

Alteration of the hydrologic cycle due to forest clearing and its consequences for rainforest succession

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Abstract

Since the 19th century, 41% of the land on Chiloé Island (41°50'S, 73°40'W) in Chile was cleared. Following clearing and burning, much of the converted land remains in sparse shrub cover. We hypothesized that the arrested conversion back to forests may reflect a nearly permanent condition associated with a rise in the water table. To evaluate this possibility we acquired data from a 60-year old evergreen forest and an area in shrub cover to parameterize two hydrologic models; one that accounts for hourly interception losses and predicts net precipitation (Gash model), the other that calculates hourly transpiration from both overstory and understory components as well as evaporation from the soil (a modified Penman–Monteith model). In addition, standpipes were installed to record water table levels over 18 months. The fraction of a total annual precipitation (~2100 mm) transpired by shrub and forest cover differed (8% versus 22%) roughly in proportion to differences in the leaf area index (2.2 versus 5.0). Although whole canopy (stomatal) conductances were similar, the aerodynamic conductance was more than three-fold higher for forests compared with shrub cover (~12 mol m⁻² s⁻¹ versus 3 mol m⁻² s⁻¹). The frequent wetting of tree canopies, combined with an average wind speed of 0.74 m s⁻¹, resulted in ~30% interception losses from forests compared with 1% of annual precipitation lost through this pathway from shrub cover. As a result of these differences, only about half of the precipitation enters the ground under forest cover compared to 90% under shrub cover. This difference in canopy interception losses accounts for a rise in the water table from an average of 45–10 cm. The high water table prevents normal tree regeneration. This condition is stable unless an effort is made to provide an elevated substrate for tree seedlings to become established.

Keywords: Evapotranspiration; Secondary shrubland; Ecosystem engineers; Water table; Penman–Monteith model; Broad-leaved evergreen forest; Chiloé Island

1. Introduction

Tree canopy removal can have profound effects on the hydrology of an ecosystem, sometimes raising the water table in areas receiving high annual rainfall (Roy, 1998), or reducing drainage and increasing runoff and erosion in semiarid areas with low rainfall (Ruprecht and Schofield, 1991).

Because of their large size, complex architecture, broad intercepting surface, and hydraulic properties, trees greatly influence hydrology of terrestrial ecosystems. Transpiration and

evaporation from the canopy are major pathways for the loss of water from forest ecosystems, hence the proposal of Jones et al. (1994) that trees are ecosystem engineers, i.e., species that exert strong control on ecosystem processes and functions, and that create essential habitat conditions (e.g., microclimate) for other species. The role of trees as ecosystem engineers can be particularly important in cool wet climates, where low inputs of radiant energy combined with high rainfall predispose towards waterlogging the soils. In such sites, a significant disturbance to the tree canopy may alter the course of succession, deterring tree establishment and favoring species that can tolerate waterlogged habitats. Such examples of arrested succession can be considered special cases of alternative stable states in plant communities (Noy-Meir, 1975; Gilpin and Case, 1976; May, 1977).

Studies involving direct measurement of interception and transpiration losses in the wet temperate uplands of the northern

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UK have shown that total evaporative losses in local forests require a latent heat supply greater than that provided by the supply of radiant energy (Calder, 1990). The difference is made up by advection of heat from air masses as they move over wet leaf surfaces in the windy uplands. The high aerodynamic roughness of tall vegetation is what allows this energy transfer; in contrast, the low aerodynamic roughness of shorter vegetation means that evaporative losses are largely determined by radiant energy inputs. Thus, in wet temperate climates such as northern UK and maritime Chile, vegetation height can have important implications for evaporative losses from wet leaf surfaces (i.e., interception; Calder, 1998).

This study addresses the consequences of deforestation by logging and anthropogenic fire on hydrologic fluxes in a North Patagonian rainforest in Chiloé Island, southern Chile. We examine the hypothesis that hydrologic changes following removal of trees lead to arrested succession because of limited or absent tree regeneration in waterlogged sites. Forest recovery in these areas would be delayed as the ecosystem becomes locked into an alternative state. The following factors would contribute to the development of such alternative conditions. Loss of an ecosystem engineer (trees) causes water saturation of soils due to reduced ET, and these new conditions may decrease soil nutrient availability and increase the concentration of toxic elements in the soil. At the same time, severe waterlogging may impair the ability of roots to absorb nutrients, due to inhibition of root activity and damage to roots due to oxygen limitation (Waring and Schlesinger, 1985; Ruthsatz and Villagrán, 1991; Larcher, 1995). This may cause further nitrogen losses due to denitrification (Pérez et al., 2003). Here, we use a simple hydrologic model to compare the water cycle in an intact evergreen rainforest ecosystem adjacent to a wet, secondary shrubland, derived from slash and burn of the original forest. We use this model to assess whether changes in water balance after tree removal can significantly affect successional processes, leading to an alternative state or arrested succession.

1.1. Study area

Our study sites were located in the Biological Station Senda Darwin, Ancud, in northern Chiloé Island (41°50'S) (Fig. 1). Annual precipitation ranges from 2000 to 2500 mm, of which 11% falls during austral summer months, January–February (Di Castri and Hajek, 1976). During 2002 there were 242 days of rain. Annual average wind speed is 2 m s^{-1} and annual mean temperature is 10°C (10-year records at Biological Station Senda Darwin; Fig. 2). Predominant soils are known as ñadis (Veit and Garleff, 1996), corresponding to the Andosol order (FAO-UNESCO, 1971). These soils present a long water saturation period and a shallow water table, especially during winter months, due to the presence of an impermeable layer of iron and aluminum oxides, or hardpan, which in these soils is found at an average of $52 \pm 3 \text{ cm}$ (mean \pm S.E., $N = 12$) below the surface. These soils are particularly developed over fluvio-glacial deposits and in depressions between relictual moraine fields (Aravena, 1991).

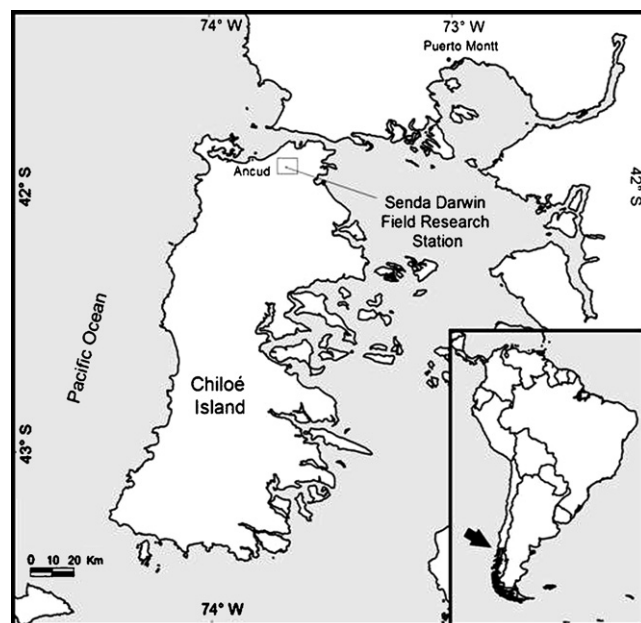


Fig. 1. Study site in Senda Darwin Biological Research Station, Chiloé Island.

From the 19th century, when Europeans settled in the Chilean Lake District (39–41°S), forest cover has declined at a fast pace due to indiscriminate use of fire, removal of timber and firewood, and opening of areas for agriculture and cattle farming (Armesto et al., 1994; Lara et al., 1996). Due to the poor drainage of post-glacial soils, which predominate in the region, clearing of forests can have dramatic and long-lasting effects on the water balance. Prairies, shrublands and wetlands occupy 72,000 h, (41%) of the land surface around Ancud on Chiloé Island (INFOR, 1999). This percentage is important when we consider that most shrublands in Chiloé Island are subjected to seasonal waterlogging and that they occur in previously forested land.

The frequent use of fire and logging (slash and burn) to clear land for livestock and farming in Chiloé Island has resulted in replacement of large areas of rainforest by low-stature ($\sim 1.5 \text{ m}$) vegetation consisting of sedges, *Baccharis patagonica* shrubs,

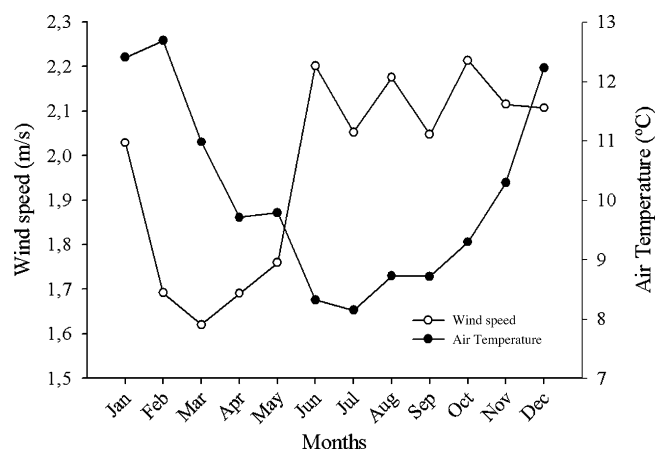


Fig. 2. Monthly average of wind speed (open circles) and air temperature (dark circles) from 10-year records at Senda Darwin Biological Station, Chiloé Island (41°50'S).

and *Sphagnum* moss. Secondary forests adjacent to these wet shrublands are dominated by *Drimys winteri*, *Podocarpus nubigena* and *Nothofagus nitida*, with an understory of *Amomyrtus meli*, *Amomyrtus luma*, *Tepualia stipularis* and *Caldcluvia paniculata*, among others, where trees are approximately 28 m height. The shrubland sites, which bear remains of the former forest such as stumps and decaying logs and snags, generally have seasonally waterlogged soils. The establishment of pioneer trees (*D. winteri* and *N. nitida*) is rare or nonexistent in comparison to drier sites, except on microsites elevated above ground level such as decaying logs or piles of woody debris (Christie and Armesto, 2003; Lusk, 1995; Papic, 2000). We selected two study sites, each one composed of a secondary forest and an adjacent secondary shrubland. We estimated ET at one paired forest–shrubland site, and measured the water table at both pairs of sites.

2. Methods

2.1. Water balance estimation

2.1.1. Model

A simple model of the water balance of a forest ecosystem makes it possible to predict the magnitude of changes in various hydrologic vectors after disturbance, such as clearcutting or slash and burning. The model was implemented in Excel, on a 1 h timestep. To obtain ET estimates, we used the Penman–Monteith equation in combination with Gash interception model. To run the model, we used meteorological inputs; parameters for the model were obtained from experimental work and literature. Water table was not directly simulated in the model but was measured independently.

A significant portion of total incident precipitation (P) in a forest stand is intercepted (I) by the tree crowns and returned to the atmosphere through evaporation without reaching the ground. Another fraction of incident precipitation enters the forest ecosystem, filtered by the canopy (throughfall, T_h , that also includes free throughfall, water that does not hit the canopy) and stems (stemflow, S_f), which together are represented by the net precipitation flux (P_{net}). A small fraction of net precipitation is intercepted by the shrub and herbaceous layers or understory, but most of it reaches the soil, where a fraction is captured by vegetation and transpired back to the atmosphere (T), and another fraction becomes drainage water. Both interception and transpiration contribute to the evapotranspiration flux (ET).

2.2. Incident precipitation (P)

We used the meteorological records at Senda Darwin Biological Station (located approximately 150 m from study sites), to determine air temperature, relative humidity, solar radiation and total precipitation data for an open area. In addition, we installed 12 rain gauges in open sites, which enabled us to obtain an additional estimate of incident precipitation when records were missing due to mechanical failure.

2.3. Throughfall (T_h) and stemflow (S_f)

We estimated net precipitation, i.e., the volume of rainfall that reaches the forest floor, which comprises direct throughfall (i.e., rainfall that falls through canopy gaps), leaf drip, and stemflow. Twelve throughfall and 10 stemflow collectors were installed inside a forested 30 m × 30 m plot. Throughfall collectors were funnels of 22 cm diameter connected with a hose to a 5 l polythene container, installed under tree canopy at 1 m above the ground. Stemflow collectors consisted of a rubber channel of 2 cm diameter that was molded around the stem to form a single, closed-loop collar. A hose led from the lowest point of the collar (1.5 m height) to a 25 l polythene container. Trees selected for the study were between 9 and 24 cm diameter at breast height and were representative of the distribution of sizes of this 60-year old forest (Aravena et al., 2002). Throughfall was measured monthly and stemflow was measured weekly. For the analysis of net precipitation we selected 20 short rainfall events (1–2 days) distributed between July 2002 and July 2003.

2.4. Interception (I)

The simple subtraction of net precipitation (P_{net}) from incident precipitation (P) can yield an overestimate of the water losses by interception due to spatial heterogeneity of throughfall. There may be downspouts where large quantities of water are draining, that are not captured by throughfall sampling. Therefore, we estimated interception based on the Gash et al. (1995) analytical model.

$$C_t = P(1 - p_c) - I + C_{t-1} \quad (1)$$

$$P_{net} = C_t - S + P * p_c \quad (2)$$

The storage of rainwater on a canopy (C_t) depends on incident precipitation (P), the fraction of area in canopy gaps (p_c), evaporation from the wet canopy (I) and water stored on the canopy at the beginning of each new increment of rainfall (C_{t-1}) (Eq. (1)). To estimate the maximum canopy storage capacity parameter (S) we ran simulations of canopy water balance during rain storms with S varied systematically, choosing the S that gave the best agreement between simulated and measured P_{net} (Eq. (2)). In this way, we determined the maximum amount of water retained by the forest canopy (4.9 mm). Excess precipitation was converted directly to drainage (Valente et al., 1997). For wet shrublands, we used an S obtained from literature (0.87 mm; Navar and Bryan, 1994).

2.5. Transpiration

To estimate transpiration from the canopy (E_c) in wet shrublands and secondary forests, we used the Penman–Monteith equation (Eq. (3)), modified by Bigelow (2001):

$$E_c = \frac{(1 - p_c)(\Delta R_n + \rho c_p \{e_s(T) - e\} g_a f)}{\lambda(\Delta + \gamma(1 + g_a/g_c))} \quad (3)$$

This equation has physical and biological parameters. In the numerator there are terms affecting the evaporative demand: net

radiation flux density (R_n); the integrated effect of atmospheric saturation deficit ($\{e_s(T) - e\}$); and aerodynamic conductance (g_a). The original equation was modified by adding $(1 - p_c)$, which represents relative canopy cover. The terms in the denominator are parameters that restrict the transfer of water vapor from leaves; specifically, the ratio of aerodynamic conductance (g_a) to canopy conductance (g_c). Additional terms are physical constants defined in [Appendix A](#).

$$g_a = \frac{\mathbf{K}^2 u(z)}{f \ln^2[(z - d)/z_0]} \quad (4)$$

Aerodynamic conductance (g_a) was calculated using the logarithmic wind-profile equation ([Monteith and Unsworth, 1990](#)) (Eq. (4)). Wind speed at instrument height $u(z)$ is assumed to be 0.74 m s^{-1} , roughness length (z_0) is assumed to equal $0.1 \times$ tree height, and zero plane displacement (d) is assumed to equal $0.65 \times$ tree height ([Campbell and Norman, 1998](#)).

Understory transpiration (E_u) was estimated by means of the following equation:

$$E_u = \frac{p_c \Delta R_n}{\lambda(\Delta + \gamma)} \quad (5)$$

This is obtained by multiplying the equilibrium evaporation rate by the fraction of canopy gaps. Parameters such as aerodynamic conductance (g_a) and canopy conductance (g_c) were derived following [Bigelow \(2001\)](#). Simulations were run on a 1 h timestep determined by the frequency of meteorological data collection.

2.6. Stomatal conductance (g_s)

Stomatal conductance was measured on a clear autumn day using an infrared gas analyzer (CIRAS-1, PP-Systems Haverhill, MA, USA). Measurements were made every 2 h, between 9 a.m. and 5 p.m., on shaded leaves of five individuals of *D. winteri* in the forest, and sun-exposed leaves of five individuals of the same species along the forest edge. The latter were used as a proxy for exposed leaves in the forest canopy. In shrublands, measurements were made on sun leaves of seven individuals of *B. patagonica*. These two species were chosen because *D. winteri* is one of the dominant trees in the forest canopy and *B. patagonica* is the most frequent and tallest shrub in wetlands generated after disturbance. High stomatal conductances at 9 a.m. were probably due to leaf wetness from condensation, so these values were discarded. Leaf stomatal conductance values were scaled up to estimate canopy conductance (g_c) ([Bigelow, 2001](#)) (Eq. (6)).

$$g_c = \frac{1}{1/Lg_s + 1/Lg_{bl}} \quad (6)$$

$$g_{bl} = \frac{D_v}{0.004 f(1/u)^{1/2}} \quad (7)$$

Estimates of stomatal conductance contributed less than 1% to the uncertainty of the analysis, so they are an insignificant

source of error ([Bigelow, 2001](#)). Boundary layer conductance (g_{bl}) was determined using the leaf dimension method ([Monteith and Unsworth, 1990](#); [Nobel, 1991](#)) (Eq. (7)), where D_v is the diffusion coefficient of water vapor in air, l is the width of the leaf in the direction of the wind, u is wind speed, and the factor 0.004 has units of $\text{m s}^{1/2}$. Leaf width (l) was 0.05 m for *D. winteri* and 0.002 m for *B. patagonica*.

2.7. Leaf area index (L)

To determine the leaf area index in forest and shrubland sites (necessary for estimating canopy conductance, g_c), we used two LAI-2000 canopy analyzers (Li-Cor, Lincoln, Nebraska, USA). We compared two simultaneous readings of the LAI-2000 taken at random points under shrub or tree canopy and in an adjacent open pasture. These measurements also provided an estimate of the proportion of canopy gaps in each site (p_c).

2.8. Water table depth

We measured the water table level in shrubland and the adjacent forest sites using PVC pipes of 1 m in length and 5 cm diameter. We installed six pipes in sites representative of each vegetation type. Pipes were perforated in the lower portion to allow the free movement of water from soil. Pipes were buried vertically in the soil until reaching the hardpan layer where further penetration was not possible. The hardpan layer was encountered at $54 \pm 5 \text{ cm}$ (mean \pm S.E.) below the ground surface in shrubland and $51 \pm 3 \text{ cm}$ (mean \pm S.E.) in forest. Water table depth records were taken monthly during 2002 and 2003, by using a hanging float placed inside the pipe. Data for shrubland and forest were compared using a repeated measures analysis of variance.

3. Results

3.1. Evapotranspiration

Evapotranspiration contributed 53% of the losses of water from the forest ecosystem ([Table 1](#)). Leaf area indices (L , $\text{m}^2 \text{ m}^{-2}$) were extremely different between forest and shrubland ([Table 2](#)), reflecting the contrasting characteristics of the canopy in both habitats. For shrubland, L was 2.2 ± 0.25 and for the forest 5.0 ± 0.1 (mean \pm 1 S.E.). These values are statistically different ($F_{(1,32)} = 51.24$, $p < 0.001$). Canopy gap fraction (p_c) estimates for each vegetation type also reflect marked differences in canopy cover. Shrubby areas were much more open than forest canopy cover, with large open spaces between shrubs ([Table 2](#)). Stomatal and boundary layer conductance varied between forest and shrubland throughout the day ([Table 3](#)). High leaf boundary layer conductance of shrubs was due to small shrub leaf-size compared to forest trees, but higher leaf area in forest brought canopy conductance up to levels comparable to shrubland ($\sim 2\text{--}4 \text{ mol m}^{-2} \text{ s}^{-1}$). High aerodynamic conductance in forest ($\sim 10\text{--}16 \text{ mol m}^{-2} \text{ s}^{-1}$) was the main factor creating increased ET compared to shrublands ($g_a \sim 3\text{--}5 \text{ mol m}^{-2} \text{ s}^{-1}$; [Fig. 3](#)).

Table 1
Major components of water balance for a forest and successional shrubland in Chiloé

	$E_c + E_u$ (mm)	E_i (mm)	ET (mm)	R_n (mm eq)	P_{net} (mm)	P (mm)
Secondary shrubland	56 (3)	171 (8)	227 (11)	224	1905 (91)	2102
Adjacent forest	296 (14)	656 (31)	952 (45)	234	1407 (67)	2102

Major components of the water balance for a 60-year old forest and a 20-year old secondary shrubland, established after forest clearing. Values in parenthesis indicate percentages with respect to total precipitation (P), which was the annual average for the northern Chiloé (2102 mm). E_c : transpiration from dry canopy; E_u : evaporation and transpiration from understory; E_i : evaporation from wet canopy; ET: evapotranspiration ($ET = E_c + E_u + E_i$); R_n : net solar radiation; P_{net} : net precipitation; P : incident precipitation.

Table 2
Leaf area index and canopy gap fraction in forest and successional shrubland in Chiloé

	L ($m^2 m^{-2}$)	p_c ($m^2 m^{-2}$)
Forest	5.0 ± 0.13	0.02 ± 0.002
Shrubland	2.2 ± 0.25	0.3 ± 0.06

Leaf area index (L) and canopy gap fraction (p_c) in young forest and secondary shrublands in northern Chiloé. Values are averages \pm 1 S.E. ($N = 24$ for shrubland and 10 for forest). L : leaf area index; p_c : canopy gap fraction.

The water balance for the forest studied (Fig. 4), according to the model, suggests that 53% of the incoming water from rainfall goes back to the atmosphere by evapotranspiration. More than half of this value corresponds to interception (I) or direct evaporation from the wet canopy. Transpiration from canopy and understory leaves contributes a lower fraction, with only 22%. Water not intercepted by the canopy reaches the soil as throughfall or stemflow. Both of these components combined account for 67% of the total precipitation. This water can be re-used by plants, taken up from the soil, or infiltrated to deeper soil layers reaching the water table. Consequently, if 53% of precipitation is returned to the atmosphere as ET, we assume that 47% of annual precipitation leaves the system either as deep drainage, overland flow, or as lateral subsurface flow.

If trees are replaced by shrubs in the hydrological model, simulating the effect of clearing of trees by slash and burn (Fig. 5), ET decreased to only 9% of the incoming rainfall, mainly because of a marked reduction in interception surfaces and canopy transpiration. These two values were estimated to be 8% and 1%, respectively. Consequently, rain falls almost directly on the soil, and net precipitation increases to 91%. This new water budget has a significant impact on the depth of the water table in disturbed forest sites (Fig. 6).

Table 3
Stomatal conductance (g_s) and boundary layer conductance (g_{bl}) measured in forest and successional shrubland in Chiloé

Hour	Forest		Shrubland	
	g_s ($mol m^{-2} s^{-1}$)	g_{bl} ($mol m^{-2} s^{-1}$)	g_s ($mol m^{-2} s^{-1}$)	g_{bl} ($mol m^{-2} s^{-1}$)
9:00	5.10	1.68	8.74	7.91
11:00	0.91	1.88	2.47	9.22
13:00	0.93	1.54	1.01	10.78
15:00	1.33	2.12	1.99	8.87
17:00	0.88	2.11	2.47	10.54

Daily stomatal conductance (g_s) and boundary layer conductance (g_{bl}) in forest and shrubland. Data from 1 day on April 2002.

3.2. Water table depth

In 20-year old shrublands, the water table was always shallower than in the adjacent forest site, despite marked seasonal fluctuations (Fig. 6). Over the entire year, the average difference in water table depth between shrubland and adjacent forest was 35 cm. We obtained a mean of 10 ± 1 cm (mean \pm S.E.) depth for the secondary shrubland in contrast to 45 ± 2 cm depth for the adjacent young forest. This difference was statistically significant ($F_{(1,20)} = 67.92$, $p < 0.001$). The water table level in secondary shrublands

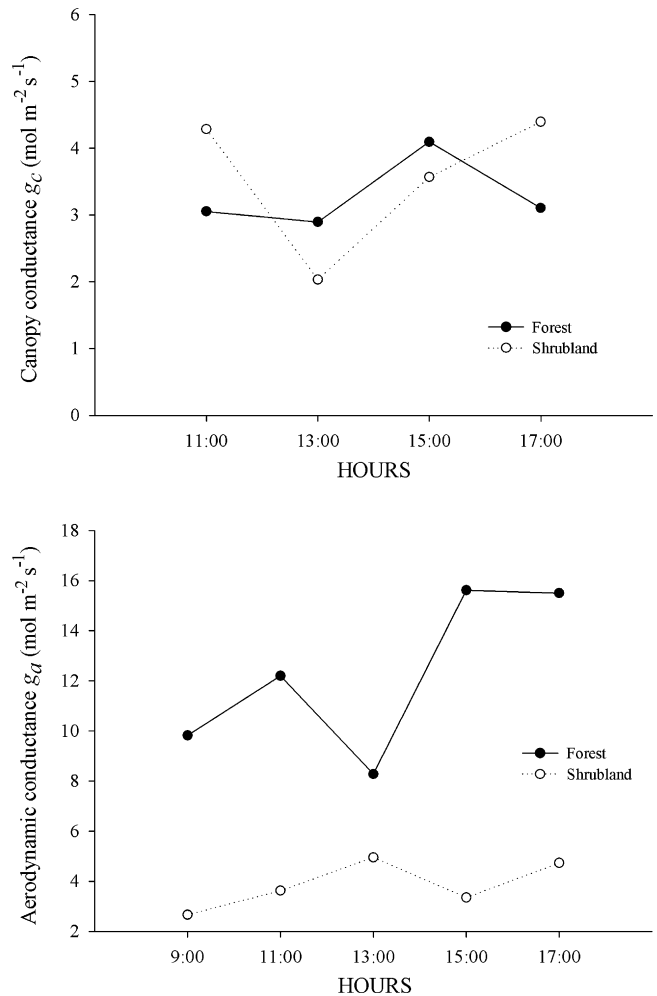


Fig. 3. Canopy (a) and aerodynamic (b) conductance from forest (closed circles) and successional shrubland (open circles) in Chiloé Islands. Measurements were made during one clear day on April 2002, from 9 a.m. to 5 p.m.

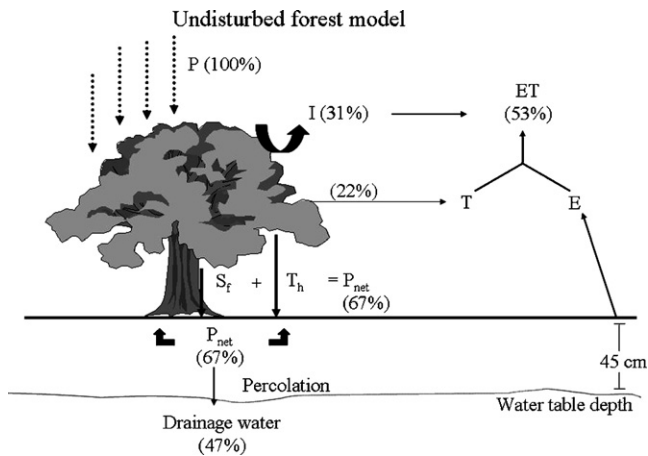


Fig. 4. Water balance model for a young (60-year old) broad-leaved, evergreen forest in northern Chiloé Island, based on parameters estimated in this work for the period 2002–2003. Percentages are relative to total precipitation (P). I : interception; T : transpiration; E : evaporation; ET : evapotranspiration; S_f : stemflow; T_h : throughfall; P_{net} : net precipitation.

frequently reached the soil surface during winter months (Fig. 6).

4. Discussion

In broad-leaved, evergreen forests, the loss of leaf area due to disturbance such as clearcutting or fire significantly reduces the interception of precipitation. In some cases, interception surfaces cannot recover rapidly, as happens when the site is

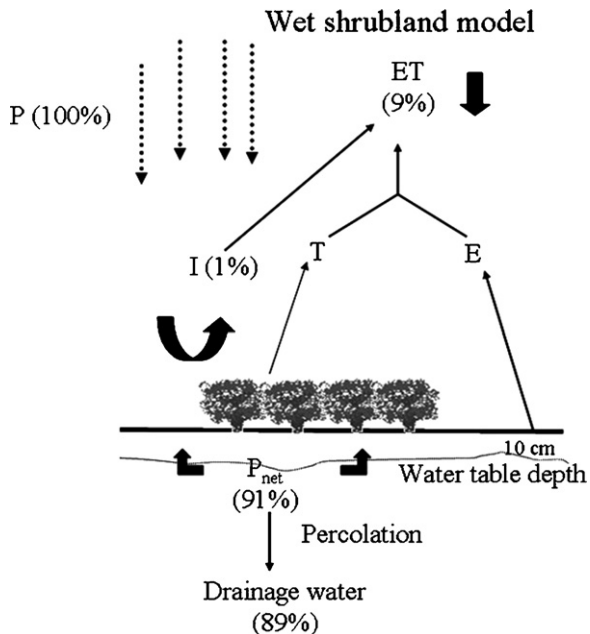


Fig. 5. Water balance model for secondary shrubland, established after clearcutting of forest in northern Chiloé Island. This picture shows differences in model parameters in response to canopy removal. Model was based on parameters estimated in this work for the period 2002–2003. Percentages are relative to total precipitation (P). I : interception; T : transpiration; E : evaporation; ET : evapotranspiration; P_{net} : net precipitation.

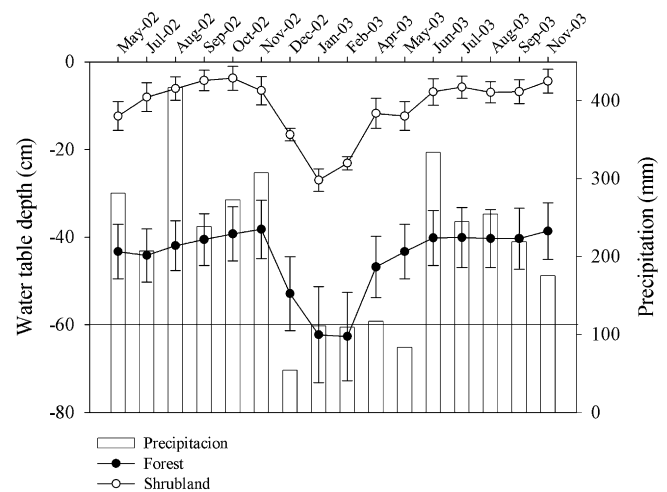


Fig. 6. Groundwater depth in a secondary shrubland and adjacent broad-leaved forest stand in northern Chiloé Island for the period 2002–2003. Circles are mean monthly values of water table depth \pm 1 S.E. in secondary shrubland (open) and forest (closed). Bars are monthly precipitation values for the same period in mm. Horizontal line at 60 cm depth indicates maximum depth of detection and the approximate position of the hardpan layer.

colonized by small-leaved shrubs that tolerate humid soils, such as *Baccharis* shrubs in the study area (Papic, 2000). The hydrological model presented here estimates that 53% of the rainfall returns to the atmosphere as water vapor in an undisturbed evergreen rain forest of northern Chiloé. In contrast, in recently colonized secondary shrublands, almost all precipitation impacts directly on the soil or on the shrub cover, which has a lower interception surface than the multi-layered, broad-leaved foliage of temperate forest (Gutiérrez et al., 2004). Accordingly, ET drops to 9% of total precipitation, a difference which is much higher than would be expected solely on the basis of the difference in leaf area index. As a direct consequence, there is an increase in the water table in disturbed sites covered by shrubs. Water saturation is exacerbated by poor drainage in these soils (Strahler and Strahler, 1984).

Historically, evaporation models have performed best in temperate humid climates, since most such models are controlled principally by meteorology rather than by the physiology of the tree species. In this study, we document that evapotranspiration differences between secondary shrublands and adjacent forest are a direct consequence of vegetative cover. An estimate of the energy that annual net radiation normally provides to a forest at this temperate latitude ($R_n/\lambda = 234$ mm) would not be enough to explain the 1111 mm of water that are actually evapotranspired (Table 1). This suggests that heat is being extracted from air masses by advection, consistent with Calder's (1998) argument about wet temperate forests. Calder (1998) has shown that in windy, wet temperate forests such as the one at our study site, enough energy can be extracted from passing air masses to fuel several times the evaporation that would be possible if radiant energy were the only energy source. Shrubs are less capable of extracting this type of energy because they are not strongly connected to the atmosphere

compared to trees (i.e., they are not as aerodynamically rough); consequently, they are much more dependent on the net radiation as a heat source for evapotranspiration. Therefore, secondary shrubland vegetation evaporates less water due to small advective energy inputs.

A biophysical model is a useful tool to explore the hydrological consequences of forest or vegetation cover disturbance (e.g., Shukla and Mintz, 1982). The analytical model of Gash et al. (1995) permitted us to estimate canopy interception and therefore water flows in the undisturbed broad-leaved forest. The simple subtraction of rainfall from net precipitation (throughfall plus stemflow) leads to overestimation of water losses by interception. Gash's model incorporates discrete rainfall events, each one comprising early wetting of the canopy, a saturation period, and a drying period when the rainfall has stopped. This model has been used to estimate interception in conifer forests of Great Britain (Gash et al., 1980), tropical rainforests of the Amazon (Lloyd et al., 1988) and evergreen broad-leaved forests in New Zealand (Pearce and Rowe, 1981), all of which have physiognomic and structural similarities to southern Chilean temperate rainforests (Armesto et al., 1996).

Rain can follow three pathways upon entering a forested ecosystem: (a) evaporation to the atmosphere from leaves and soil surface (evapotranspiration), (b) infiltration to deeper soil layers, including lateral transfer across geological strata, and (c) runoff and streamflow. Evapotranspiration is one of the fundamental factors regulating water flow through streams and rivers draining a forested basin (Aber and Federer, 1992; Larcher, 1995; Jarvis et al., 1997; Kimball et al., 1997; White et al., 1998). Because chemical flows are intimately linked to the hydrological cycle, disturbance events that alter the hydrological flows can have impacts on the nutrient budgets of terrestrial and aquatic ecosystems (Likens et al., 1978; Jackson et al., 2001). Several studies have documented the relationship between nutrient flows and storage and hydrologic pathways (Likens et al., 1978; Godoy et al., 1999; Salmon et al., 2001; Perakis and Hedin, 2002). The changes in evapotranspiration that may occur after disturbances that alter the vegetation cover of a basin (Swift et al., 1975; Huber et al., 1985; Whitehead and Kelliher, 1991), may affect local hydrology including overland and deep water flows.

These hydrologic changes associated with anthropogenic disturbance to forests have spread rapidly through the rural landscape of southern Chile, especially during the past decades (Willson and Armesto, 1996; Armesto et al., 2001), and can have broad consequences on successional processes and tree regeneration. Recent studies (Papic, 2000; Díaz, 2004) have postulated an interruption of the successional process following clearing of forests, and their replacement by open shrublands, because of waterlogging of soils. This alteration of the depth of the water table would be difficult to reverse, at least for a long period until drainage of the sites changes and canopy cover recovers to its pre-disturbance condition. Tree regeneration in these secondary shrublands is severely limited (Díaz and Armesto, 2007), presumably because seedlings of most pioneer tree species that should

colonize open areas are not capable of surviving in seasonally waterlogged sites. It has been documented in disturbed shrublands in Chiloé Island that tree regeneration is restricted to the surface of logs, stumps, and accumulations of woody detritus (Lusk, 1995; Christie and Armesto, 2003). The establishment of tree seedlings in high rainfall sites is favored by the presence of coarse woody debris. Papic (2000) suggests that the presence of woody debris on the disturbed areas could favor colonization of tree species in early succession on Chiloé forests, preventing the monopolization of substrate by shrub species such as *Baccharis* and buffering the negative effects of waterlogging. The establishment of pioneer trees, e.g., *D. winteri* and *N. nitida*, seems to be very slow or scanty when compared with drier sites (Aravena et al., 2002).

5. Conclusion

The notable contrast between the estimated hydrological fluxes for the forest area before and after a disturbance emphasizes the importance of the analysis of hydrological cycles in forested catchments under silvicultural management, and the importance of trees as ecosystem engineers. Changes in land use are one of the most important human impacts in southern Chilean forests (Lara et al., 1996; Armesto et al., 2001). Postglacial soils are broadly characterized by poor drainage and they occupy large areas of Chiloé Island (Aravena, 1991) and the Lake District (Veit and Garleff, 1996). This soil type was colonized by forest (Villagrán et al., 1986; Villagrán, 1990a,b; Moreno and León, 2003; Abarzúa et al., 2004; Moreno, 2004) during the Holocene at different rates depending on drainage conditions, following deglaciation. The recent expansion of waterlogged areas due to human disturbance to forest cover has created open lands of low productivity (e.g., shrub- and moss-invaded pastures). This trend can be seen as a reversal of Holocene forest expansion. Absent active efforts to restore microsites where trees can germinate readily, the impacts of earlier human activities on this landscape will be felt for an exceedingly long time.

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Appendix A. Symbols used in the model and in the text

Symbol	Units	Value	Definitions
C_t	mm	^a	Depth of water on canopy
d	m	^a	Zero place displacement
D_v	$\text{m}^2 \text{s}^{-1}$	22.5×10^{-6}	Molecular diffusion coefficient of water vapor in air atmospheric vapor pressure
E	kPa	^a	Atmospheric vapor pressure
$e_s(T)$	kPa	^a	Saturated vapor pressure at temperature T
ET	mm s^{-1}	^a	Evapotranspiration
E_c	mm s^{-1}	^a	Transpiration from dry canopy
E_u	mm s^{-1}	^a	Evaporation and transpiration from understory
I	mm s^{-1}	^a	Evaporation from wet canopy
f	$\text{M}^3 \text{mol}^{-1}$	0.0245	Converts conductance from units of $\text{mol m}^{-2} \text{s}^{-1}$ to m s^{-1} at 25 °C and sea level atmospheric pressure
g_a	$\text{mol m}^{-2} \text{s}^{-1}$	^a	Aerodynamic conductance
g_{bl}	$\text{mol m}^{-2} \text{s}^{-1}$	^a	Boundary layer conductance
g_c	$\text{mol m}^{-2} \text{s}^{-1}$	^a	Canopy conductance
g_s	$\text{mol m}^{-2} \text{s}^{-1}$	^a	Stomatal conductance
I	mm	^a	Interception
K	~	0.41	von Karman's constant
l	m	^a	Leaf width
L	$\text{m}^2 \text{m}^{-2}$	^a	Leaf area index
P	mm	^a	Precipitation
p_c	$\text{m}^2 \text{m}^{-2}$	^a	Canopy gap fraction (=1 – canopy cover)
P_{net}	mm	^a	Net precipitation (throughfall + stemflow)
R_n	$\text{J m}^{-2} \text{s}^{-1}$	^a	Net radiation
S	mm	^a	Maximum canopy water storage capacity
S_f	mm	^a	Stemflow
T_h	mm	^a	Throughfall
u	m s^{-1}	^a	Wind speed
z	m	10	Height of meteorological instruments
z_0	m	^a	Roughness length
γ	kPa K^{-1}	0.0664	Psychrometer constant at 25 °C
Δ	kPa K^{-1}	^a	Rate of increase in saturated vapor pressure with temperature
λ	J g^{-1}	2435	Latent heat of vaporization of water at 25 °C
ρ	g m^{-3}	1184	Air density at 25 °C

^a Measured or estimated values.

References

- Abarzúa, A.M., Villagrán, C., Moreno, P.I., 2004. Deglacial and postglacial climate history in east central Isla Grande de Chiloé, southern Chile (43°S). *Quater. Res.* 62, 49–59.
- Aber, J.D., Federer, C.A., 1992. A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. *Oecologia* 92, 463–474.
- Aravena, J.C., 1991. Análisis de la estructura y la Flora de los bosques de Chiloé Continental e Insular. Tesis de Magíster en Ciencias Biológicas con mención en Botánica, Facultad de Ciencias, Universidad de Chile.
- Aravena, J.C., Carmona, M.R., Pérez, C.A., Armesto, J.J., 2002. Changes in tree species richness, stand structure and soil properties in a successional chronosequence of forest fragments in northern Chiloé Island, Chile. *Rev. Chilena Hist. Nat.* 75, 339–360.
- Armesto, J.J., León-Lobos, P., Arroyo, M.T.K., 1996. Los bosques templados del sur de Chile y Argentina: una isla biogeográfica. In: Armesto, J.J., Villagrán, C., Arroyo, M.T.K. (Eds.), *Ecología de los bosques nativos de Chile*. Editorial Universitaria, Santiago, pp. 23–27.
- Armesto, J.J., Villagrán, C., Donoso, C., 1994. Desde la era glacial a la industrial: La historia del bosque templado chileno. *Ambiente y Desarrollo X*, 66–72.
- Armesto, J.J., Rozzi, R., Caspersen, J., 2001. Temperate forests of North and South America. In: Chapin, F.S., Sala, O.E., Huber-Sannwald, E. (Eds.), *Global Biodiversity in a Changing Environment. Scenarios for the 21st Century*. Springer, New York, pp. 223–249.
- Bigelow, S., 2001. Evapotranspiration modeled from stands of three broad-leaved tropical trees in Costa Rica. *Hydrol. Process.* 15, 2779–2796.
- Calder, I.R., 1990. *Evaporation in the Uplands*. Wiley, Chichester, UK.
- Calder, I.R., 1998. Water use by forests, limits and controls. *Tree Physiol.* 18, 625–631.
- Campbell, G.S., Norman, J.M., 1998. *An Introduction to Environmental Biophysics*, 2nd ed. Springer-Verlag, New York.
- Christie, D.A., Armesto, J.J., 2003. Regeneration microsites and tree species coexistence in temperate rain forests of Chiloé Island, Chile. *J. Ecol.* 91, 776–784.
- Di Castri, F., Hajek, E.R., 1976. *Bioclimatología de Chile Santiago*. Editorial de la Universidad Católica de Chile, Chile.
- Díaz, M.F., 2004. Limitantes biológicas e hidrológicas de la sucesión secundaria en bosques de Chiloé. Tesis de Doctorado en Ciencias mención Ecología y Biología Evolutiva, Facultad de Ciencias, Universidad de Chile, Santiago.
- Díaz, M.F., Armesto, J.J., 2007. Limitantes físicos y bióticos de la regeneración arbórea en matorrales sucesionales de la Isla Grande de Chiloé, Chile. *Revista Chilena de Historia Natural* 80, 13–26.
- FAO-UNESCO, 1971. *Soil Map of the World-1:5000000, South America*. UNESCO, IV París.
- Gash, J.H.C., Lloyd, C.R., Lachaud, G., 1995. Estimating sparse forest rainfall interception with an analytical model. *J. Hydrol.* 170, 79–86.
- Gash, J.H.C., Wright, I.R., Lloyd, C.R., 1980. Comparative estimates of interception loss from three coniferous forests in Great Britain. *J. Hydrol.* 48, 89–105.

- Gilpin, M.E., Case, T.J., 1976. Multiple domains of attraction in competition communities. *Nature* 261, 40–42.
- Godoy, R., Oyarzún, C., Bahamondes, J., 1999. Flujos hidroquímicos en un bosque de *Nothofagus pumilio* en el Parque Nacional Puyehue, sur de Chile. *Rev. Chilena Hist. Nat.* 72, 579–594.
- Gutiérrez, A.G., Armesto, J.J., Aravena, J.C., 2004. Disturbance and regeneration dynamics of an old-growth North Patagonian rain forest in Chiloé Island, Chile. *J. Ecol.* 2, 598–608.
- Huber, A., Oyarzún, C., Ellies, A., 1985. Balance hídrico en tres plantaciones de *Pinus radiata*. II. Humedad del suelo y evapotranspiración. *Bosque* 6, 74–82.
- INFOR, 1999. Informe Regional de la Décima Región. Catastro y evaluación de recursos vegetacionales nativos de Chile.
- Jackson, R.B., Carpenter, S.R., Dahm, C.N., McKnight, D.M., Naiman, R.J., Postel, S.L., Running, S.W., 2001. Water in a changing world. *Ecol. Appl.* 11, 1027–1045.
- Jarvis, P.G., Massheder, J.M., Hale, S.E., Moncrieff, J.B., Rayment, M., Scott, S.L., 1997. Seasonal variation of carbon dioxide, water vapor, and energy exchanges of a boreal black spruce forest. *J. Geophys. Res.* 102, 28953–28966.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *OIKOS* 69, 373–386.
- Kimball, J.S., White, M.A., Running, S.W., 1997. BIOME-BGC simulations of stand hydrologic processes for BOREAS. *J. Geophys. Res.* 102, 29043–29051.
- Lara, A., Donoso, C., Aravena, J.C., 1996. La conservación del bosque nativo de Chile: problemas y desafíos. In: Armesto, J.J., Villagrán, C., Arroyo, M.T.K. (Eds.), *Ecología de los bosques nativos de Chile*. Editorial Universitaria, Santiago, pp. 335–362.
- Larcher, W., 1995. *Water Relations. Physiological Plant Ecology*. Springer-Verlag, Berlin, Heidelberg, pp. 215–275.
- Likens, G.E., Bormann, F.H., Pierce, R.S., Reiners, W.A., 1978. Recovery of a deforested ecosystem. *Science* 199, 492–496.
- Lloyd, C.R., Gash, J.H.C., Shuttleworth, W.J., Marques, A.D.O., 1988. The measurement and modelling of rainfall interception by Amazonian rain forest. *Agric. For. Meteorol.* 43, 277–294.
- Lusk, C., 1995. Seed size, establishment sites and species coexistence in a Chilean rain forest. *J. Veg. Sci.* 6, 249–256.
- May, R.M., 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* 269, 471–477.
- Monteith, J.L., Unsworth, M.H., 1990. *Principles of Environmental Physics*, 2nd ed. Edward Arnold, United Kingdom.
- Moreno, P.I., 2004. Millennial-scale climate variability in northwest Patagonia over the last 15,000 year. *J. Quat. Sci.* 19, 35–47.
- Moreno, P.I., León, A.L., 2003. Abrupt vegetation changes during the last glacial to Holocene transition in mid-latitude South America. *J. Quat. Sci.* 18, 787–800.
- Navar, J., Bryan, R.B., 1994. Fitting the analytical model of rainfall interception of Gash to individual shrubs of semi-arid vegetation in northeastern Mexico. *Agric. For. Meteorol.* 68, 133–143.
- Nobel, P.S., 1991. *Physicochemical and Environmental Plant Physiology*. Academic Press, San Diego, CA.
- Noy-Meir, I., 1975. Stability of grazing systems: an application of predator-prey graphs. *J. Ecol.* 65, 459–481.
- Papic, C., 2000. Regeneración de plántulas arbóreas sobre material leñoso en descomposición en un bosque sucesional de Chiloé, Chile. Tesis de Magíster en Ciencias con mención en Biología, Facultad de Ciencias, Universidad de Chile.
- Pearce, A.J., Rowe, L.K., 1981. Rainfall interception in a multi-storied, evergreen mixed forest: estimates using Gash's analytical model. *J. Hydrol.* 49, 341–353.
- Perakis, S.S., Hedin, L.O., 2002. Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds. *Nature* 415, 416–419.
- Pérez, C.A., Carmona, M.R., Armesto, J.J., 2003. Non-symbiotic nitrogen fixation, net nitrogen mineralization and denitrification in evergreen forests of Chiloé Island, Chile: a comparison with other temperate forests. *Gayana Bot.* 60, 25–33.
- Roy, V., 1998. Impacts of the modification of the hydrological regime by clearcutting and draining forested wetlands on growth of natural and planted seedlings. Ph.D. Dissertation. Université Laval, Québec, Canada.
- Ruprecht, J.K., Schofield, N.J., 1991. Effects of partial deforestation on hydrology and salinity in high salt storage landscapes. I. Extensive block clearing. *J. Hydrol.* 129, 19–38.
- Ruthsatz, B., Villagrán, C., 1991. Vegetation pattern and soil nutrients of a Magellanic moorland on the Cordillera de Piuchué, Chiloé Island, Chile. *Rev. Chilena Hist. Nat.* 64, 461–478.
- Salmon, C.D., Walter, M.T., Hedin, L.O., Brown, M.G., 2001. Hydrological controls on chemical export from an undisturbed old-growth Chilean forest. *J. Hydrol.* 253, 69–80.
- Shukla, J., Mintz, Y., 1982. Influence of land surface evapotranspiration on the earth's climate. *Science* 215, 1498–1501.
- Strahler, A.N., Strahler, A.H., 1984. *Elements of Physical Geography*, 3rd ed. John Wiley & Sons, New York, Chichester, Brisbane, Toronto, Singapore.
- Swift, L.W., Swank, W.T., Mankin, J.B., Luxmoore, R.J., Goldstein, R.A., 1975. Simulation of evapotranspiration and drainage from mature and clear-cut deciduous forests and young pine plantation. *Water Resour. Res.* 11, 667–673.
- Valente, F., David, J.S., Gash, J.H.C., 1997. Modelling interception loss for two sparse eucalypt and pine forests in central Portugal using reformulated Rutter and Gash analytical methods. *J. Hydrol.* 190, 141–162.
- Veit, H., Garleff, K., 1996. Evolución del paisaje cuaternario y los suelos en Chile central-sur. In: Armesto, J.J., Villagrán, C., Arroyo, M.T.K. (Eds.), *Ecología de los bosques nativos de Chile*. Editorial Universitaria, pp. 29–50.
- Villagrán, C., 1990a. Glacial Climates and their effects on the history of vegetation of Chile. A synthesis based on palynological evidence from Isla de Chiloé. *Rev. Palobot. Palynol.* 65, 17–24.
- Villagrán, C., 1990b. Glacial, late glacial and post glacial climate and vegetation of the Isla Grande de Chiloé, southern Chile (41–44°S). *Quat. South America Antarctic Peninsula* 8, 1–15.
- Villagrán, C., Armesto, J.J., Leiva, R., 1986. Recolonización postglacial de Chiloé insular: evidencias basadas en la distribución geográfica y los modos de dispersión de la flora. *Rev. Chilena Hist. Nat.* 59, 19–39.
- Waring, R.H., Schlesinger, W.H., 1985. *Hydrology of Forest Ecosystems. Forest Ecosystems. Concepts and Management*. Academic Press, Inc., pp. 94–120.
- White, J.D., Running, S.W., Thornton, P.E., Keane, R.E., Ryan, K.C., Fagre, D.B., Key, C.H., 1998. Assessing simulated ecosystem processes for climate variability research at Glacier National Park, USA. *Ecol. Appl.* 8, 805–823.
- Whitehead, D., Kelliher, F.M., 1991. A canopy water balance model for a *Pinus radiata* stand before and after thinning. *Agric. For. Meteorol.* 55, 109–126.
- Willson, M.F., Armesto, J.J., 1996. The natural history of Chiloé: on Darwin's trail. *Rev. Chilena Hist. Nat.* 69, 149–161.