Extreme environments in the forests of Ushuaia, Argentina

Hector D'Antoni,¹ Lynn Rothschild,¹ Cynthia Schultz,² Seth Burgess,² and J. W. Skiles¹

Received 27 June 2007; revised 21 August 2007; accepted 4 October 2007; published 20 November 2007.

[1] A survey over two mountain slopes (Glaciar Martial and Cerro Guanaco) in the vicinity of Ushuaia (Tierra del Fuego, Argentina) showed normal results for the region in terms of chlorophyll concentration in the leaves of the dominant tree species Nothofagus antarctica, N. pumilio and N. betuloides, and soil variables such as temperature, moisture, pH, and concentration of nitrogen, sodium and potassium. Solar radiation, on the other hand, showed high values of ultraviolet over the 200-400 nm range, suggesting that the environment is extreme in terms of incoming solar radiation. The forest canopy absorbs and/or reflects a significant amount of that radiation. In separate analyses we showed that these tree species contain UVabsorbing pigments (cvanidin, delphidin, and flavonol glycosides). We submit that the rippled and glossy surface of leaves serves as a reflection/backscattering mechanism that protects their inner structure and function. The presence of krummholz (= twisted, dwarf trees) in the upper end of the forest shows the effects of an extreme environment. Citation: D'Antoni, H., L. Rothschild, C. Schultz, S. Burgess, and J. W. Skiles (2007), Extreme environments in the forests of Ushuaia, Argentina, Geophys. Res. Lett., 34, L22704, doi:10.1029/2007GL031096.

1. Introduction

[2] The *Isla Grande de Tierra del Fuego* is the largest landmass at the southern tip of South America. This unique territory is often under the direct influence of the springtime "Ozone hole" that hovers above Antarctica. Ushuaia is the main town of the big island and one of its remarkable features is the upper timberline of the nearby Andean mountains. With the seasons, the top of these mountains is viewed either as solid rock and debris devoid of life or covered by snow (some with permanent ice). The upper timberline is a straight line that marks the upper end of the forest and identifies an *extreme environment* for complex life in the Andes of Tierra del Fuego, and elsewhere (Figure 1).

[3] The breakthrough finding of UV-C in the Bolivian Altiplano by Rothschild and Rogoff followed by our finding in Lago Argentino stimulated us to investigate the upper timberline in Tierra del Fuego as an extreme environment. Extreme environments can be characterized by their low or high pH [*Palacios et al.*, 2004; *Amaral Zettler et al.*, 2004], low or high temperature [*Huber*, 2004; *Lipps*, 2004] high salt concentration or hypersaline, high concentration of metals [*Amils*, 2004], great pressure as found at 2000 m below the surface of marine and some freshwater environmetation.

ments or ice [*Tung et al.*, 2006] lack of water or oxygen [*Hoehler*, 2005], and exposure to extreme solar radiation in the infrared and the ultraviolet bands of the electromagnetic spectrum [*Cockell et al.*, 2005]. Research in Astrobiology focuses on extreme environments because they provide analogs of the environments where early developmental stages of life may have taken place and, by extension, where life may have developed in other worlds. Modern extreme environments are used to acquire insight into their structure and functions and to develop and test mechanistic hypotheses to be used subsequently to build predictive models.

2. Biological Relevance of Ambient UV-C Radiation

[4] Nucleic acids have a strong absorbance around 260 nm due to the aromatic π -electron system of pyrimidine and purine bases [Parson and Gross, 1980; Tevini, 1993]. Proteins have an absorbance maximum at about 280 nm due to the absorption by the aromatic amino acids phenylalanine, tyrosine and triptophane [Grossweiner, 1976]. Some lipids absorb in the UV range because of their single or conjugated π -electron systems of their highly unsaturated fatty acids (as linoleic acid) that are part of the complex membrane lipids. Abscisic acid (a phytohormone) and Indole Acetic Acid (IAA), a growth hormone or auxin, also absorb in the UV range [Caldwell et al., 1986; Coohill, 1989; Rundel, 1983]. From these effects, fundamentally results of laboratory work, projections are made to microbiology, plant and animal biology. It is clear that the shorter the UV wavelength, the more energy is to be found in the photons and the more powerful the effects. However, short wave radiation is more bound to reflection, bouncing and backscattering [Weber et al., 1959].

[5] For fieldwork in Tierra del Fuego we developed a survey-style protocol to measure ecosystem parameters such as soil pH, temperature, humidity, ions (Na, K, and N) concentration, in plants we measured chlorophyll absorbance in the red and near infrared, and we recorded solar radiation in the UV band, air temperature and relative humidity. We measured these parameters at the top, in the middle and at the bottom of the forests growing on the slopes of the Andes at Glaciar Martial and Cerro Guanaco. These data are not enough to make hard statistical analyses but rather to generate testable hypotheses and an intensive research program. As shown in results, most variables behave as expected except for the UV solar radiation that exhibits high values probably due to the effects of the global ozone depletion and the ozone hole.

[6] Tree growth is often very stunted at the upper timberline where the last trees form a low, densely matted belt known as krummholz (from the German *krumm*, twisted; and *holz*, wood) [*Mueller-Dombois and Ellenberg*,

¹NASA Ames Research Center, Moffett Field, California, USA.

²Geology Department, San Jose State University, San Jose, California, USA.

Copyright 2007 by the American Geophysical Union. 0094-8276/07/2007GL031096

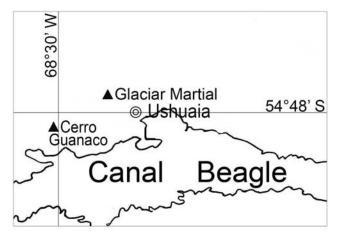


Figure 1. Location of Glaciar Martial (first transect) and Cerro Guanaco (second transect) in the vicinity of Ushuaia.

2002]. Originally this life form was considered genetically determined [Holtmeier, 1981] but the term was subsequently used to designate all genetically or environmentally determined stunted and dwarf trees at the timberland [Norton and Schönenberger, 1984; Barrera et al., 2000]. Generally, trees do not grow in places where the mean temperature of the warmest month is less than 10°C [Williams, 1961; Tranquillini, 1979; Grace, 1989]. The aerodynamic roughness of forest vegetation allows air circulation among the branches making the temperature of above-ground tissues closely coupled to the air temperature. Shorter vegetation has tissue temperature and microclimates that depend upon other climate variables, notably radiation and wind speed. At this level, water stress occurs in late winter and early spring, when soil water is frozen [Grace, 1989]. Studying plant species distribution across two contrasting treeline ecotones in the Spanish Pyrinees, Camarero and Gutiérrez [2002] found that regeneration concentrated near the krummholz area and over the rocky substrates, and suggested that krummholz may modify microenvironment conditions and increase seedling survival. Summarizing this vegetation-analysis approach, Wardle [1973] observed that, at higher altitudes, woody plants can occur as shrubs and krummholz, by benefiting from warmer day-time temperatures close to the ground. For New Zealand, Wardle [1973] observes that wind-depressed timberlines and stunted woody vegetation occur in exposed mountains. The main ranges are less exposed, but locally they host krummholz-forming species. Deciduous Nothofagus species are absent in New Zealand, but dominate widely in the drier and colder environment of the southern Andes [Wardle et al., 2001].

[7] Nothofagus pumilio is a deciduous tree species that dominates the upper tree line of the Chilean and Argentinean Andes in this latitudinal range [Lara et al., 2005]. In Tierra del Fuego, the Nothofagus krummholz zone at the upper timberline is formed by the deciduous species Notofagus antarctica ("ñire") and N. pumilio ("lenga"). The krummholz here is a belt of variable width from a few to several hundred meters. Barrera et al. [2000] studied changes, both structural (density, height, basal area, above-ground tree biomass, leaf area index), and functional (leaf phenology, growth rate, fine litter fall, leaf decomposition) in N. pumilio forests along an altitudinal gradient in Tierra del Fuego (Argentina). They found that dead stems increased with elevation in erect forests, but the trend was inverted in krummholz. The authors suggest that krummholz is not only a morphological response to the adverse climate but also a life-form (biotype) with functional advantages. Along those lines, Frangi et al. [2005] analyzed the nutrient cycling of the N. pumilio krummholz finding fast turnover, storage in branch biomass, faster cycles of retention and recycling, greater dependence on biotic recycling of nutrients, and morphological characteristics associated to leaf size, number, duration, etc. By studying isozyme polymorphisms, Premoli [2003] provided evidence of clinal variation with elevation in N. pumilio and tested the hypothesis that different growth forms of that species in the forests of the southern Andes will display continuous genetic variation with elevation. Overall, the results showed that the populations from low-elevations were more variable than those from high elevations. Pollmann and Hildebrand [2005] analyzed the structure and composition of species in timberline ecotones of the southern Andes concluding that on the wind-exposed side, growth forms were characterized by single stemmed habit and long branches running uphill. These growth form changes were apparently controlled by changes in abiotic factors and climate rather than genetically determined.

[8] We do not see a conflict between the genetic and the structural-functional points of view but two complementary approaches to a single problem. Consequently, we conducted our survey by measuring biotic and abiotic parameters at the upper timberline and then down to the middle of the slope and to the foothills.

3. Materials and Methods

[9] For this work we took measurements along two slopes (Glaciar Martial and Cerro Guanaco) between the surroundings of the upper timberline and the foothills. Samples were numbered (1) around the upper timberline, (2) half the way down and under the foliage, and (3) at the foothill level.

[10] The samples consisted of: (a) latitude, longitude and elevation, (b) forest composition, (c) chlorophyll concentration estimates, (d) soil temperature at 20 cm below the surface, (e) soil moisture at about 20 cm below the surface, (f) soil pH, (g) concentration of nitrogen in soil, (h) concentration of sodium in soil, (i) concentration of potassium in soil, and (j) solar irradiance.

[11] An eTrex handheld GPS (Garmin) was used to determine latitude, longitude and elevation of each sampling site, forest composition consists of two dominant tree species, *N. antarctica* and *N. pumilio* [*Bisheimer and Fernandez*, 2000]. We used a Minolta SPAD 502 to estimate chlorophyll concentration from the ratio of absorbance in the red and in the infrared, soil temperature was measured with a digital thermometer at 20 cm below the surface, soil moisture was measured with a Field Scout TDR 100 instrument (Spectrum Technologies, Inc.), pH was measured in situ with a portable pH probe (Shindengen pH Pro), nitrogen, sodium and potassium concentration was determined with N-, Na-, and K-specific Cardi-Horiba instruments (Spectrum Technologies, Inc.). For solar radia-

				Air		Chloroph.	Soil					
Site and	Latitude,	Longitude,	Elevation,	Temperature,	Percent	SPAD	Temperature,	Soil %	Soil	Soil	Soil [Na],	Soil [K],
Time	S	W	m	deg C	Humidity	Units	deg C	Humidity	pН	[N], ppm	ppm	ppm
Glaciar Martial												
GM1, 13:37	54°47′30″	68°22′25″	572	20.0	41.0	41.0	7.3	33.2	6.6	13	1400	50
GM 2, 15:06	54°47′55″	68°22′50″	452	14.7	64.0	32.4	6.8	14.8	5.8	14	1400	40
GM 3, 16:32	54°48′20″	68°21′35″	245	13.4	56.9	38.2	9.3	4.8	6.1	14	1600	70
Cerro Guanaco												
CG 1, 12:41	54°48′40″	68°32′10″	655	12.8	59.4	n/a	8.7	9.0	6.7	13	1600	80
CG 2, 14:08	54°48′58″	68°33′00″	504	14.2	62.5	34.8	5.2	10.9	5.5	14	1700	100
CG 3, 15:06	54°49'10"	68°31′45″	485	18.5	52.0	42.4	8.2	4.0	6.9	15	1700	250

Table 1. Measurements at Glaciar Martial (GM) and Cerro Guanaco (CG)

tion we used a USB-4000 Spectrometer by Ocean Optics, connected to a Dell Inspirion PC laptop. The spectroradiometer was fitted with a Toshiba TCD 1304AP CCD detector with an L4 collection lens, a UV4 window upgrade and a OVFL-200-850 variable longpass order-sorting filter to eliminate second- and third-order effects and render a clean first order spectrum. The pixel size is 8 μ m \times 200 μ m with a well depth of approximately 100,000 electrons. The sensitivity is of 130 photons/count at 400 nm and 60 photons/count at 600 nm. The 600 lines grating is blazed at 400 nm and the collection window is a CC-3-DA directattach Cosine Corrector with a Spectralon diffuser for the UV-NIR range. The optical resolution is 0.3 nm, signal-tonoise 300:1 at full signal, the stray light is <0.05 % at 600 nm, <0.10 % at 435 nm. The best efficiency (>30%) of this outfit is in the 250-800 nm. This outfit was calibrated in factory for irradiance and wavelength, according to the NIST Handbook 120-2E for Optical Radiation Measurements. Because of its CCD technology, our spectroradiometer takes one "snapshot" of solar irradiance every 100 μ s. We take the average of 10 readings and apply a Boxcar smoothing of five averaged spectra. The spectra were taken around noon, on January 7, 2007 (Glaciar Martial) and on January 8, 2007 (Cerro Guanaco) under clear sky and within the solar angle of 52° above the horizon (>75% erythema exposure [Madronich, 1993]). All the other measurements were done as shown in Table 1.

4. Results

4.1. Glaciar Martial Transect

[12] GM 1 is high in the 400–315 nm band, and the highest in the 270–250 nm band. GM 2 has the lowest values for the range of 400–250 nm. This record was taken in the *Nothofagus* forest and shows that the canopy absorbs and/or reflects a significant part of the UV-band from 400 nm through 250 nm. GM 3 is high in the 400–315 nm band, then values go down to a minimum at 300 nm and rise again to reach 4 $\mu W^* cm^{-2*} nm^{-1}$ at wavelength 250 nm (Table 1).

[13] Glaciar Martial (Table 1) exhibits a strong soil moisture gradient from the top sample to the bottom one, pH is lowest in the middle sample, N, Na, and K are slightly more abundant in the bottom sample. Cerro Guanaco (Table 1) exhibits changes among samples in soil humidity, pH, N, Na, and K. Overall, these changes fall within the values we recorded in our survey of 11 forest locations in Tierra del Fuego. Soil temperature is probably the highest of the year, and reaches its maximum in the zones of naked soil.

4.2. Solar Irradiance in the Ultraviolet

4.3. Cerro Guanaco Transect

[14] CG 1 exhibits high values of UV-A (315–400 nm), then falls to a few $\mu W^* cm^{-2*} nm^{-1}$ between 303 and 280 nm, where the values rise 8 $\mu W^* cm^{-2*} nm^{-1}$ at wavelength 250 nm. CG 2 shows less that 20 $\mu W^* cm^{-2*} nm^{-1}$ UV-A, almost no UV-B down to 303 nm and around 1 $\mu W^* cm^{-2*} nm^{-1}$ all the way to 250 nm (Figure 2). This record was taken under the *Nothofagus* forest canopy that absorbs and/or reflects a significant part of the UV spectrum. CG 3 was also taken under the forest canopy that shields the ground from UV-A and UV-B down to around 300 nm where it rises to reach 12 $\mu W^* cm^{-2*} nm^{-1}$ at 250 nm (Table 1 and Figure 3).

5. Discussion

[15] The upper timberline zone of Tierra del Fuego can be characterized as an extreme environment for solar radiation. The high levels of UV-A (400–320 nm) and part of the UV-

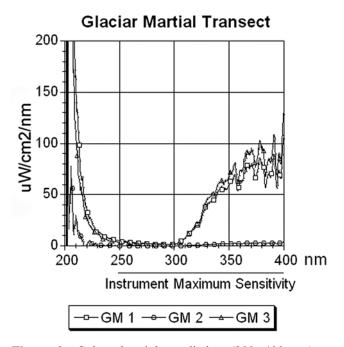


Figure 2. Solar ultraviolet radiation (200–400 nm) at Glaciar Martial. GM 1 was recorded at 572 m, GM 2 at 452 m, and GM 3 at 245 m.

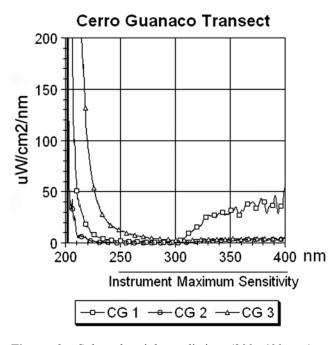


Figure 3. Solar ultraviolet radiation (200–400 nm) at Cerro Guanaco. CG 1 was recorded at 665 m, CG 2 at 504 m and CG 3 at 485 m.

B (320 to 300 nm) in three of the spectra discussed in this article suggests that plants and other organisms are exposed to potentially damaging fluxes of UV-A and UV-B radiation. From Figures 2–3 it is evident that UV-C reaches the surface in sizeable amounts; we see a rise of the solar irradiance curve with a 1/x shape that starts at around 260 nm and continues rising until it reaches the 200 nm wavelength when all spectra drop to zero. This is related to the spectrometer design with a minimum recording limit set at 200 nm and maximum sensitivity starting at 250 nm. A natural limit occurs nearby due to the strong absorption by carbon dioxide (CO₂) at 190 nm.

[16] Our data must be compared with laboratory-derived data in regards to damaging important biomolecules. The absorption spectrum for DNA shows peaks between 280 and 260 nm and a steep rise from 240 through 220 nm. Similar cases can be made for vital molecules of proteins, fats and hormones. Thus, high UV-A, UV-B and, as we have shown, UV-C radiation fluxes makes the upper timberline an extreme environment.

[17] How can the forest survive the current UV fluxes? *Mayoral* [1994] reported the finding of cyanidin, delphidin, and flavonol glycosides in extracts from leaves of *Nothofagus* using reverse phase HPLC techniques. She found three consistent maxima in HPLC of the three species of *Nothofagus* growing in Tierra del Fuego. While the deciduous species, *N. antarctica* and *N. pumilio* showed narrow peaks of these compounds in the graphs, the evergreen species *N. betuloides* shows thicker areas of concentration of these pigments in the graphs suggesting a larger concentration of protective pigments in leaves that will be active over longer time periods. The presence of UV-absorbing pigments in the leaves of *Nothofagus* trees shows that this taxon has developed and kept a protective system in place to

prevent UV radiation from reaching targets such as DNA, proteins (including that of the functional center of photosystem II), and lipids in the leaves. In addition, the leaves have a rippled profile and glossy surface that can be viewed as an apparatus for reflection. Such a mechanism may have been selected in response to the need to backscatter the energy-laden shorter waves of UV. This interpretation based on chemical and genetic grounds should not exclude the structural and functional views nor those based on changes in the abiotic components of the environmental complex. We submit the UV band of the electromagnetic spectrum has a significant role in the definition of the extreme environment at the upper timberline. The organisms' abilities to cope with the lower temperatures, frozen soils and the consequent water stress, the strong winds and the destructive exposure to UV-A, UV-B and, as we have shown, UV-C are put to test in the upper timberline. A sequence of variations (a cline) that loses diversity with the increase of elevation was found in Nothofagus [Premoli, 2003]. This sequence of genetic variations may originate by the molecular effect (breakage of chemical bonding) of high energy UV radiation and the following repair process. The resulting phenotype would be then selected by biotic (competition, herbivory, etc.) and abiotic (radiation, temperature, wind, water stress, etc.) factors. Successful plants will carry UV-blocking pigments (cyaniding, delphidin, and flavonol glycosides) to protect cellular structure and function, DNA repair mechanisms, and the ability to cope with temperature, wind and water stress.

[18] These views require further fieldwork, monitoring of certain variables, data analysis and modeling.

[19] Acknowledgments. This research was funded by the NASA Astrobiology Institute, for project number 6, "Hindcasting Ecosystems" (D'Antoni and Skiles) of the Ames Team (Des Marais).

References

- Amaral Zettler, L., A. Laatsch, A. Dhillon, C. Palacios, E. Zettler, F. Gomez Gomez, E. Gonzalez Toril, R. Amils, and M. Sogin (2004), Diversidad microbiana en el Río Tinto (España): Una aproximación a los tres dominios, *Int. J. Astrobiol.*, 8–9, suppl. 1.
- Amils, R. (2004), Relevancia del Ciclo del Hierro en la búsqueda de vida en Marte, Int. J. Astrobiol., 8–9, suppl. 1.
- Barrera, M. D., J. L. Frangi, L. L. Richter, M. H. Perdomo, and L. B. Pinedo (2000), Structural and functional changes in Nothofagus pumilio forest along an altitudinal gradient in Tierra del Fuego, Argentina, *J. Veg. Sci.*, 11, 179–188.
- Bisheimer, M. V., and E. M. Fernández (2000), Arboles de los Parques Nacionales del Sur: Arboles Autóctonos Característicos de los Bosques Andino-Patagónicos de la Argentina, 176 pp., Grafica, Buenos Aires.
- Caldwell, M. M., L. B. Camp, C. W. Warner, and S. D. Flint (1986), Action spectra and their key role in assessing biological consequences of solar UV-B radiation change, in *Stratospheric Ozone Reduction, Ultraviolet Radiation and Plant Life, NATO ASI Ser., Ser. G Ecol. Sci.*, vol. 8, edited by R. C. Worrest and M. M. Caldwell, pp. 87–112, Springer, Berlin.
- Camarero, J., and E. Gutiérrez (2002), Plant species distribution across two contrasting treeline ecotones in the Spanish Pyrenees, *Plant Ecol.*, 162(2), 247–257.
- Cockell, C. S., A. C. Schuerger, D. Billi, E. J. Friedmann, and C. Panitz (2005), Effects of a simmulated Martian UV flux on the cyanobacterium Chroococcidiopsis sp. 029, *Astrobiology*, 5(2), 127–140.
- Coohill, T. P. (1989), Ultraviolet action spectra (280–380 nm) and solar effectiveness spectra in higher plants, *Photochem. Photobiol.*, 50, 451–457.
- Frangi, J. L., M. D. Barrera, L. L. Richter, and A. E. Lugo (2005), Nutrient cycling in Nothofagus pumilio forests along an altitudinal gradient in Tierra del Fuego, Argentina, *For. Ecol, Manage.*, 217(1), 80–94.
- Grace, J. (1989), Tree lines, Philos. Trans. R. Soc. London, Ser. B, 324, 233-245.

- Grossweiner, L. I. (1976), Photochemical inactivation of enzymes, *Curr. Topics Radiat. Res. Q.*, *11*, 141–199.
- Hoehler, T. M. (2005), Cretaceous Park? A commentary on microbial paleomics, Astrobiology, 5(2), 95–99.
- Holtmeier, F.-K. (1981), What does the term "Krummholz" really mean? Observations with special reference to the Alps and the Colorado Front Range, *Mt. Res. Dev.*, 1(3-4), 253–260.
- Huber, H. (2004), Hyperthermophillic microorganisms—A possibility for extraterrestrial life?, *Int. J. Astrobiol.*, 3, suppl. 1.
- Lara, A., R. Villalba, A. Wolodarsky-Franke, J. C. Aravena, B. H. Luckman, and E. Cuq (2005), Spatial and temporal variation in Nothofagus pumilio growth at tree line along its latitudinal range (35°40′-55°S) in the Chilean Nades, J. Biogeogr., 32(5), 879–893.
- Lipps, J. H. (2004), Life and death on icy worlds, Int. J. Astrobiol., 4, suppl. 1.
- Madronich, S. (1993), UV radiation in the natural and perturbed atmosphere, in UV-B Radiation and Ozone Depletion. Effects on Humans, Animals, Plants, Microorganisms, and Materials, edited by M. Tevini, pp. 17–69, Lewis, Boca Raton, Fla.
- Mayoral, A. C. (1994), HPLC reversed-phase analyses of phenolic compounds in extracts from leaves of *Nothofagus antarctica*, *N. pumilio* and *N. betuloides*, technical report, NASA Ames Res. Cent., Moffett Field, Calif.
- Mueller-Dombois, D., and H. Ellenberg (2002), Aims and Methods of Vegetation Ecology, 547 pp., Blackburn, Caldwell, N. J.
- Norton, D. A., and W. Schönenberger (1984), The growth forms and ecology of Nothofagus solandri at the alpine timberline, Craigieburn Range, New Zealand, *Arct. Alp. Res.*, *16*(3), 361–370.
- Palacios, C., L. Amaral Zettler, E. Zettler, F. Gomez Gomez, E. Gonzalez Toril, R. L. Amils, and M. Sogin (2004), Biodiversidad microbiana del Río Tinto (Huelva, España), un ecosistema extremadamente acido y cargado de metales pesados, *Int. J. Astrobiol.*, 9, suppl. 1.
- Parson, P. G., and P. Gross (1980), DNA damage and repair in human cells exposed to sunlight, *Photochem. Photobiol.*, 32, 635-641.
- Pollmann, W., and R. Hildebrand (2005), Structure and composition of species in timberline ecotones of the southern Andes, in *Mountain Eco*systems, edited by G. Broll and B. Keplin, pp. 117–151, Springer, Berlin.

- Premoli, A. C. (2003), Isozyme polymorphisms provide evidence of clinal variation with elevation in *Nothofagus pumilio*, *J Hered.*, 94(3), 218– 226.
- Rundel, R. D. (1983), Action spectra for inactivation of biologically effective UV radiation, *Plant Physiol.*, 58, 360–366.
- Tevini, M. (1993), Molecular biological effects of ultraviolet radiation, in UV-B Radiation and Ozone Depletion. Effects on Humans, Animals, Plants, Microorganisms and Materials, edited by M. Tevini, pp. 1–15, Lewis, Boca Raton, Fla.
- Tranquillini, W. (1979), *Physiological Ecology of the Alpine Timberline: Tree Existence at High Altitudes with Special Reference to the European Alps*, Springer, New York.
- Tung, H. C., P. B. Price, N. E. Bramall, and G. Vrdoljak (2006), Microorganisms metabolizing on clay grains in 3-km-deep greenland, Astrobiology, 6(1), 69–86.
- Wardle, P. (1973), New Zealand timberlines, Arct. Alp. Res., 5(3), A127–A135.
- Wardle, P., C. Ezcurra, C. Ramirez, and S. Wagstaff (2001), Comparison of the flora and vegetation of the southern Andes and New Zealand, N. Z. J. Bot., 39, 69–108.
- Weber, R. L., M. W. White, and K. V. Manning (1959), College Physics, McGraw-Hill, New York.
- Williams, P. J. (1961), Climatic factors controlling the distribution of certain frozen ground phenomena, *Geogr. Ann.*, 43(3–4), 339–347.

H. D'Antoni, L. Rothschild, and J. W. Skiles, NASA Ames Research Center, M.S. 239-20, Moffett Field, CA 94035-1000, USA. (hector.l.dantoni@ nasa.gov)

S. Burgess and C. Schultz, Geology Department, San Jose State University, San Jose, CA 95192, USA.