

Comparative ecology of temperate rainforests of the Americas along analogous climatic gradients

Ecología comparativa de los bosques lluviosos templados de Norte y Sudamérica a lo largo de gradientes climáticos análogos

PAUL B. ALABACK

U.S. Forest Service, Pacific Northwest Research Station
Post Office Box 20909, Juneau, AK 99802 USA. (Fax: 907-586-7848)

ABSTRACT

A definition for temperate rainforest and its applications to world forest type distribution is presented. Southern Chile and the Pacific coast of North America are the largest expanses of temperate rainforest. Although both regions have important similarities in climate, dramatic differences in the species composition of flora and fauna are evident. Analogous forest types occur at similar levels of summer rainfall in both zones. In Chile sea-level glaciers and associated subantarctic vegetation types begin at 10-15 degrees lower latitude than in North America. Biomass accumulations achieve world record status in coniferous forest types in both regions, although conifer forest types are rare in Chile. Structure and composition of forests in both zones reflect chronic disturbance by wind and rain, and periodic catastrophic disturbance by intense storms, landslides, or vulcanism. Ecological analogs exist for many common plant species.

Detailed comparative studies are needed between the principal rainforest regions of the world to more clearly identify how biogeographical, climatic and historical factors have influenced evolution of forest structure and function. The prospect of global climatic change also underscores the need for comparative data on ecosystem processes along analogous climatic gradients, especially at high latitudes where the most pronounced changes are expected to occur.

Key words: Temperate rainforests, climate, biogeography, plant ecology, Alaska, *Nothofagus*, *Picea*.

RESUMEN

Se presenta una definición de bosque lluvioso templado y su aplicación a la distribución geográfica mundial de bosques. El sur de Chile y la costa noroeste de Norteamérica tienen las áreas de bosques lluviosos templados más grandes en todo el mundo. Ambas regiones son semejantes en clima, pero son muy diferentes en cuanto a la composición de especies de plantas y animales. En ambas regiones los tipos de bosques análogos están en lugares que reciben la misma cantidad de lluvias durante el verano. En Chile, los glaciares adyacentes al mar, y la mayoría de los tipos de bosques análogos comienzan 10-15 grados de latitud antes que en Norteamérica. La acumulación de biomasa más alta de todo el mundo ocurre en bosques de coníferas de ambas regiones, aunque los bosques de coníferas son escasos en Chile. La estructura y composición de los bosques de ambas regiones son una función de perturbaciones frecuentes causadas por vientos y lluvias y de perturbaciones más raras causadas por tempestades fuertes, derrumbes, avalanchas, o vulcanismo. Existen análogos ecológicos para muchas especies de plantas en ambas regiones.

Estudios comparativos de bosques lluviosos del mundo son necesarios para entender cómo la biogeografía, el clima y la historia han influido la evolución del funcionamiento y estructura de estos bosques. La posibilidad de cambios en el clima en un futuro próximo también subraya la necesidad de obtener datos comparativos sobre los procesos de ecosistemas a lo largo de gradientes análogos de clima, sobre todo a altas latitudes, en donde se producirían los cambios más significativos de clima y de función ecológica.

Palabras claves: Bosques lluviosos, clima, biogeografía, *Nothofagus*, *Picea*, ecología, Alaska.

INTRODUCTION

The term temperate rainforest has been applied to a broad range of forest types in both popular and scientific publications. These forests have been the focus of intense public debate on both conservation

and management throughout their geographic range. They include some of the longest-lived and massive tree species as well as the largest remaining virgin landscapes outside of the tropics (Franklin & Warring 1980, Veblen *et al.* 1976). They also occur at high latitudes where their sensitivity to and history of rapid climatic change make them ideal subjects for monitoring global climatic change.

Many critical scientific questions relating to landscape level processes may be best studied in temperate rainforests since their fauna and landscapes are more intact than in most other ecosystem types. Important decisions on conservation and management options for these pristine ecosystems will also require that we understand in much greater detail how temperate rainforests respond to both logging and climatic perturbations.

Research emphasis has been much different in temperate rainforests of the northern and southern hemispheres. In the northern hemisphere much attention has been paid to the relation of structure to function and of the unique attributes of "old-growth" forests (Alaback & Juday 1989, Franklin *et al.* 1981, Graham & Cromack 1982, McKee *et al.* 1982, Spies *et al.* 1988, Spies & Franklin 1988, Waring & Franklin 1979). Succession research has focused on post-logging, fire and wind caused disturbances (e.g. Alaback 1982, Cline *et al.* 1980, Halpern 1989, Harcombe 1986, Kellman 1969) although some work has been done on revegetation following mass movements and vulcanism (Dale 1989, Miles & Swanson 1986, Smith & Commandeur 1986) and fluvial dynamics (Fonda 1974, McKee *et al.* 1982). Much of the classic work on post-glacial succession was conducted in the northern temperate rainforest zone of Southeast Alaska (Cooper 1937, Crocker & Major 1955, Reiners *et al.* 1971).

In southern Chile research has focused on gap dynamics of old-growth forests and succession following mass movement events (e.g. Armesto & Figueroa 1987, Veblen 1989, Veblen *et al.* 1981). Little work has been done on post-glacial succession, and on the relation of forest structure to function (Kunkel 1955, Veblen 1982, Weinberger 1974, Young 1972).

Although many sites spread throughout the temperate zone are commonly referred to as temperate rainforests there have been few attempts to compare the ecological characteristics of these widely scattered forests. Most comparisons have been made of temperate rainforests with climatically disparate environments, or of forests with

a common vegetational history. A close examination of sites with a temperate rainforest climate located at the far corners of the earth where vegetation evolved more or less independently might provide some unique insights as to how climate influences forest evolution and function. Consideration of the disturbance regimes and functional characteristics of these disparate forest types are also needed to determine what adaptations to the rainforest environment are shared between these floristically distinct locales. In particulari would like to ask the question how do the two largest temperate rainforests regions in the world compare; and to what degree do historical factors influence present day ecosystem functioning, as we understand them, and what are the research opportunities for comparative studies in this forest zone?

A definition for temperate rainforest

The term temperate rainforest is not new to ecology, but has been applied to a range of vegetative types throughout the world (Alaback & Juday 1989, de Laubenfels 1975, Köppen 1918, Kuchler 1949, Veblen *et al.* 1983, Webb 1978). One of the most distinctive features of rainforest climate is cool summers and wet weather year around. An ecological consequence of this unique climate is frequent disturbance by wind, and the lack of fire as an important factor in forest dynamics. In the southern hemisphere lightning caused fires appear to be rare events (Veblen *et al.* 1983, Wardle *et al.* 1983). Throughout the northern hemisphere fire plays a key role, either as a infrequent catastrophic event in humid regions, or as a chronic event in drier climates. Only in the coastal rainforest is fire of minor importance (Harris & Farr 1974).

Rainforests are difficult to distinguish floristically or physiognomically from related forest types (Cockayne 1971, de Laubenfels 1975, Webb 1968, 1978). The upper canopy is often composed of a large number of species with few in a position of dominance, and trees form clumped patterns reflecting gap-phase disturbance

regimes (Armesto *et al.* 1986). Epiphytes are often associated with rainforests, but they also frequent timberline and arctic environments with a high frequency of fog.

De Laubenfels (1975) has proposed presence of a dense and continuous understory layer and the absence of annual herbaceous plants as key factors distinguishing rainforests from seasonal forests. Understory plants in many mesophytic temperate forests, however, are light limited so that their relative abundance may reflect more the structure and disturbance history of the upper canopy than regional climate (e.g. Alaback 1982). Understory density does not work well in distinguishing seasonal and rainforest types in Pacific Northwest temperate forests. In Chilean rainforests understory density varies dramatically with climate largely because of the requirements of the bamboo (*Chusquea* spp, Veblen 1989).

As a whole temperate rainforest ecosystems are quite distinct from those of the tropics. Temperate zone forests have proportionately fewer species in the upper canopy. Canopy trees tend to have smaller more coriaceous or even needle shaped leaves in the temperate rainforest formation, although conifers can occur in some lowland tropical rainforests (New Guinea, Queensland, Fiji, Borneo, Malaya). Temperate rainforests have proportionately fewer lianas when compared with the tropics (Webb 1978, De Laubenfels 1975). Dense mats of mosses and liverworts often carpet the forest floor and the upper canopy.

Cloudforests, or high elevation forests in the wet tropics share many characteristics in common with high latitude rainforests (c.f. Chapman & White 1970, Cockayne 1971, Robbins 1961). The lack of seasonality in growth and higher overstory diversity may be key distinguishing characters. Soils in cloudforests tend to be better drained and with less accumulation of organic matter than high latitude low elevation rainforests (Cockayne 1971, Robbins 1961) although much variation occurs in relation to rainfall and bedrock type (Chapman & White 1970, Holdgate 1961).

Cloudforests may be less productive and shorter in stature than corresponding high latitude rainforests because of their exposure to winds at the high elevations in which they typically occur (e.g. Howard 1969, Byer & Weaver 1977).

Many phytogeographers have distinguished the needle-leaved forests of the northern hemisphere from the evergreen broad-leaved forests of the southern hemisphere, implying they are ecologically distinct entities. Although it is generally true that the northern hemisphere forests have cooler winters and that conifers are well adapted to these cool temperatures (Sprugel 1989), climate alone does not consistently distinguish these forest types. Some conifers occur in southern hemisphere types (e.g. Podocarpaceae, Cupressaceae, Araucariaceae) while conifers are exclusive dominants of forests with analogous climates in the northern Pacific coast of North America (Waring & Franklin 1979). For northern ecologists it seems to be an apparent contradiction to see lush broad-leaved evergreen rainforests (suggestive of a subtropical environment) growing adjacent to icefields as in southern Chile and New Zealand. In part because of this commonly made distinction between northern and southern rainforests few comparisons have been made of the principal components of the world temperate rainforest formation.

For purposes of discussion the temperate rainforest climatic zone could be defined with the following four factors:

- 1) greater than 1,400 mm annual precipitation, 10% or more occurring during the summer months
- 2) cool frequently overcast summers, July (or austral January) isotherm < 16°C
- 3) fire infrequent, and not an important evolutionary factor
- 4) dormant season caused by low temperatures, may be accompanied by transient snow.

Applying this definition to the temperate forest zone results in a striking global pattern (Fig. 1). Large land masses in ge-

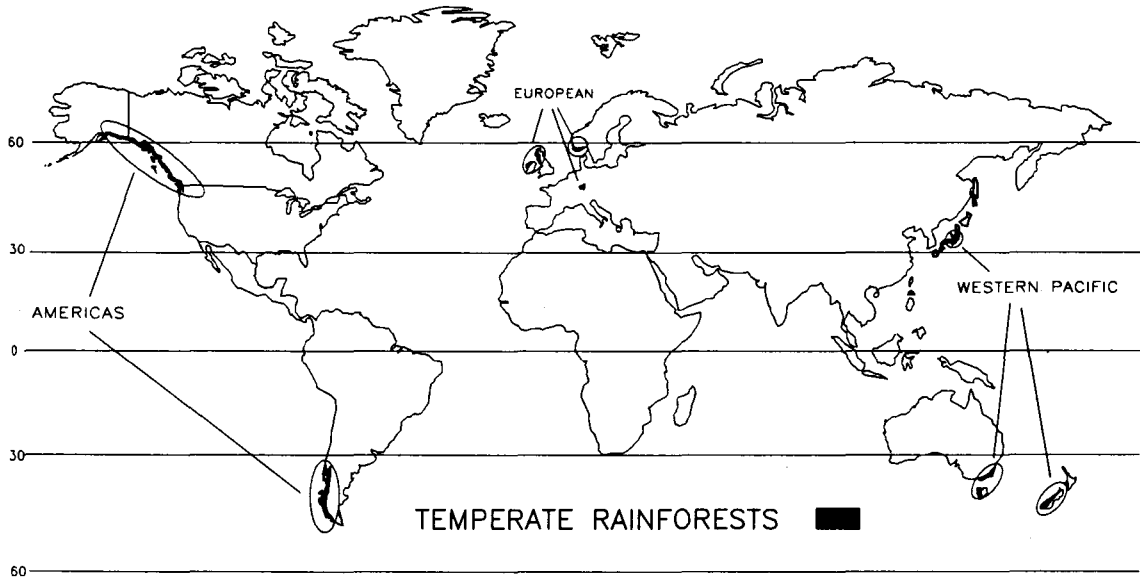


Fig. 1: World distribution of temperate rainforests. Ellipses indicate principal regions with temperate rainforests. This figure represents potential maximum (historical) distribution and does not take account of current land-use practices.

Distribución mundial de bosques lluviosos templados. Las elipses indican regiones principales con bosques lluviosos. Esta figura representa la distribución histórica (máximo) y no considera las reducciones en área debido al impacto reciente del hombre.

neral have continental climates that influence much of the coastal zone, or at least produce rain-shadows preventing the development of rainforest. The principal rainforest zones are along the northern Pacific coast of North America, from a narrow band along the Olympic Peninsula in Washington State (46°N), to a broad band reaching the coastal cordillera in British Columbia and southeastern Alaska (61°N); and along a similar latitudinal range and physiographic pattern in southern Chile from approximately Valdivia in the coast and Conguillío in the Andes (38°S) south to western Tierra del Fuego (55°S). All other rainforest zones are in isolated patches in mid-montane regions or in smaller islands, with the possible exception of western south island, New Zealand. This global pattern closely matches the temperature driven classification of Köppen (1949) type CFb, except that CFb includes more of central Chile, northeastern Asia (Sakhalin Island, central Honshu) and the high elevation *Nothofagus* forests of New Guinea.

Geology and vegetation history

Southern Chile and the northern Pacific coastline show a strikingly similar geologic history, resulting in a complex maze of fjords, channels, and extensive low elevation ice fields (Fig. 2). Miller *et al.* (1977) summarized the timing and extent of glacial advance and retreat in the two regions and concluded that they were sufficiently similar to treat them as analogous physical environments (specifically the Mediterranean sites). It should be pointed out, however, that a major contrast with the two regions lies in the dynamics of the geologic plates. Southern Chile abuts one of the world most active subduction zones, resulting in high frequency volcanic and associated mudflow and landslide disturbances (Veblen *et al.* 1981). By contrast volcanic activity is rare within most of the northern Pacific rainforest zone. Major volcanic eruptions are confined to interior mountain ranges such as the Cascades and the non-forested arctic terrain in the Aleutian islands and western Alaska.

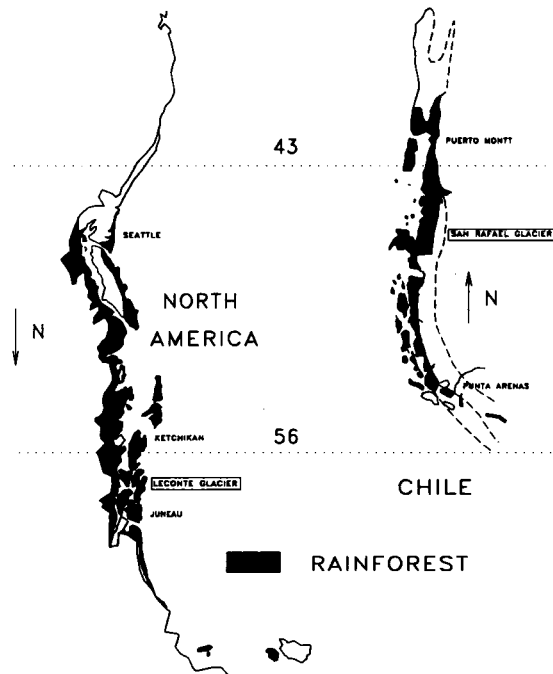


Fig. 2: Distribution of rainforests in North America and Chile. Included in the general rainforest regions are non-forest types such as alpine, bog, and permanent snowfield regions. Glaciers noted on each coastline represent the equatorial-most tidewater glaciers.

Distribución general de bosques lluviosos en Norteamérica y en Chile. Las áreas de bosque también incluyen en parte otros tipos de vegetación, como praderas, pantanos, glaciares, etc. Los glaciares indicados en cada costa representan la latitud más baja de un glaciar que alcanza el nivel del mar.

The presence of glaciers and icefields may be a key factor constraining species richness in the coolest portions of each coastline (Fig. 3). Contemporary forest communities have existed in many poleward parts of these coastlines for less than 3,000 years. At the highest latitudes in both coastlines only 5 plant species can become forest trees. Tree species richness of the northern Pacific coast monotonically increases until reaching the limit of the rainforest zone or the forest zone in the south. In South America by contrast tree species richness remains at around 5 species until passing the principal icefield regions after which tree species richness rapidly increases, generally exceeding the level of forests in comparable climates in the northern Pacific. A similar pattern has been observed in freshwater algal commu-

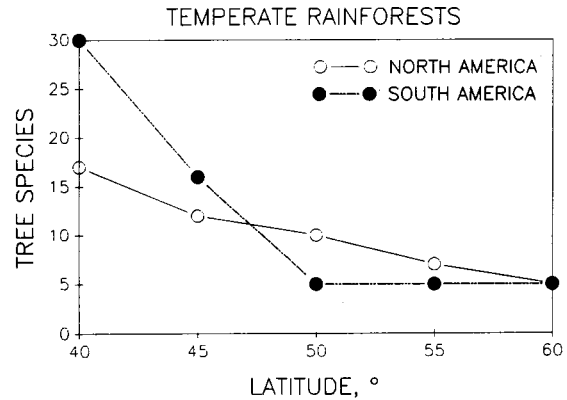


Fig. 3: Tree diversity patterns within the rainforest regions of Chile and North America. Includes total number of taxa within each geographic region per degree of latitude.

Modelos de la diversidad de árboles dentro de las regiones de bosques lluviosos de Chile y de Norteamérica. Se indica el número total de especies dentro de cada región por grado de latitud.

nities along the Chilean coast (Soto 1991). Perhaps because of the narrowness of the peninsula of southern South America, glacial advances or some related biogeographical factors have made more effective barriers to species migration in South America than in corresponding regions in North America, despite less ice advance in South America and widespread vulcanism (Markgraf 1989, 1990)*.

Diversity of rainforest shrubs and herbs does not show a clear pattern in relation to climate. Many species persist along the entire range, sometimes becoming more important at high latitudes due to the diminished density of overstory dominants (Alaback & Juday 1989).

Although the floras of Chile and the northern Pacific coast of North America evolved independently a significant number of species occur principally in these two locations or have close analogs in each (Hultén 1968, Moore 1983). The fossil record shows no evidence that the common tree genera in southern South America

* MARKGRAF V (1990) Quaternary history of temperate ecosystems in North and South America. Presented at the Workshop Comparative studies of North and South American temperate ecosystems: theory, approaches and limitations. Termas de Chillán, Chile, January 5-10, 1990.

ever occurred in North America or vice versa. Yet several herbaceous species occur only in the high latitude temperate rainforests of North America and southern Chile (Heckard 1963, Moore 1972, Raven 1963). Over 20 species of plants occur in both Tierra del Fuego and the Pacific coasts of North America. Of these at least 7 occur only in these two locales (the others having large distributions in Europe or Asia) including species of *Osmorhiza*, *Fragaria*, and *Carex*. A leading hypothesis is that these species are products of long distance dispersal by birds (e.g. terns, plovers, other shore birds). The ability of these species to flourish in both environments provides further evidence of the comparability of the environments in both rainforest regions.

Climate

Numerous authors have been struck by the climatic similarity of Chile and western North America (Mooney *et al.* 1977, Moldencke 1976). In the rainforest region the comparison is not nearly as precise as it is for the Mediterranean zones (Instituto Geográfico Militar 1979, Franklin & Dyness 1973, Farr & Harris 1979). Precipitation magnitude and seasonal pattern appear to be comparable, although the lack of climatic stations in exposed coastline locales in Chile make precise comparisons highly tentative (Fig. 4). Overall, the

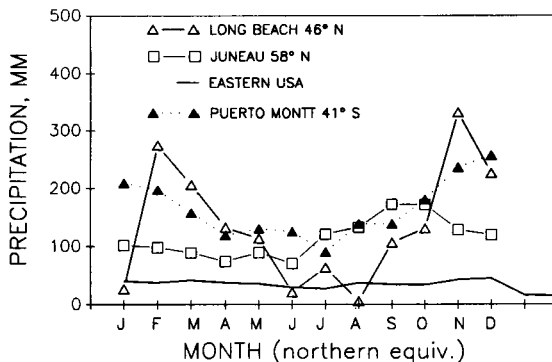


Fig. 4: Rainfall patterns of selected sites in the rainforest region of North America and South America. Based on 20 year averages.

Modelos de la distribución de las lluvias de algunas localidades dentro de las regiones de bosques lluviosos de Chile y de Norteamérica. En base a promedios de veinte años.

Chilean sites resemble the temperature patterns of the Washington coast but with the rainfall patterns of coastal Alaska.

In both regions rugged topography causes a wide range in temperature and rainfall over short distances (U.S. Weather Bureau 1989, Weinberger 1974). The high degree of local variation in precipitation in the rugged terrain of both coastlines makes interpretation of rainfall data difficult at best. In Juneau at sea level, for example, annual rainfall varies by a factor of 2-3x within a 4 km radius. In both regions however, heavy rainfall and low temperatures combine to produce among the highest runoff rates in the temperate zone (Di Castri 1976). This high runoff rate leads to rapid rock weathering and soils formation, and to high frequencies of landslides and other mass wasting types of erosion (Alexander 1988, Bishop & Stevens 1964, Veblen *et al.* 1981).

Both Chilean and northern Pacific coastlines appear to have a steady decline in growing season temperatures which is closely related to species richness and tree productivity (Farr & Harris 1979, Holdgate 1961). In the southern hemisphere climates tend to be more maritimes so that cool climates begin at much lower latitudes than in North America. The rainforest of North America begins at nearly 10° higher latitude than it does in South America. In Chile tidewater glaciers begin at only 45°S, or nearly 12° lower in latitude than tidewater glaciers in Alaska (Fig. 2). Despite these cool summer temperatures, however, winter temperatures are much higher throughout the Chilean coastline than in most of the northern Pacific rainforest. Growing season temperatures, appear to be much more closely matched between the two regions (Fig. 5). The monthly temperatures for Long Beach, Washington and Puerto Montt, Chile for example are nearly identical.

Presumably growing season temperatures are more important to productivity and related ecosystem nutrient budgets than are winter temperatures making comparison between these regions an appropriate one. Winter photosynthesis can, however, play a significant role in carbon uptake

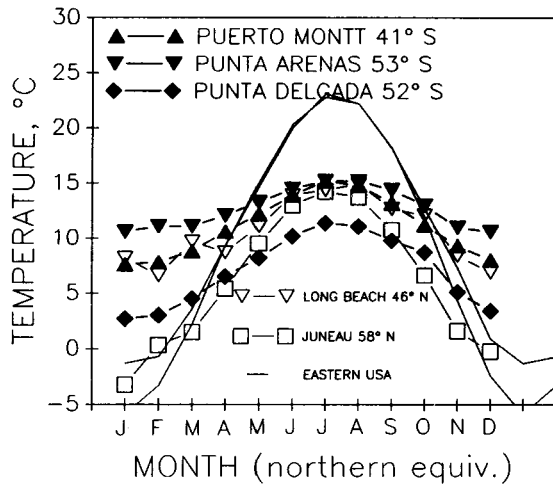


Fig. 5: Mean monthly temperatures in the rainforest region of North America and South America. Based on 20 years averages.

Temperaturas promedio mensuales de algunas localidades dentro de las regiones de bosques lluviosos de Chile y Norteamérica. En base a promedios de veinte años.

in cool northern climates and thus would be expected to be of even greater importance in Chile (Waring & Franklin 1979). Forest productivity data for the Chilean coast could provide a valuable reference on how a more attenuated distribution of temperature could influence carbon uptake. Some models of global climatic change predict a climate more like southern Chile for northern rainforests sites, making this comparison a particularly important one.

As in many tropical regions, the limit of rainforest along both coastlines is mostly a function of precipitation rather than temperature (De Laubenfels 1975). Forest extends to the highest latitudes where heavy rainfall persist (e.g. the contrast the climate of Punta Delgada, Chile and Adak Island, Alaska). Wind may also play a role in restricting forest growth as in the case of the Aleutian Islands in Alaska where planted *Picea* seedlings only survive in sheltered microsites (Alden & Bruce 1989), or in the exposed moorelands of the southern Chilean coast (Holdgate 1961, Young 1972).

A key consequence of the unique climate of temperate rainforests is the rapid rate of soils morphogenesis. High rates of runoff result in rapid leaching and

podzol formation in temperate rainforests (Alexander 1988, Bowers 1987, Holdgate 1961). Heavy accumulations of organic matter and nutrient immobilization lead to the development of a hardpan layer, impeding water drainage (Ugolini & Mann 1986). Without chronic disturbance, soils in southeast Alaska are hypothesized to develop into waterlogged acidic, peat-like soils which can only support stunted bog-like forest plants. The causes of bog formation and the determinants of the ecotone between bog and forest have been long debated in both hemispheres (Hennon 1986, Holdgate 1961, Neiland 1971). A leading hypothesis is that the balance between bog and forest may reflect changes in regional climates (Winkler 1988). In both regions cupressid tree species have rapidly diminished their former geographic range or are experiencing disease and decline (*Fitzroya cupressoides*, *Chamaecyparis nootkatensis*). For *Chamaecyparis* it appears that the forest-bog ecotone is a key factor. Another cupressid, *Pilgerodendron uvifera* although uncommon, plays a similar ecological role in Chile.

Forest structure and composition along a climatic gradient

Along the more than 15 degrees of latitude in each coastline temperate rainforest species composition and structure changes continuously both in response to changes in temperature and moisture. Along the North American coast a steady decline in accumulated temperature is closely related to declines in forest productivity and tree height (Farr & Harris 1979) and to increases in soil organic matter and litter depth. Similar trends occur along the Chilean coast (Holdgate 1961, Weinberger 1974). Much of the temperature differences are due to not only diminishing global insolation but also due to higher summer cloudiness and rainfall. Moisture-laden clouds are particularly effective in decreasing insolation at high latitudes because of low solar altitudes.

The key characteristic that distinguishes major forest formations and that of the

temperate rainforest zone itself is the duration and intensity of cool summer rain (Fig. 6, Veblen *et al.* 1983). Although summer rains occur in other temperate forest types they are usually associated with intense storms of short duration and so do not lead to a cool climate. In temperate rainforests long periods of fog, drizzle, and light rain are common. This may be why the cloud forests of the tropics share so much in common both climatically and biologically with temperate rainforests. Within the temperate rainforest zone duration of summer rains are closely associated with forest structure and composition.

In the most equatorial portion of the rainforest zone short summer droughts and temperatures over 25°C are common, but moisture is still freely available, making it a nearly ideal environment for tree growth. Forest productivity and biomass accumulation is greatest in this zone, which includes the Olympic rainforest in Washington and southern British Columbia and the Valdivian rainforest in Chile. In the Pacific Northwest forest biomass commonly exceeds 1,200 mt/ha as compared with 150-300 mt/ha in eastern North America or typical broadleaf sites in Chile (Franklin & Waring 1980). Dominant tree species in North America are *Picea sitchensis*, *Tsuga heterophylla*, *Pseudotsuga menziesii* and *Thuja plicata* (Franklin

& Dryness 1973, Roemer *et al.* 1988). Understory plants vary from dense thickets of woody broadleaf evergreen shrubs to low growing herbaceous carpets depending on soil moisture and exposure.

A rich diversity of evergreen trees dominate the Valdivian rainforest including various combinations of *Nothofagus dombeiyi*, *N. nitida*, *Aextoxicon*, *Laurelia*, *Drimys*, *Weinmannia*, *Podocarpus* and *Fitzroya*. The dense lush multilayered forest is reminiscent of the physiognomy of a subtropical rainforest. In *Fitzroya* sites biomass can approach 1,000 mt/ha, whereas typical *Nothofagus* sites only attain 200-300 mt/ha (Alaback 1989). On many of these sites *Chusquea* bamboos form an almost impenetrable thicket underneath a patchy upper canopy. Understory tree and shrub species also contribute to this thicket of undergrowth. Herbaceous species are less prominent than in the coniferous forests of the northern Pacific. Summer rain is approximately 40% of annual precipitation (C. Pérez, pers. comm.).

In the North Patagonian rainforest and the spruce rainforest of the northern Pacific the overstory is less diverse and productivity lower than in the Valdivian rainforest. Within this zone the greatest change in overstory species richness and productivity occurs in both hemispheres. In North America *Picea sitchensis*, *Tsuga heterophylla*, *Abies amabilis* and *Thuja plicata* are the dominant species (Alaback & Juday 1989, Gagnon and Bradfield 1986, Roemer *et al.* 1988). Pure stands of *Picea* and *Tsuga* are common with few trees reaching intermediate crown positions. The understory is dominated by deciduous ericaceous woody shrubs and evergreen herbs which play a key role in providing winter habitat for mammals and birds (Alaback 1982). Forest biomass is generally 25-50% that of the Olympic or related *Pseudotsuga* forest in the Pacific Northwest (Alaback 1990). Summer rainfall ranges from 10 to 20 percent of annual precipitation.

In the most poleward sites a distinctly open and depauperate forest develops. In Alaska this subarctic rainforest is best

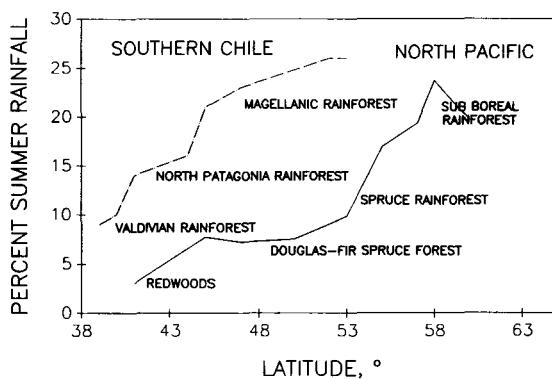


Fig. 6: Distribution of forest types within the rainforest region of North America and Chile in relation to climate.

Distribución de los tipos de bosques dentro de las regiones de bosques lluviosos de Norteamérica y de Chile en relación al clima.

represented in Prince William Sound with a mixture of *Picea sitchensis*, *Tsuga heterophylla*, and *T. mertensiana* (Alaback & Juday 1989, Borchers *et al.* 1989, Cooper 1942, Eck 1984). Growing sites are poor and mature canopies of 20-35 m are common (Farr & Harris 1979, Young 1972). Thickets of *Rubus spectabilis* and other tall woody shrubs are less common than in the spruce rainforest type. The understory is dominated by ericaceous woody shrubs and carpets of bryophytes and ferns on the forest floor.

In the Magellanic or subantarctic rainforest the overall physiognomy is much more similar to the northern conifer forests than in any other type. The absence of *Chusquea* bamboos makes for a much more open, mossy forest. The understory is often low and patchy with ericaceous species such as *Gaultheria* and *Pernettya* and extensive carpets of bryophytes on the forest floor. *Nothofagus betuloides*, *Drimys winteri* or *N. pumilio* are overstory dominants. Severe wind and cool temperatures are common during the growing season in both locales. The landscape in both hemispheres is a dynamic fine-grained mosaic of bog or moorland, icefields and rainforest. These are among the least well known rainforest types.

Forest dynamics

Temperate rainforests are extremely dynamic systems with disturbances occurring at several spatial and temporal scales. In the Valdivian and Olympic rainforest zones catastrophic disturbance appears to be an important component of stand structure, whether caused by fire, landslides or volcanism (Franklin & Waring 1980, Veblen *et al.* 1981). At higher latitudes and along exposed coastlines continual disturbance by wind may become a more important factor (Armesto & Figueroa 1987, Harris 1989, Taylor 1990). Forest stand structure is often an integration of both scales of disturbance due to the longevity of dominant trees both in Chile and North America. *Picea* and *Tsuga* are least moderately shade tolerant and can regenerate effectively under partial

forest canopies, although forests with a high component of *Picea* are normally subject large scale catastrophic disturbances. In the Valdivian Andes *Nothofagus* species by contrast appear to require catastrophic disturbance for regeneration (e.g. Veblen *et al.* 1983). The mixed forest of myrtles, laurels and podocarps appears the most ecologically analogous to the *Tsuga* forests of North America (Armesto & Figueroa 1987).

The first work on plant succession in the temperate rainforest zone focused on succession following deglaciation (Cooper 1937, Croker & Major 1955, Reiners *et al.* 1971). A simple chronosequence was used to characterize this succession from bryophytes (e.g. *Rhacomitrium* spp.), to a shrub stage (*Salix* spp.), to a *Picea sitchensis* forest, finally to a climax *Tsuga heterophylla* forest. This primary succession can proceed remarkably quickly, with a dense mature *Picea* forest established on land scraped bare by glaciers only two centuries ago.

In North America *Alnus sinuata* is widely recognized for playing an important role in soils nutrition following deglaciation by fixing atmospheric nitrogen (Croker & Major 1955). Following establishment of *Alnus* forests, *Picea* seedlings grow slowly in the understory, eventually overtopping the short-lived *Alnus*. The nitrogen-rich soils then allow for rapid growth of *Picea* and the establishment of a pure *Picea* forest within two centuries of deglaciation (Cooper 1937). In Chile *Gunnera chilensis* appears to play a similar role to *Alnus*, although few field studies have been conducted to verify how important its nitrogen fixation is to soils development and plant succession following glacial retreat (Veblen *et al.* 1989).

Recent work on post glacial succession has emphasized plant life history strategies and competitive relationships to examine if succession truly follows the facilitation model of Connell & Slatyer (1977) or simply relay floristic (Egler 1954). Preliminary results of some of this work suggests that post glacial succession is a far more complex and multi-faceted process than first believed. For example in Glacier

Bay the original work was done only on the eastern arm of the Bay where glacial retreat occurred rapidly (Cooper 1937). In the western arm where calcareous parent materials predominate a wide range of plant successional trajectories develop following deglaciation. The speed of deglaciation and physical processes associated with it such as scour, fill, and other soils changes lead to divergent successional pathways. It also appears that late seral species occur at the earliest stages of the succession, imposing some constraints on the facilitation model.

Erosional events are distinctly different in the two regions. In Alaska and British Columbia, because of the lower winter temperatures heavy wet snow accumulates much more readily than in Chile resulting in frequent snow avalanches on steep slopes. The mainland coast is particularly prone to avalanching as it combines steep glaciated topography with heavy snowfall. Landslides occupy only a small fraction of the landscape and are often associated with stream channels (Swanston & Swanson 1976). In southern Chile avalanche caused erosion appears to be less common, but increased ruggedness of the terrain and heavy rainstorms appear to result in high frequency slope failures.

Few studies have been conducted on succession following landslides or mudflows in the northern temperate zone (Dale 1989, Miles & Swanson 1986, Smith & Commandeur 1986). Chronosequences are difficult to establish because of the individualistic nature of each disturbance event and the wide range of soil conditions which may result from different kinds of disturbances or within different terrains contained in a single landslide area. The succession resembles post glacial succession in its dominance by nitrogen fixing species such as *Lupinus* and *Alnus* and early establishment of *Picea*. Similarly in Chile the nitrogen fixer *Gunnera chilensis* is an early colonizing species, along with the climax species, *Nothofagus dombeyi*. Much of the climax old growth *Nothofagus* and *Fitzroya* is presumed to originate from landslide or mudflow events. Yet little information is available

on the timing and nature of primary succession either following deglaciation or hillslope failures in the region (Veblen *et al.* 1981).

Secondary succession also proceeds rapidly in the northern temperate rainforest zone. Following windthrow or logging most of the pre-disturbance propagules survive intact allowing growth release of tree seedlings and layering or resprouting of shrubs and herbs. The most characteristic aspect of the succession is an extended period of species impoverished understory vegetation following the establishment of a dense overstory canopy layer. Less than 1% of the understory biomass of old growth forests are maintained in these younger forests for 100 years or more (Alaback 1982, 1984). As stands mature shade tolerant shrubs and tree seedlings invade the understory, often leading to a dense secondary canopy layer. Only after the principal overstory stratum senesces, and begins to follow a pattern of gap-phase dynamics does the full structural diversity of shrubs, herbs, and tree seedlings develop (Alaback 1990). Many herbaceous species (e.g. *Cornus canadensis*, *Rubus pedatus*, *R. lasiococcus*, *Oxalis oregona*) which are important sources of highly nutritious forage are most abundant in chronically disturbed old growth or in the oldest age class of seral dominants (500-1,000 years old) (Alaback 1982, 1990, Spies & Franklin 1988).

Few data are available on how the structure of secondary forests compares with primary forest in southern Chile and how long it takes for this forest to become ecologically equivalent to the original forest. The ecological value of secondary forests should become a key question as human activity extends into these southern forests in coming decades.

Aggressive woody understory species can cause regeneration problems with chronic disturbances, impeding the succession towards climax species. *Chusquea* forms impenetrable thickets following canopy gap creation, impeding regeneration of *Nothofagus* (Veblen 1982, Veblen *et al.* 1983). In North America *Rubus spectabilis* can similarly exclude other woody seed-

ings under partial canopies, especially along floodplains and other riparian sites. The presence of these species by themselves can play a pivotal role in determining ecosystem response to disturbance.

In the North Patagonian and Magellanic rainforest the greatest similarity of ecosystem response to disturbance probably occurs, however neither region has been intensively studied. Both have chronic wind disturbance and overstory species with a range of shade tolerance. Shade tolerant trees and shrubs rapidly reoccupy forest sites by resprouting or by releasing established seedlings that survived the disturbance (e.g. Alaback 1990). In Alaska *Tsuga mertensiana* resembles *Nothofagus* in that it seldom regenerates under itself, and appears to require a large scale disturbance to be maintained in the stand. Little work has been done on dynamics of *Tsuga mertensiana* or *Nothofagus betuloides*. More detailed information on gap sizes and survivorship under partial canopies will be needed to answer questions about what kind of disturbances are needed to maintain present stand structure in both regions.

Predictions and summary

The unique cool and wet climate of the temperate rainforest should create distinct ecological stresses to which these forests must adapt. This climate should lead to rapid soils development and immobilization of nutrients, eventually leading to bog formation, unless the soil horizons are disturbed. Low growing season temperatures should also contribute to paludification by allowing greater accumulation of organic matter. Soils disturbance should be beneficial to maintain long-term productivity on such sites.

Shade tolerant species should become increasingly important along the latitudinal gradient of the rainforest. This implies rapid ecosystem recovery to disturbance, and important influences of surviving propagules on forest regeneration and structure. The dense vegetation and high cloud cover should work together to suppress understory diversity in secondary forests until a patchy overstory canopy

develops. Overall productivity of these ecosystems should be heavily influenced by soils fertility. An excess amount of water should lead to drainage of water, oxygenation of soils, and soil temperature as being limiting growth factors.

During the past several decades research on the functional ecology of temperate rainforests in North America has generated several general hypotheses about how climate influences forest growth and structure. Forest leaf area, for example has been used to estimate potential productivity and site growing potential of both secondary and primary forests (Waring & Franklin 1980). The growth form and physiology of trees in the Pacific Northwest has also been attributed to unique climatic conditions. But without good replication it is difficult to determine how important these factors really were to the evolution of present day ecosystems. The analogous climatic gradients in North and South America provide a unique opportunity to test many of these ideas, while at the same time providing some insights as to how historical factors influence ecosystem structure and function.

Thus despite the striking contrast in biota the physical environment and history of the Northern Pacific coast and the extreme southern coast of Chile provide a unique opportunity for comparative ecological studies. The extremely wet and cool climatic conditions also provide unique physiological conditions for plants and soils. Key questions that might be addressed in such studies might be: what is the relative importance of biogeographical factors and physical environment in regulating the evolution of forest ecosystem structure and function; of how might the structure and dynamics of temperate rainforests change with an increase in precipitation and temperature (as has often been proposed under a global warming scenario)?

ACKNOWLEDGMENTS

Funding for this research was provided by the USDA Forest Service Pacific Northwest Research Station, and by the USDA Office of International and Community

Development program for scientific exchange, and the Mellon Foundation. I am indebted to Juan Armesto, Steward Pickett, and their students for organizing the conference which stimulated this synthesis.

LITERATURE CITED

- ALABACK PB (1989) Logging of temperate rainforests and the greenhouse effect-some ecological factors to consider. pp. 195-202 in EB Alexander, (ed.) *Proceed. Watershed '89*. March 21-23, 1989, Juneau, AK. USDA Forest Service, Region 10, Juneau.
- ALABACK PB (1990) Dynamics of old-growth temperate rainforests in Southeast Alaska. In: AM Milner and JD Wood (eds.) *Proceedings of the 2nd Glacier Bay Science Symposium*, September 19-22, 1988, Gustavus, Alaska. National Park Service, Alaska Region, Anchorage, Ak.
- ALABACK PB (1984) A comparison of old-growth and second-growth western hemlock-Sitka spruce forests in Southeast Alaska. pp. 219-226. In: WR Meehan, TR Merrell, Jr and TA Hanley (eds.) *Fish and Wildlife Relationships in old-growth forests: Proceedings of a symposium held in Juneau, Alaska*, 12-15 April 1982. American Institute of Fishery Research Biologists.
- ALABACK PB (1982) Forest community structural changes during secondary succession in southeast Alaska. In: JE Means, (ed.) *Forest Succession and stand development research in the Northwest*. Proceedings of Corvallis, Oregon Symposium, March 26, 1981. Oregon State University Forest Research Laboratory, Corvallis, OR, pp. 70-79.
- ALABACK PB (1982) Dynamics of understory biomass in Sitka spruce-western hemlock forests of Southeast Alaska. *Ecology* 63: 1932-1948.
- ALABACK PB, & GP JUDAY (1989) Structure and composition of low elevation old-growth forest in research natural areas of Southeast Alaska. *Natural Areas Journal* 9: 27-39.
- ALDEN J & D BRUCE (1989) Growth of historical Sitka spruce plantations at Unalaska Bay, Alaska. USDA Forest Service General Technical Report. PNW-GTR-236. Pacific Northwest Research Station. Portland, OR. 18 pp.
- ALEXANDER EB (1988) Rates of soil formation: implications for soil-loss tolerance. *Soil Science* 145: 37-45.
- ARMESTO JJ & FIGUEROA J (1987) Stand structure and dynamics of rainforests in the Chiloé archipelago. *Journal of Biogeography* 14: 367-376.
- ARMESTO JJ, JD MITCHELL & C VILLAGRAN (1986) A comparison of spatial patterns of trees in some tropical and temperate forests. *Biotropica* 18: 1-11.
- BISHOP DM & ME STEVENS (1964) Landslides on logged areas in southeast Alaska. USDA Forest Service Res Pap NOR-1. Pacific Northwest Research Station. 18 p. Juneau.
- BORCHERS SL, J WATTENBARGER & R AMENT (1989) Forest plant associations of Montague Island, Chugach National Forest: preliminary results. pp. 29-46. In: EB Alexander, ed. *Watershed 89, Proceed. of the Conference* 21-23 March, 1989, Juneau, AK. USDA Forest Service Region 10, Juneau, AK.
- BOWERS F (1987) Effects of windthrow on soil properties and spatial variability in Southeast Alaska. Ph.D. diss. University of Washington, Seattle. 200 pp.
- BYER MD & PL WEAVER (1977) Early secondary succession in an elfin woodland in the Luquillo Mtns of Puerto Rico. *Biotropica* 9: 35-47.
- CHAPMAN JD & F WHITE (1970) The evergreen forests of Malawi. Commonwealth Forestry Institute, Oxford. 190 pp. illus.
- CLINE SP, AB BERG & HM WIGHT (1980) Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *Journal of Wildlife Management* 44: 773-786.
- COCKAYNE L (1971) The subtropic and subantarctic rainforests of New Zealand. pp 109-136. In: SR Eyre (ed.) *World Vegetation Types*. Columbia University Press. New York.
- CONNELL JH & RO SLATYER (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111: 1119-1144.
- COOPER WS (1942) Vegetation of the Prince William Sound Region, Alaska; with a brief excursion into post-Pleistocene climatic history. *Ecological Monographs* 12: 1-22.
- COOPER WS (1937) The recent ecological history of Glacier Bay: an initial report upon a long term study. *Ecology* 4: 355-65.
- CROCKER RL & J MAJOR (1955) Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. *Journal of Ecology* 43: 427-448.
- DALE VH (1989) Wind dispersed seeds and plant recovery on the Mount St. Helens debris avalanche. *Canadian Journal of Botany* 67: 1434-1441.
- DE LAUBENFELS DJ (1975) Mapping the world's vegetation. *Syracuse Geographical Series* 4. Syracuse Press, Syracuse, NY.
- ECK KC (1984) Forest characteristics and associated deer habitat values, Prince William Sound Island. pp 235-246. In: WR Meehan, TR Merrell and TA Hanley, (eds.) *Fish and wildlife relationships in old-growth forests*. *Proceed. Symposium*. Juneau, AK 12-15 April 1982. American Inst. Fishery Research Biol. and USDA Forest Service Pacific Northwest Research Station, Portland, OR.
- EGLER FE (1954) Vegetation science concepts: I Initial floristic composition a factor in old field vegetation development. *Vegetatio* 4: 412-417.
- DI CASTRI F (1976) *Bioclimatología de Chile*. Vicerrectoría Académica de la Universidad Católica de Chile, Santiago. 128 pp.
- FARR WA & AS HARRIS (1979) Site index of Sitka spruce along the Pacific coast related to latitude and temperatures. *Forest Science* 25: 145-153.
- FONDA RW (1974) Forest succession in relation to river terrace development in Olympic National Park, Washington. *Ecological Monographs* 55: 927-942.
- FRANKLIN JF, K CROMACK, W DENSON, AW McKEE, C MASER, J SEDELL, F SWANSON & GP JUDAY (1981) Ecological characteristics of old-growth Douglas-fir forests. USDA Forest Service Gen Tech Rep PNW-118. Pacific Northwest Research Station, Portland, OR.
- FRANKLIN JF & CT DYRNESS (1973) *The Natural Vegetation of Washington and Oregon*. USDA Forest Service Pac. Northwest For. Range Exp. Stn., Portland, Oregon. Gen. Tech. Rep. PNW-8, 417 pp. illus.
- FRANKLIN JF & RH WARING (1980) Distinctive features of the Northwestern coniferous forest: development, structure, function. pp. 59-89. In: War-

- ing RH (ed.) Forests: fresh perspectives from ecosystems analysis Proc. 40 th Ann. Biol. Colloq. Oregon State Univ. Press. Corvallis, OR.
- GAGNON D & GE BRADFIELD (1987) Gradient analysis of west central Vancouver Island forests. Canadian Journal of Botany 65: 822-833.
- GODLEY EJ & NT MOAR (1973) Vegetation and pollen analysis of two bogs on Chiloé. New Zealand Journal of Botany 11: 255-268.
- GRAHAM RL & K CROMACK Jr (1982) Mass, nutrient content and decay rate of dead boles in rain forests of Olympic National Park. Canadian Journal of Forest Research. 12: 511-521.
- HALPERN CB (1989) Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology 70: 704-720.
- HARCOMBE PA (1986) Stand development in a 130-year old spruce-hemlock forest based on age structure and 50 years of mortality data. Forest Ecology and Management 14: 41-58.
- HARRIS AS (1989) Wind in the forests of Southeast Alaska and guides for reducing damage General Technical Report PNW-GTR-244. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 63 pp.
- HARRIS AS & WA FARR (1974) The forest ecosystems of southeast Alaska 7. Forest ecology and timber management. USDA Forest Service Gen. Tech. Rep. PNW-25. 109 pp.
- HECKARD LR (1963) Amphitropical relationships in the herbaceous flora of the Pacific Coast of North and South America: the Hydrophyllaceae. Quarterly Review of Biology 38: 117-123.
- HENNON PE (1986) Pathological and ecological aspects of decline and mortality of *Chamaecyparis nootkatensis* in southeast Alaska. Ph. D. diss. Oregon State University, Corvallis. 279 pp.
- HOLDGATE MW (1961) Vegetation and soils in the south Chilean islands. Journal of Ecology 49: 559-580.
- HOWARDS RA (1969) The ecology of an elfin forest in Puerto Rico. 8. Studies of stem growth and form and of leaf structure. Journal of the Arnold Arboretum 49: 381-418.
- HULTEN E (1968) Flora of Alaska and neighboring territories. A manual of the vascular plants. Stanford Univ. Press. Stanford. 1008 pp.
- INSTITUTO GEOGRAFICO MILITAR (1982) Biogeografía. pp. 95-221. En Tomo III, Colección Geografía de Chile. Santiago.
- KELLMAN MC (1969) Plant species interrelationships in a secondary succession in coastal British Columbia. Syesis 2: 201-212.
- KOPPEN W (1918) Klassifikation der klimate nach temperature niederschlag, und jahreslauf. Petermann's Mitteilungen 64: 193-203.
- KOCHLER AW (1949) A geographical system of vegetation. The Geographical Review 37: 233-240.
- KUNKEL G (1955) Beobachtungen über klima und vegetation in Sudchile. Abhandlungen der Deutschen Akademie der Wissenschaften zu Berlin. Klasse für Chemie, Geologie und Biologie. Jahrgang Nr. 9.
- MARKGRAF V (1989) Paleoclimates in Central and South America since 18,000 BP based on pollen and lake-level records. Quaternary Reviews 8: 1-24.
- McKEE AW, G LAROI & JF FRANKLIN (1982) Structure composition and reproductive behavior of terrace forests south fork Hoh River, Olympic National Park. pp. 22-29. In: EE Starkey, JF Franklin and JW Matthews (eds.) Ecological Research in National Parks of the Pacific Northwest. USDI Nat. Park Serv., Coop. Park Studies Unit. Corvallis. 142 pp.
- MILES DWR & FJ SWANSON (1986) Vegetation composition on recent landslides in the Cascade Mountains of western Oregon. Canadian Journal of Forestry Research 16: 739-744.
- MILLER PC, DE BRADBURY, E HAJEK, V LAMARCHE & NJW THROWER (1977) Past and present environment. p 27-In H Mooney (ed.) Convergent evolution in Chile and California: Mediterranean climate ecosystems. Dowden, Hutchinson and Ross, Inc., Stroudsburg.
- MOLDENKE AR (1976) Evolutionary history and diversity of the bee faunas of Chile and Pacific North America. Wasmann Journal of Biology 34: 147-177.
- MOONEY HA (1977) Convergent evolution in Chile and California. Mediterranean climate ecosystems. US/IBP Synthesis Series 5. Dowden, Hutchinson & Ross, Inc., Stroudsburg.
- MOORE DM (1972) Connections between cool temperate floras with particular reference to southern South America. pp. 115-138. In: DH Valentine (ed.) Taxonomy, phytogeography and evolution. Academic Press. London.
- MOORE DM (1983) Flora of Tierra del Fuego. Missouri Botanical Garden, St. Louis. 396 pp.
- NEILAND BJ (1971) The forest bog complex of southeast Alaska. Vegetatio 26: 3-62.
- RAVEN PH (1963) Amphitropical relationships in the floras of North and South America. Quarterly Review of Biology 38: 151-177.
- REINERS WA, IA WORLEY & DB LAWRENCE (1971) Plant diversity in a chronosequence at Glacier Bay, Alaska. Ecology 52: 55-59.
- ROBBINS RG (1971) Montane vegetation of New Guinea. pp. 109-136. In: SR Eyre (ed.) World Vegetation Types. Columbia University Press. New York.
- ROEMER HL, J POJAR & KR JOY (1988) Protected old-growth forests in coastal British Columbia. Natural Areas Journal 8: 146-159.
- SMITH RB & PR COMMANDEUR (1986) Soils, vegetation and forest growth on landslides and surrounding logged and old-growth areas on the Queen Charlotte Islands. British Columbia Ministry of Forests, Land Management Report No. 41. 95 pp. Victoria, B.C.
- SOTO D (1991) Food web structure and species dominance in zooplanktonic assemblages of South American temperate lakes and ponds. Revista Chilena de Historia Natural (this issue).
- SPIES TA & JF FRANKLIN (1988) Old-growth and forest dynamics in the Douglas-fir region of western Oregon and Washington. Natural Areas Journal 8: 190-201.
- SPIES TA, JF FRANKLIN & TB THOMAS (1988) Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69: 1689-1702.
- SPRUGEL DG (1989) The relationship of evergreenness, crown architecture, and leaf size. The American Naturalist 133: 465-479.
- SWANSTON DN & FJ SWANSON (1976) Timber harvesting mass erosion, and steep-land forest geomorphology in the Pacific Northwest. pp. 199-221. In: Geomorphology and Engineering. DR Coates (ed) Hutchison and Ross (Publ.).
- TAPPEINER JC II & PB ALABACK (1989) Early establishment and vegetative growth of understory species in the western hemlock - Sitka spruce forests

- of Southeast Alaska. Canadian Journal of Forestry Research 67: 318-326.
- TAYLOR AH (1990) Disturbance and persistence of Sitka spruce (*Picea sitchensis* (Bong) Carr.) in coastal forests of the Pacific Northwest, North America. Journal of Biogeography 17: 47-58.
- UGOLIN FC & DH MANN (1979) Biopedological origin of peatlands in southeast Alaska. Nature 281: 366-368.
- VEBLEN TT (1982) Growth patterns of *Chusquea* bamboos in the understory of Chilean *Nothofagus* forest and their influences in forest dynamics. Bulletin of the Torrey Botanical Club 109: 474-487.
- VEBLEN TT (1989) *Nothofagus* regeneration in treefall gaps in northern Patagonia. Canadian Journal of Forestry Research 19: 365-371.
- VEBLEN TT, DH ASHTON, S RUBULIS, DC LORENZ & M CORTES (1989) *Nothofagus* stand development on in-transit moraines, Casa Pangué Glacier, Chile. Arctic and Alpine Research 21: 144-155.
- VEBLENT TT, RJ DELMASTRO & JE SCHLATTER (1976) The conservation of *Fitzroya cupressoides* and its environment in southern Chile. Environmental Conservation 3: 291-301.
- VEBLEN TT, Z DONOSO, FM SCHLEGEL & RB ESCOBAR (1981) Forest dynamics in south-central Chile. Journal of Biogeography 8: 211-247.
- VEBLEN TT, FM SCHLEGEL & JV OLTREMARI (1983) Temperate broad-leaved evergreen forest of South America pp. 5-31. In: Ovington JD (ed.) Ecosystems of the world. Vol. 10. Temperate broad leaved evergreen forests. Elsevier, New York.
- WARDLE P, MJA BULFIN & J DUGDALE (1983) Temperate broad-leaved evergreen forests of New Zealand. pp. 33-72 In: JD Ovington (ed.). Temperate broad-leaved evergreen forests. Ecosystems of the World 10. Elsevier, New York.
- WARING RH & JF FRANKLIN (1979) Evergreen coniferous forests of the Pacific Northwest. Science 204: 1380-1386.
- WEBB LJ (1968) Environmental relationships of the structural types of Australian rain forest vegetation. Ecology 49: 296-311.
- WEBB LJ (1978) A general classification of Australian rainforests. Australian Plants 76: 349-363.
- WEINBERGER P (1974) The regeneration of the Araucano-Patagonic *Nothofagus* species in relation to microclimatic conditions. Tuatara 22: 245-265.
- WINCKLER M (1988) Effect of climate on development of two Sphagnum bogs in south-central Wisconsin. Ecology 69: 1032-1043.
- YOUNG SB (1972) Subarctic rain forest of Magellanic Chile: distribution, composition, and age and growth rate studies of common forest trees. Antarctic Research Series 20: 307-372.