\text{Sclerophyll Index} = (\text{Lignin} + \text{Cellulose}) / \text{Crude Protein} \times 100 \tag{3}$$

5.1.6 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) was recorded using upward sighting tubes; the understorey stratum of low shrubs and ground stratum (< 2m in height) was recorded using downward sighting tubes.

5.1.7 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).

$$N = a \text{ Log}_{10} A + b \tag{4}$$

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 1988). 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 (4).

5.2 Results

5.2.1 Evaporative Coefficients of Chilean Climate Stations

Emberger Pluviothermic Quotient (Q) and Evaporative Coefficient (k) of each Meteorological Station in Chile are listed in Appendix 1 — in a gradient from the cool temperate perhumid climate with deciduous *Nothofagus* forests, to the cool temperate humid climate with evergreen *Nothofagus* and *Cryptocarya* forests to the warm temperate sub-humid climate with sclerophyll forests and matorrals of *Cryptocarya* and *Quillaja*, to the warm temperate arid climate with *Flourensis – Heliotropium* steppe-like matorrals, to almost barren per-arid climate of northern Chile (± *Atriplex atacamensis* and *Acacia caven*).

The Emberger Pluviothermic Quotient (Q) (Emberger 1955) and the Evaporative Coefficient

(k) (Specht 1972) were shown to be closely related (Figure 2a).

5.2.2 Foliage Attributes of the Overstorey Stratum

Although the number of data is small, the measures of sclerophylly of leaves — Leaf Specific Weight (Specht & Rundel 1990) and the Sclerophyll Index (Loveless 1961) — are related (Figure 2b). The sclerophylly of all leaves that are produced on new shoots during the short foliage-growth phenophase is related to the Evaporative Coefficient (k) of the meteorological site (Specht & Specht 2010).

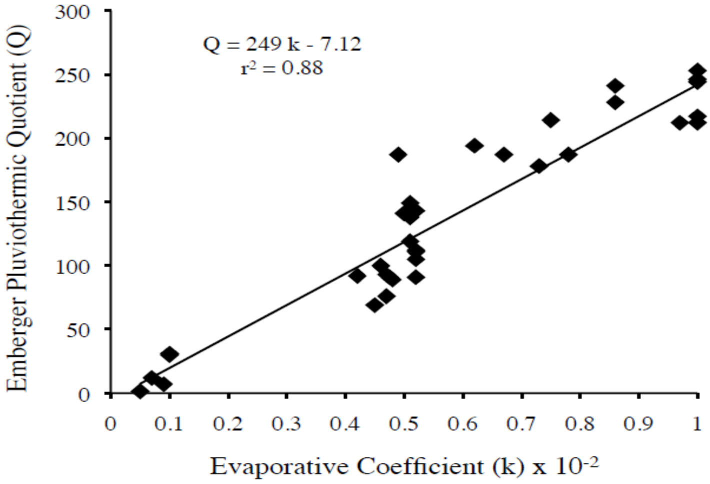

Figure 2a. Statistical relationship of the Emberger Pluviothermic Quotient (Q = 2000 Annual Precipitation / (Mean maximum temperature of hottest month^2 – Mean minimum temperature of coldest month^2) (Emberger 1955) and the Evaporative Coefficient (k), the slope of the linear relationship between the monthly Moisture Index (the ratio of Actual to Potential Evapotranspiration) and Available Soil Water (Specht 1972) — based on Chilean data (Specht 1988).

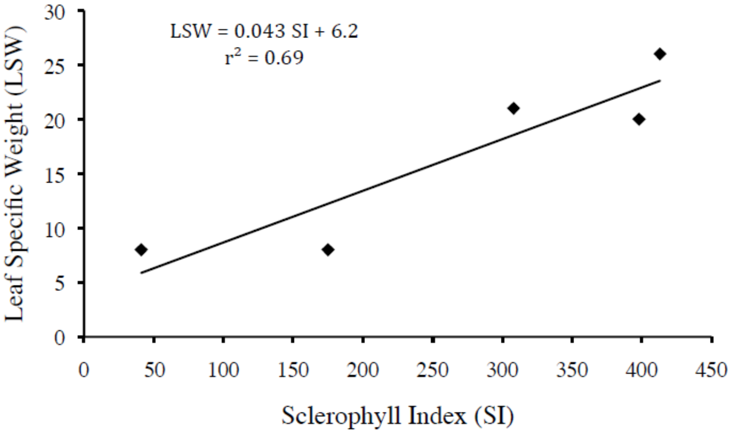

Figure 2b. Statistical relationship of the Leaf Specific Weight (dry weight of the lamina of the leaf per unit area, mg cm^{-2}) (Specht & Rundel 1990) and the Sclerophyll Index (Lignin + Cellulose / Crude Protein x 100) (Loveless 1961) of leaves — based on Chilean data (Specht 1988).

5.2.3 Foliage Projective Covers of Overstorey and Understorey Strata

The effect of evaporative aerodynamics as the atmosphere flows over and through the plant community during the season of foliage shoot growth is shown in Figure 3 where the Foliage Projective Covers of overstorey (FPCo) and overstorey plus understorey strata (FPCo+u) are plotted against the Evaporative Coefficient (k) for meteorological sites in (1) the cool temperate, perhumid *Nothofagus obliqua* forest, (2) the warm temperate, sub-humid matorral of *Quillaja saponaria* with *Lithraea caustica* and (3) the warm temperate, per-arid *Acacia caven* espinal.

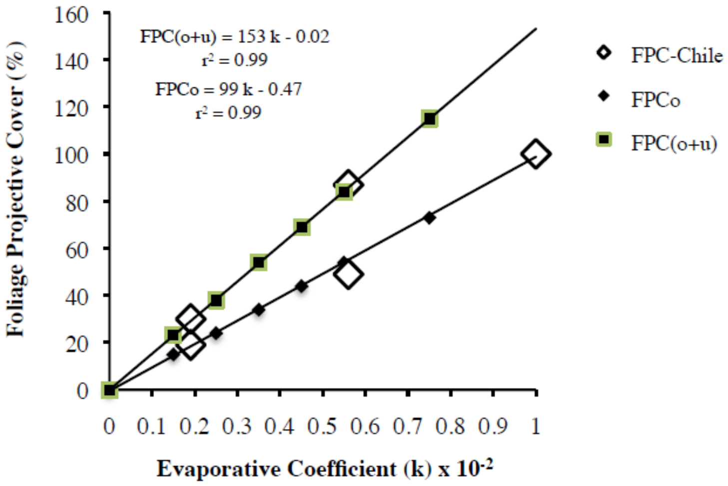

Figure 3. Relationship of the Foliage Projective Covers in overstorey and in (overstorey + understorey) strata of major plant communities in Australia with the Evaporative Coefficient (k), the slope of the linear relationship between the monthly Moisture Index (the ratio of Actual to Potential Evapotranspiration) and Available Soil Water (Specht 1972, 1983)

The Foliage Projective Covers at three Chilean sites are shown:

1. Cool temperate, per-humid *Nothofagus obliqua* closed-forest at Punta Tumbes (36° 37’S, 73° 06’W, 120m) with an Evaporative Coefficient (k) of 1.0 x 10^{-2}.
2. Warm temperate, sub-humid (*Quillaja saponaria* + *Lithraea caustica*) matorral near Santiago (33° 27’S, 70° 42’W, 520m) with an Evaporative Coefficient (k) of 0.56 x 10^{-2}.
3. Warm temperate, per-arid *Acacia caven* (espinal) near Colina (33° 12’S, 70° 40’W, 542m) with an Evaporative Coefficient (k) of 0.19 x 10^{-2}.

As had been demonstrated in Australia, the Foliage Projective Cover (FPC%) and leaf attributes (Leaf Area - cm^2 and Leaf Specific Weight - mg cm^{-2}) of overstorey leaves in each plant community is correlated with the Evaporative Coefficient (k) during the season of shoot growth. Table 1 shows the ranges of these attributes that are recorded in the per-humid, humid, sub-humid, semi-arid and arid zones in the temperate climate of both Australia and Chile. The range of Stand Heights (m) in each of these plant communities, at maturity, is also shown.

Table 1. Foliage Projective Cover (FPC%), foliage attributes (Leaf Area, Leaf Specific Weight) and Stand Height in the overstorey stratum of major plant communities on median-nutrient soils in temperate Australia and Chile — relationship with the Evaporative Coefficient (k)

Climatic Zone	Per-humid	Humid	Sub-humid	Semi-arid	Arid
Evaporative Coefficient (k) x 10^{-2}	1.0-0.75	0.75-0.55	0.55-0.45	0.45-0.35	<0.35
Stand Height (m)	30-(*)-20	20-14	14-111	11-7	<7
FPC (%)	100-65	65-45	45-35	35-25	<25
Leaf Area (cm^2)	20-16	16-10	10-7	7-4	<4
Leaf Specific Weight (mg cm^{--2})	12-16	16-28	28-40	40-50	>50

* Emergent trees

5.2.4 Alpha Biodiversity (species richness, number of species per hectare)

Gloria Montenegro compiled the ecomorphological characters of four plant communities typical of the Mediterranean-climate zone of Central Chile during August 1984 (Montenegro 1988, Tables 29-32). The number of overstorey species increases from one (*Acacia caven*) in the Arid Climatic Zone, to two (*Prosopus chilensis* and *Acacia caven*) in the Semi-Arid Climatic Zone, to four (*Lithraea caustica, Quillaja saponaria, Cryptocarya alba* and *Kageneckia oblonga*) in the Sub-Humid Climatic Zone, to nine (*Nothofagus obliqua, Laurelia sempervirens, Persea lingue, Aextoxicon punctatum, Myrceugenia apiculata, M. planiceps, Chusquea quila, Gevuina avellana* and *Lomatia dentata*) in the Per-Humid Climatic Zone.

The species richness of these overstoreys is correlated with the Evaporative Coefficients of these climatic zones (Figure 4).

Species richness of the overstorey in perhumid climates declines from about nine trees per hectare in the sclerophyllous evergreen forest to four or five per hectare in the deciduous *Nothofagus* forests (see the section on ‘Major Plant Communities in Chile’ above). As mean annual solar radiation declines with latitude, the foliage shoot growth produced annually declines, thus resulting in lower species richness of the overstorey (Specht & Specht 1999, Figures 17.2 and 17.5). At even higher latitudes in the Austral Region of Chile, overstorey trees no longer survive thus leaving only the understorey wet-heathland species, *Sphagnum* moss and other cryptogams (Moore 1979).

The species richness of both plants and resident vertebrates (small mammals, birds, amphibia, lizards, snakes) in an ecosystem is determined by the annual fixation of solar energy by the Foliage Projective Cover of the overstorey (Braithwaite *et al.* 1985; Specht 1988, 1994, 2012; Specht & Specht 1999; Specht & Tyler 2010).

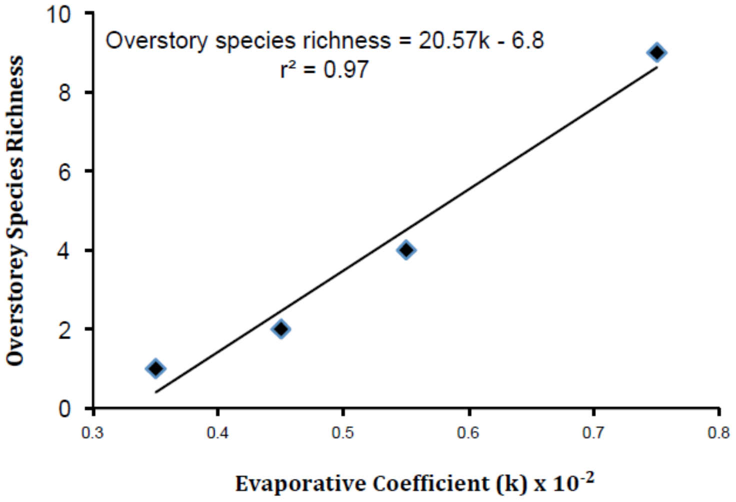

Figure 4. Species richness (number of species) in the overstorey of Chilean plant communities in the Arid, Semi-arid, Sub-humid and Per-humid Climatic Zones (after Montenegro 1988, Tables 29-32)

6. Discussion

The structure, growth and biodiversity of Chilean vegetation are explored from the arid north, through the Mediterranean-climate zone of Central Chile to the evergreen and semi-deciduous *Nothofagus* vegetation in the south and into the treeless wet-heath vegetation of the Magellanic islands. The northern Desert Zone has four to six genera of plants that have been recorded in Australia, while the southern vegetation reveals many relationships with the cool temperate vegetation of Australia with which Chile was conjoined in the Gondwanan assembly during the Late Mesozoic.

The structures of plant communities — Foliage Projective Covers and leaf attributes, Leaf Areas and Leaf Specific Weights — in the climatic gradient from the arid to humid zones in the temperate climate of Chile are similar to those in the temperate south of Australia. As the species richness (number of species per hectare) is related to the solar energy that is fixed annually by the leaves in the overstorey (the Leaf Area Index, area of all leaves per hectare) is also similar, similar values are shown in Chile and Australia.

Although the majority of genera in the plant communities of Chile are different from those in Australia, the structure and alpha biodiversity (species richness) are very similar.

References

Acosta, M. C., Mathiasen, P., & Premoli, A. C. (2014). Retracing the evolutionary history of *Nothofagus* in its geo-climatic context: new developments in the emerging field of phylogeology. *Geobiology, 12*, 497-510.

APG II (Angiosperm Phylogeny Group). (2003). An ordinal classification for the families of flowering plants. *Botanical Journal of the Linnean Society, 141*, 399-436.

Arianoutsou, M., & Groves, R. H. (Eds) (1994). *Plant-Animal Interactions in Mediterranean-Type Ecosystems*. Tasks in Vegetation Science, No. 31. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Avila, G., Aljaro, M. E., Araya, S., Montenegro, G., & Kummerow, J. (1975) The seasonal cambium activity of Chilean and Californian shrubs. *American Journal of Botany, 62*, 473-478.

Bowman, V. B., Francis, J. E., Askin, R. A., Riding, J. R., & Swindles, G. T. (2014). Latest Cretaceous – earliest Paleogene vegetation and climate change at the high southern latitudes: palynological evidence from Seymour Island, Antarctic Peninsula. *Palaeogeography, Palaeoclimatology, Palaeoecology, 408*, 26-47.

Braithwaite, R. W., Winter, J. W., Taylor, J. A., & Parker, B. S. (1985). Patterns of diversity and structure of mammalian assemblages in the Australian tropics. *Australian Mammalogist, 8*, 171-186.

Carpenter, R. J., Wilf, P., Conran, J. G., & Cúneo, N. R. (2014). A Paleogene trans-Antarctic distribution for *Ripogonum* (Riponogonaceae: Liliales)? *Palaeontologia Electronica*, *17*(3), 39A*; 9p*.

Conrad, C. E., & Oechel, W. C. (Eds) (1982). *Dynamics and Management of Mediterranean-Type Ecosystems*. Pacific Southwest Forest and Range Experimental Station, Berkeley, Calif., USA.

Dell, B., Hopkins, A. J. M., & Lamont, B. B. (Eds) (1986). *Resilience in Mediterranean-Type Ecosystems*. Tasks for Vegetation Science, No. 16. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Dettmann, M. E. (1990). Antarctica: Cretaceous cradle of austral temperate rain forests? *Geological Society of London Special Publication*, *47*, 89-105.

Dettmann, M. E. (1992). Structure and floristics of Cretaceous vegetation of southern Gondwana: implications for angiosperm biogeography. *Palaeobotanist, 41*, 224-233.

Di Castri, F., & Hajek, E. R. (1976) *Bioclimatologia de Chile*. Vicerrectoria Academica, Universidad Católica de Chile, Santiago, Chile. (129 pp.)

Di Castri, F., & Mooney, H. A. (Eds) *Mediterranean Type Ecosystems. Origin and Structure*. Springer-Verlag, Berlin, Germany.

Emberger, L. (1955). Une classification biogéographique des climats. *Rev. Trav. Lab. Bot. Fac. Sci., Montpellier, 7*, 3-43.

Frakes, L. A. (1979). *Climates throughout Geologic Time*. Elsevier, Amsterdam, The Netherlands, 310 pp.

Gajardo, R. (1994). *La Vegetación Natural de Chile. Clasificación y Distribución Geográfica*. Editorial Universitaria, Santiago, Chile, 165 pp.

Gandolfo, M. A., Hermsen, E. J., Zamaloa, M. C., Nixon, K. C., González, C. C., Wilf, P., Cúneo, & Johnson, K. (2011). Oldest known *Eucalyptus* macrofossils are from South America. *PLoS ONE, 6*(6), e21084.

Goodall, D. W. (General Editor) (1975-2005). *Ecosystems of the World*. Vols 1-30. Elsevier, Amsterdam, The Netherlands.

Hajek, E. R. (1988) Clmate data for Chile. In: *Mediterranean-type Ecosystems. A Data Source Book*. (Ed. R. L. Specht), pp. 115-116. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Hajek, E. R., & di Castri, F. (1975) *Bioclimatografia de Chile*. Dirección de Investigacion, Universidad Católica de Chile, Santiago, Chile. (225 pp.)

Hajek, E. R., & Gajardo, R. (1988) Climate stations in Chile. In: *Mediterranean-type Ecosystems. A Data Source Book*. (Ed. R. L. Specht) pp. 113-114. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Hajek, E. R., Specht, R. L., & Hutley, L. B. (1988) Climate data for Chile – Growth Indices. In: *Mediterranean-type Ecosystems. A Data Source Book*. (Ed. R. L. Specht) p. 116. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Hallam, A. (1984). Distribution of fossil marine invertebrates in relation to climate. Pp. 107-125. In: *Fossils and Climate*. (Ed. P. J. Brenchley), Wiley, Chichester and New York, N.Y.

Heddle, E. M., & Specht, R. L. (1975). Dark Island heath (Ninety-Mile Plain, South Australia). 8. The effect of fertilizers on composition and growth, 1950-1972. *Australian Journal of Botany, 23*, 151-164.

Herbert, D. A. (1935) The relationships of the Queensland flora. *Proceedings of the Royal Society of Queensland, 39*, 115-118.

Hooker, J.D. (1847). *The botany of the Antarctic voyage of the H.M. discovery ships Erebus and Terror in the years 1839-1843, 1, Flora Antarctica*. Reeve Bros, London. Reprinted 1963, J. Cramer, Weinheim.

Hopkins, B. (1955). The species-area relations of plant communities. *Journal of Ecology, 43*, 409-426.

Jaccard, P. (1928). Die statistische-floristische Methode als Grundlage der Pflanzensoziologie. *Handb. Biol. Arbeitsmeth. Abderhalden* XI, **5**, 165-202.

Jeffrey, D. W. (1964). The formation of polyphosphate in *Banksia ornata*, an Australian heath plant. *Australian Journal of Biological Sc*ience, *17*, 845-854.

Jeffrey, D. W. (1967). Phosphate nutrition of Australian heath plants. 1. The importance of proteoid roots in *Banksia* (Proteaceae). *Australian Journal of Botany, 15*, 403-412.

Jeffrey, D. W. (1968). Phosphate nutrition of Australian heath plants. II. The formation of polyphosphate by five heath species. *Australian Journal of Botany, 16*, 603-613.

Kooyman, R. M., Wilf, P., Barreda, V. D., Carpenter, R. J., Jordan, G. J., Sniderman, J. M. K., Allen, A., Brodribb, T. J., Crayn, D., Shield, T. S., Laffan, S. W., Lusk, C. H., Rossetto, M., & Weston, P. H. (2014). Paleo-Antarctic rainforest into the modern Old World tropics: the rich past and threatened future of the "southern wet forest survivors". *American Journal of Botany, 101*(12), 1-15.

Kruger, F. J., Mitchell, D. T., & Jarvis, J. U. M. (Eds) (1983). *Mediterranean-Type Ecosystems. The Role of Nutrients.* Springer-Verlag, Berlin, Germany.

Kummerow, J., Avila, G., Aljaro, M. E., Araya, S., & Montenegro, G. (1982). Effect of fertilizer on fine root density and shoot growth in the Chilean matorral. *Botanical Gazette, 143*, 498-504.

Kummerow, J., Montenegro, G., & Krause, D. (1981) Biomass, phenology and growth. In: *Resource Use by Chaparral and Matorral. A Comparison of Vegetation Function in Two Mediterranean Type Ecosystems*. (Ed. P. C. Miller) Springer-Verlag, New York.

Lisker, F., & Läufer, A.L. (2013). The Mesozoic Victoria Basin: vanished link between Antarctica and Australia. *Geology, 41*, 1043-1046.

Long, G., & Pons, A. (Eds) (1982). *Bioclimatologie Méditerraneenne*. Vol. 131. Bulletin de la Société Botanique de France, Paris, France.

Loveless, A. R. (1961). A nutritional interpretation of sclerophylly based on differences in the chemical composition of sclerophyllous and mesophyllous leaves. *Annals of Botany, 25*, 168-184.

Montenegro, G. (1984) *Atlas de Anatomia de Especies Vegetales Autóctonas de la Zona Central*. Ediciones Universidad Católica de Chile, Santiago, Chile.

Montenegro, G. (1988). Ecomorphological characters: Chile. In: *Mediterranean-type Ecosystems. A Data Source Book.* (Ed. R. L. Specht) pp. 42-45. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Montenegro, G. (1994). *Landscape Degradation in Mediterranean-Type Ecosystems*. Proceedings of the Seventh International Conference on Mediterranean Ecosystems. *Noticiero de Biologia, 2*(3).

Montenegro, G., & Teillier, S. (1988) Species richness of plant communities in the Mediterranean-climate region of Chile. In: *Mediterranean-type Ecosystems. A Data Source Book*. (Ed. R. L. Specht) p. 87. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Montenegro, G., Gatti, R., & Riveros, F. (1976). Modificaciones foliares en *Acacia caven* (Mol.) Hook. et Arn. por efecto de la contaminación ambiental. *Medio Ambiente, 2*, 29-34.

Montenegro, G., Rivera, O., & Bas, F. (1978). Herbaceous vegetation in the Chilean matorral: Dynamics of growth and evaluation of allelopathic effects of some dominant shrubs. *Oecologia, 36*, 237-244.

Montenegro, G., Aljaro, M. E., & Kummerow, J. (1979). Growth dynamics of Chilean matorral shrubs. *Botanical Gazette, 140*, 114-119.

Montenegro, G., Araya, S., Aljaro, M. E., & Avila, G. (1982). Seasonal fluctuations of vegetative growth in roots and shoots of central Chile shrubs. *Oecologia, 53*, 235-237.

Montenegro, G., Avila, G., & Schatte, P. (1983). Presence and development of lignotuber in shrubs of the Chilean matorral. *Canadian Journal of Botany, 61*, 1804-1808.

Mooney, H. A., & Conrad, C. E. (Eds) (1977). *Proceedings of the symposium on the environmental consequences of fire and fuel management in Mediterranean ecosystems.* USDA Forest Service General Technical Report WO-3, USDA, Washington, DC, USA.

Mooney, H. A., & Kummerow, J. (1971). The comparative water economy of representative evergreen sclerophyll and drought deciduous shrubs of Chile. *Botanical Gazette, 132***,** 245-252.

Moore, D. M. (1978). Southern oceanic wet-heathlands (including Magellanic moorland). In: *Ecosystems of the World, 9A. Heathlands and Related Shrublands. Descriptive Studies*. (Ed. R. L. Specht) pp. 489-497. Elsevier, Amsterdam, The Netherlands.

Orshan, G., Montenegro, G., Avila, G., Walckowiak, A., & Mujica, A. M. (1985) Plant growth forms of Chilean matorral. A monocharacter growth form analysis along an altitudinal transect from sea level to 2000 m. a. s. l. *Bulletin Soc. Bot. Fr., 131, Act. Bot. 1984*, 411-425.

Rauh, W. (1985). The Peruvian-Chilean Deserts. In*: Ecosystems of the World*. Vol. 12A. (Eds. M. Evanari, I. Noy-Meir & D. W. Goodall) pp. 239-267. Elsevier, Amsterdam, The Netherlands.

Roy, J., Aronson, J., & Di Castri, F. (Eds) (1995). *Times Scales of Biological Responses to Water Constraints. The Case of Mediterranean Biota*. SPB Academic Publishing, Amsterdam, The Netherlands.

Rundel, P. W. (1981) The matorral zone of central Chile. In: *Ecosystems of the World*, 11. *Mediterranean-type Shrublands*. (Eds F. di Castri, D. W. Goodall & R. L. Specht) pp. 175-201. Elsevier, Amsterdam, The Netherlands.

Rundel, P. W. (1988). Leaf structure and nutrition in mediterranean-climate sclerophylls. In: *Mediterranean-type Ecosystems. A Data Source Book*. (Ed. R. L. Specht) pp. 157-167. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Sanmartin, I., & Ronquist, F. (2004). Southern Hemisphere biogeography inferred by event-based models: plant versus animal patterns. *Systematic Biology, 53*, 216-243.

Sauquet, H., Ho, S. Y. W., Gandolfo, M. A., Jordan, G. J., Wilf, P., Weston, P. H., Anderson, C. L., Barker, N. P., Cantrill, D. J., Bayly, M. J., Broham, L., Brown, G. K., Carpenter, R. J., Lee, D. M., Murphy, D. J., Sniderman, J. M. K., & Udovicic, F. (2012). Testing the impact of calibration on molecular divergence times using a fossil-rich group: the case of *Nothofagus* (Fagales). *Systematic Biology, 61*,289-313.

Schmaltz, J. (1991) Deciduous forests of southern South America. In: *Ecosystems of the World, 7. Temperate Deciduous Forests*. (Eds E. Röhrig & B. Ulrich) pp. 557-578. Elsevier, Amsterdam, The Netherlands.

Specht, R. L. (1957a). Dark Island heath (Ninety-Mile Plain, South Australia). 4. Soil moisture patterns produced by rainfall interception and stem-flow. *Australian Journal of Botany, 5*, 137-150.

Specht, R. L. (1957b). Dark Island heath (Ninety-Mile Plain, South Australia). 5. The water relationships in heath vegetation and pastures on the Makin Sand. *Australian Journal of Botany, 5*, 151-172.

Specht, R. L. (1963). Dark Island heath (Ninety-Mile Plain, South Australia), 7. The effect of fertilizers on composition and growth, 1950-60. *Australian Journal of Botany, 11*, 67-94.

Specht, R. L. (1973). Structure and functional response of ecosystems in the Mediterranean climate of Australia. In: *Mediterranean Type Ecosystems. Origin and Structure*. (Eds F. di Castri & H. A. Mooney). pp. 113-120. Springer-Verlag, Berlin, Germany.

Specht, R. L. (1981). Growth indices - Their rôle in understanding the growth, structure and distribution of Australian vegetation. *Oecologia, Berlin, 50*, 347-356.

Specht, R. L. (1983). Foliage projective covers of overstorey and understorey strata of mature vegetation in Australia. *Australian Journal of Ecology, 8*, 433-439.

Specht, R. L. (1988). Climatic control of ecomorphological characters and species richness in mediterranean ecosystems of Australia. In: *Mediterranean-type Ecosystems. A Data Source Book*. (Ed. R. L. Specht) Pp. 149-155. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Specht, R. L. (1994). Species richness of vascular plants and vertebrates in relation to canopy productivity. In: *Plant-Animal Interactions in Mediterranean-Type Ecosystems*. (Eds M. Arianoutsou & R. H. Groves). Pp. 15-24. Cambridge University Press, Cambridge, England.

Specht, R. L. (2011). Development of ecosystem research. *International Scholarly Research Network (ISRN) Ecology,* 2011, ID 897578, 20. http://dx.doi.org/10.5402/2011/897578

Specht, R. L. (2012). Biodiversity of terrestrial ecosystems in tropical to temperate Australia. *International Journal of Ecology, 2012,* ID 359892, 15. http://dx.doi.org/10.1155/2012/35982

Specht, R. L. (2014). Management of biodiversity in Australia. *Macrothink Journal of Environment and Ecology, 5*(2), 186-205.

Specht, R. L., & Cleland, J. B. (1961). Flora conservation in South Australia. 1. The preservation of plant formations and associations recorded in South Australia. *Transactions of the Royal Society of South Australia, 85*, 177-196.

Specht, R. L., & Cleland, J. B. (1963). Flora conservation in South Australia. 2. The preservation of species recorded in South Australia. *Transactions of the Royal Society of South Australia, 87*, 63-92.

Specht, R. L., & Groves, R. H. (1966). A comparison of the phosphorus nutrition of Australian heath plants and introduced economic plants. *Australian Journal of Botany, 14*, 201-221.

Specht, R. L., & Moll, E. J. (2014). Structure and alpha biodiversity of major plant communities in South Africa, a close biogeographical relation with Australia. *Macrothink Journal of Environment and Ecology, 5*(2), 48-88.

Specht, R. L., & Morgan, D. G. (1981). The balance between the foliage projective covers of overstorey and understorey strata in Australian vegetation. *Australian Journal of Ecology, 6*, 193-202.

Specht, R. L., & Rundel, P. W. (1990). Sclerophylly and foliar nutrient status of mediterranean-climate plant communities in southern Australia. *Australian Journal of Botany, 38*, 459-474.

Specht, R. L., & Specht, A. (1989a). Canopy structure in *Eucalyptus* -dominated communities in Australia along climatic gradients. *Acta Oecologia, Oecologia Plantarum, 10*, 191-213.

Specht, R. L., & Specht, A. (1989b). Species richness of overstorey strata in Australian plant communities. The influence of overstorey growth rates. *Australian Journal of Botany, 37*, 321-336.

Specht, R. L., & Specht, A. (1989c). Species richness of sclerophyll (heathy) plant communities in Australia. The influence of overstorey cover. *Australian Journal of Botany, 37*, 337-350.

Specht, R. L., & Specht, A. (1999 Hardback; 2002 Paperback). *Australian Plant Communities. Dynamics of Structure, Growth and Biodiversity.* Oxford University Press, Melbourne, 492 pp.

Specht, R. L., & Specht, A. (2010). The ratio of foliar nitrogen to foliar phosphorus — A determinant of leaf attributes and height in life-forms of subtropical and tropical plant communities. *Australian Journal of Botany, 58*, 527-538.

Specht, R. L., & Tyler, M. J. (2010). The species richness of vascular plants and amphibia in major plant communities in temperate to tropical Australia: Relationship with annual biomass production. *International Journal of Ecology*, 17. http://dx.doi.org/10.1155/2010/635852

Specht, R. L., & Yates, D. J. (1990). Climatic control of structure and phenology of foliage shoots in dicotyledonous overstorey and understorey strata of subtropical plant communities in eastern Australia. *Acta Oecologia, Oecologia Plantarum, 11*, 215-233.

Specht, R. L., Rayson, P., & Jackman, M. E. (1958). Dark Island heath (Ninety-Mile Plain, South Australia). 6. Pyric succession: Changes in composition, coverage, dry weight, and mineral nutrient status. *Australian Journal of Botany, 6*, 59-88.

Specht, R. L., Roe, E. M. & Boughton, V. H. (Eds) (1974). *Conservation of Major Plant Communities in Australia and Papua New Guinea.* Australian Journal of Botany Supplement

No. 7, 667 pp.

Specht, R. L., Grundy, R. I., & Specht, A. (+ Ruhama Berliner) (1990). Species richness of plant communities — relationship with community growth and structure. *Israel Journal of Botany, 39,* 465-480.

Specht, R. L., Yates, D. J., Sommerville, J. E. M., & Moll, E. J. (1991). Foliage structure and shoot growth in heathlands in the mediterranean-type climate of southern Australia and South Africa. *Ecologia Mediterranea, 16,* 195-207.

Specht, R. L., Dettmann, M. E., & Jarzen, D. M. (1992). Community associations and structure in the Late Cretaceous vegetation of southeast Australia and Australasia. *Palaeogeography, Palaeoclimatology, Palaeoecology, 94*, 283-309.

Specht, R. L., Specht, A., Whelan, M. B. & Hegarty, E. E. (1995). *Conservation Atlas of Plant Communities in Australia.* Centre for Coastal Management, Southern Cross University, Lismore, N.S.W., Australia, 1073 pp.

Tenhunen, J. D., Catarino, F. M., Lange, O. L. & Oechel, W. C. (Eds) (1987). *Plant Response to Stress. Functional Analysis in Mediterranean Ecosystems.* Springer-Verlag, Berlin, Germany.

Veblen, T. T., Schlegel, F. M., & Oltremari, J. V. (1983). Temperate broad-leaved evergreen forests of South America. In: *Ecosystems of the World.* Vol. 10. *Temperate Broad-leaved Evergreen Forests*. (Ed. J. D. Ovington). pp. 5-31. Elsevier, Amsterdam, The Netherlands.

Weston, P. H., & Hill, R. S. (2013). Southern (Austral) Ecosystems. *Encylopedia of Biodiversity, 6,* 612-619.

Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon 21*, 213-251.

Wilf, P., Cúneo, Escapa, I. G., Pol, D., & Woodburne, M. O. (2013). Splendid and seldom isolated: the paleobiogeography of Patagonia. *Annual Review of Earth and Planetary Sciences, 41*, 561-603.

Woodell, G. M. (Ed.) (1990). *The Earth in Transition. Patterns and Processes of Biotic Impoverishment*. Cambridge University Press, New York, NY, USA.

Appendix 1. Chilean climate stations, vegetation types, Emberger Pluviothermic Quotient (Q), Evaporative Coefficients (k) and Smax (maximum soil moisture storage in the wettest month of the year)

(Hajek & di Castri 1975; Di Castri & Hajek 1976; Hajek 1988; Hajek *et al.* 1988)

Climate Station	Vegetation type	Emberger Quotient (Q)	Evaporative Coefficient ($k \times 10^{-2}$)	Smax (mm)
Cool Temperate – Perhumid	**Region of deciduous forests**			
Concepción	*Nothofagus obliqua* +	228	0.86	300+

(36° 50’S, 73° 02’W, 15m)	*Persea lingue*			
Contulmo (38° 02’S, 73° 13’W, 30m)	(?)	(?)	1.00	300+
Coyhaique (45° 29’S, 71° 33’W, 140m)	*Nothofagus pumilo*	217	1.00	300+
Cullinco (38° 22’S, 72° 15’W, 377m)	*Nothofagus obliqua* + *Laurelia sempervirens*	241	0.86	300+
Lonquimay (38° 26’S, 71° 15’W, 900m)	*Nothofagus obliqua*	244	1.00	300+
Osorno (40° 35’S, 73° 09’W, 24m)	*Nothofagus obliqua* + *Laurelia sempervirens*	214	0.75	300+
Punta Carranza (35° 36’S, 72° 38’W, 30m)	*Nothofagus glauca*	253	1.00	300+
Punta Tumbes (36° 37’S, 73° 06’W, 120m)	*Nothofagus obliqua*	246	1.00	300+
Rio Bueno (40° 19’S, 72° 55’W, 58m)	*Nothofagus obliqua* + *Laurelia sempervirens*	212	1.00	300+
Temuco (38° 45’S, 72° 35’W, 114m)	*Nothofagus obliqua* + *Laurelia sempervirens*	217	1.00	300+
Cool Temperate - Humid	**Region of deciduous & sclerophyll forests**			
Angol (El Verg) (37° 49’S, 72° 39’W, 77m)	*Nothofagus obliqua* + *Cryptocarya alba*	143	0.52	300+
Balmaceda (45° 54’S, 71° 43’W, 520m)	*Festuca pallescens* + *Mulinum spinosum*	89	0.48	300+
Chillán (36° 36’S, 72° 02’W, 118m)	*Cryptocarya alba*	141	0.50	300+
Constitución (35° 20’S, 72° 56’W, 7m)	*Nothofagus glauca*	178	0.73	300+
Lineares (35° 51’S, 71° 36’W, 157m)	*Cryptocarya alba*	138	0.51	300+
Los Angeles (37° 28’S, 72° 21’W, 130m)	*Nothofagus obliqua* + *Cryptocarya alba*	187	0.49	300+
Molina (35° 05’S, 71° 16’W, 235m)	*Cryptocarya alba* + *Quillaja saponaria*	119	0.51	300+
Panimávida (35° 46’S, 71° 24’W, 197m)	*Cryptocarya alba* + *Quillaja saponaria*	149	0.51	300+
Punta Lavapié (37° 08’S, 73° 35’W, 46m)	*Nothofagus obliqua*	212	0.97	300+
Rio Cisnes (44° 45’S, 72° 00’W, 700m)	*Nothofagus pumilio*	105	0.52	300+

Sewell (El Teniente) (34^{o} 06'S, 70^{o} 22'W, 2134m)	*Shuquiraga oppositifolia*	187	0.67	300+
Traiguén (38^{o} 15'S, 72^{o} 40'W, 170m)	*Nothofagus obliqua* + *Cryptocarya alba*	187	0.78	300+
Victoria (38^{o} 13'S, 72^{o} 21'W, 360m)	*Nothofagus obliqua*	194	0.62	300+
Warm Temperate - Sub-humid	**Region of sclerophyll forests & matorrals**			
Cauquenes (35^{o} 59'S, 72^{o} 22'W, 177m)	*Acacia caven* + *Maytenus boaria*	92	0.42	300+
Curicó (34^{o} 58'S, 72 13'W, 225m)	*Cryptocarya alba* + *Peumus boldus*	93	0.47	300+
Rancagua (34 10'S, 70^{o} 45'W, 500m)	*Quillaja saponaria*	76	0.47	287
Rengo (34^{o} 24'S, 70^{o} 52'W, 139m)	*Cryptocarya alba* + *Peumus boldus*	76	0.47	280
San Fernando (34^{o} 35'S, 71^{o} 00'W, 342m)	*Cryptocarya alba* + *Peumus boldus*	112	0.52	300+
Santiago (33^{o} 27'S, 70^{o} 42'W, 520m)	*Quillaja saponaria* + *Lithraea caustica*	100	0.56	155
Talca (35^{o} 26'S, 71^{o} 40'W, 97m)	*Quillaja saponaria*	91	0.52	300+
Valparaiso (33^{o} 01'S, 71^{o} 38'W, 41m)	*Cryptocarya alba* + *Peumus boldus*	111	0.52	224
Warm Temperate - Semi-arid	**Region of matorrals & sclerophyll forests**			
Los Andes (32^{o} 50'S, 70^{o} 37'W, 616m)	(?)	(?)	0.48	100
Quillota (32^{o} 53'S, 71^{o} 16'W, 128m)	*Cryptocarya alba* + *Peumus boldus*	69	0.45	118
Warm Temperate - Arid	**Region of steppe-like matorrals**			
La Serena (29^{o} 54'S, 71^{o} 15'W, 32m)	*Flourensis thurifera* + *Heliotropium stenophyllum*	30	0.10	30
Punta Tortúga (29^{o} 55'S, 71^{o} 22'W, 25m)	*Flourensis thurifera* + *Heliotropium stenophyllum*	31	0.10	27

Warm Temperate - Per-arid	**Desert region**			
Antofagasta (23° 42’S, 70° 24’W, 94m)	(?)	(?)	0.08	2
Caldera (27° 03’S, 70° 58’W, 28m)	*Skytanthus acutus*	7	0.09	8
Potrerillos (26° 30’S, 69° 27’W, 2850m)	*Atriplex atacamensis*	12	0.07	5
Refresco (25° 19’S, 69° 52’W, 1850m)	Absolute desert	1.4	0.05	2

Copyright Disclaimer