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Abiotic factors related to the incidence of the *Austrocedrus chilensis* disease syndrome at a landscape scale

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ABSTRACT

In this paper, the incidence of the *A. chilensis* disease syndrome in the "16 de Octubre" Valley (Chubut, Argentinean Patagonia) was related to landscape climatic, topographic and edaphic attributes, using remote sensing, geographic information systems and statistical methods. A strong relationship between the occurrence and incidence of the *A. chilensis* disease syndrome and site variables related to poor soil drainage was found. Non-allophanized soils with fine textures on flat and wavy soil phases, geomorphologies associated to alluvial processes, and low elevations and gentle slopes were positively related to the incidence of the disease. These relationships at a landscape scale agree with previous studies carried out at the stand level. A logistic predictive model of diseased occurrence was developed for the study area considering aspect, elevation, slope, mean annual precipitation and soil phase (classified according to predominant slopes).

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1. Introduction

The cordilleran cypress [*Austrocedrus chilensis* (D. Don) Pic. Serm. & Bizzarri] is an endemic Cupressaceae of the Andean forests of Patagonia. In Argentina, it is discontinuously distributed between 37°7' and 39°30'S latitude and, more continuously distributed between 39°30' and 43°44'S latitude, along a 60–80 km wide strip (Pastorino et al., 2006). It covers ca. 141,000 ha spreading over a strong west–east precipitation gradient that ranges from more than 1700 to 500 mm in the Patagonian steppe fringe. This forest species inhabits very different ecological niches (Veblen et al., 1995). *A. chilensis* forests are an important economic resource for the Andean region, their high quality wood being used for construction and woodworking (Díaz-Vaz, 1985). Their importance relates also to aesthetic roles, as these forests surround most of the tourist cities and villages in the area.

Widespread mortality of *A. chilensis* occurs throughout its range in Argentina. The syndrome was detected about 60 years ago and is locally known as "mal del ciprés". Symptoms are manifested as a progressive withering and defoliation, crown thinning, decay of the main roots and, finally, the death of the tree. Recently, the magnitude of *A. chilensis* disease syndrome was quantified in an area of interest, using remote sensing techniques. It was shown that the affected forest covered 24% of the total surface of *A. chilensis* (La Manna et al., 2008a).

"Mal del ciprés" has been considered a forest decline disease by many authors (Calí, 1996; Filip and Rosso, 1999; La Manna and Rajchenberg, 2004a,b). This type of disease is the result of complex interactions between biotic and abiotic factors and they typically have an unresolved etiology (Manion, 1991; Manion and Lachance, 1992). Wood-rotting basidiomycetes and *Phytophthora* species were considered to act as opportunistic fungi (Barroetaveña and Rajchenberg, 1996; Greslebin et al., 2005). According to dendro-chronological studies, the onset of the disease is related to climatic and geologic events and radial growth decline may occur for 75 years before dying (Calí, 1996). It was alleged that site conditions favoring poor internal drainage act as predisposing factors that enhance the development of the disease (Bacalá et al., 1998; La Manna and Rajchenberg, 2004a,b).

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The causal agent of this syndrome has been recently elucidated. The biotic agent is a fungus of the genus *Phytophthora* (*P. austrocedrae* Gresl. & E. M. Hansen), which has been recently isolated, described, and shown to fulfill Koch's postulates (Greslebin and Hansen, 2007; Greslebin et al., 2007). However, the degree of aggressiveness of *P. austrocedrae* is still unknown (Greslebin and Hansen, 2007). This pathogen, which penetrates the plant through the roots, is an aquatic mould which needs water for dispersion and it is generally associated with poor drained soils. The disease was shown to be originated in the root system with necrotic inner bark lesions at the lower stem (Greslebin et al., 2007). Diseased forests where *P. austrocedrae* was not detected were rarely found (Greslebin et al., 2007). Studies on *A. chilensis* forests in Chile identified the aphid *Cinara cupressi* (Homoptera: Aphididae) associated to defoliation symptoms and forest mortality (Baldini et al., 2004). These studies did not assess the root system or lower stem health, thus the influence of *Phytophthora* cannot be discarded. Even though the cause of *A. chilensis* disease syndrome is still a topic of discussion (El Mujtar and Andenmatten, 2007), *P. austrocedrae* seems to be the most probable biotic causal agent.

Phytophthora species can be potentially destructive, according to the experience in other forests from around the world. Many *Phytophthora* species are known as virulent pathogens of forests, plantations, fruit trees and ornamentals (Erwin and Ribeiro, 1996). "Sudden oak death" caused by *P. ramorum* has reached epidemic levels in coastal forests of central California (Meentemeyer et al., 2004; Venette and Cohen, 2006). *Phytophthora lateralis* is an introduced root pathogen that attacks Port-Orford-cedar (*Chamaecyparis lawsoniana*) and it is extremely virulent. Symptoms and death occurs in seedlings and saplings within a few weeks (Goheen et al., 2005). *Phytophthora cinnamomi* causes a widespread disease on *Pinus occidentalis*, affecting mainly mature stands, but also plantations and natural regeneration (Jung and Dobler, 2002). *Phytophthora kernoviae* have been recently identified and it was proved to cause bleeding stem lesions on mature *Fagus sylvatica* (Brasier et al., 2005). *Phytophthora alni* sp. nov. causes the lethal root and collar rot disease of *Alnus* sp. (Brasier et al., 2004). Infected trees show yellowish foliage, a dieback of the crown, and necroses of the inner bark (Jung et al., 2007), similar to *A. chilensis* forests affected by *Phytophthora* (Greslebin et al., 2007).

One axiom of the contemporary ecology is that the patterns at one scale of observation are not necessarily those that occur at some different scale of observation (Wiens, 1999). Previous studies about edaphic factors related to the *A. chilensis* disease syndrome were performed at microsite level, comparing pairs of diseased/asymptomatic plots inside the stands but the relationship between the disease and the soil factors have never been evaluated at a landscape scale. These studies showed that the affected trees tended to develop in poorer drained soils (La Manna and Rajchenberg, 2004a,b); however, the association with the site conditions may change according to the scale of analysis (Oline and Grant, 2002). Another study carried out in Nahuel Huapi National Park showed that *A. chilensis* stands were more prone to develop symptoms when occurring at sites with higher precipitation and moderate elevations (Bacalá et al., 1998). This study, which is the only previous analysis of abiotic factors at a broad scale, included a low number of stands.

Recent developments in remote sensing and geographical information systems have resulted in the potential for great increases in both the quality and quantity of habitat-level information that can be obtained and analyzed. Statistical techniques coupled with geographical information systems have fostered the development of predictive host habitat distribution models. Data on species/communities-habitat associations have

been widely used for ecological studies resulting in practical conservation and management (Iverson et al., 1997; Marsden and Fielding, 1999; Schadt et al., 2002; Van Staden et al., 2004). The habitat-association approach facilitates the investigation of abiotic factors associated with the *A. chilensis* disease syndrome and it can be used to develop predictive models for estimating disease occurrence. Knowing the association of the disease with climatic, geomorphic and edaphic factors at a large scale should allow the generation of risk maps (Meentemeyer et al., 2004; Van Staden et al., 2004; Fernández and Solla, 2006), an important tool for developing forest management criteria.

The objectives of the present study were to identify the relationship between the incidence of the *A. chilensis* disease syndrome and climatic, topographic, and edaphic features at the landscape scale, and to create a predictive model that relates the disease occurrence to site conditions. We hypothesized that the spatial distribution of the *A. chilensis* disease syndrome at a landscape scale is controlled by climatic, topographic, and edaphic features that affect drainage and predicted that the incidence would be higher in sites with higher precipitation, gentler slopes, nearer to water streams and in fine-textured non-allophanized soils.

2. Materials and methods

2.1. Study area

The study was carried out in the "16 de Octubre" Valley (Chubut province, 43°10'S), which concentrates 9% of the total area of *A. chilensis* pure forests in Argentina (Carabelli and Claverie, 2005). A 10 m resolution distribution map of the *A. chilensis* disease syndrome in the "16 de Octubre" Valley based on SPOT PAN and XS satellite images was used (La Manna et al., 2008a). In order to build the map 100 patches of diseased trees, 50 patches of trees in asymptomatic dense forests and 80 patches of trees in asymptomatic thin forests were identified in the field. Dense and thin forests were distinguished according to canopy openness. The location and perimeter of each patch was determined using a global positioning system. The criteria for the selection of the training sites were a minimum size of 400 m², and an edge sector of at least 10 m with the similar forest health than the sampled polygon. The diseased patches were recognized according to typical symptoms: withering, defoliation, crown thinning and mortality. All along the "16 de Octubre" Valley, *A. chilensis* disease symptoms were associated to *Phytophthora* attacks (Greslebin et al., 2005; Greslebin and Hansen, 2007). According to the training sites identified in the field, the digital numbers for each type of *A. chilensis* vegetation were determined and a supervised classification was done. The map was intensively checked and corrected on the basis of field information, using an iterative approach between image processing and field check. The overall classification accuracy was of 75% and the classification accuracy for discriminating *A. chilensis* affected patches from asymptomatic dense patches was 85% (La Manna et al., 2008a).

In order to identify the relationship between the disease and site conditions, only those patches greater than 900 m² were considered and the study was centered in a sector of the map comprising 4520 ha of *A. chilensis* forests. This sector was intensively checked in the field and with the support of aerial photographs, in order to ensure the validity of the map.

2.2. Site attribute layers

In order to characterize the site, climatic, topographic, geomorphologic and edaphic thematic layers were compiled. The mean annual precipitation layer was obtained from isohyets of

the study area (Irisarri et al., 1995; Giraut et al., 2002). Elevation, slope and aspect were derived from a 30 m resolution digital elevation model based on Aster images and provided by Eckert and Leuggern (2006). Because aspect is a circular variable, both relative south aspect or degrees from the north and relative east aspect or degrees from the west were used in the analysis rather than aspect itself (Anchorena and Cingolani, 2002). For example, if aspect is absolute north (0°), the relative south aspect is 0° and the relative east aspect is 90° ; if aspect is absolute east (90°), the relative south aspect is 90° and the relative east aspect is 180° . The geomorphology layer was extracted from Martínez (2003). The layer of distance to streams was obtained from a digitized map provided by the Military Geographical Institute of Argentina (IGM), and corrected according to the interpretation of a SPOT satellite image. The soil thematic layer was extracted from a semi-detailed soil map (scale 1:50,000) specifically developed for “16 de Octubre” Valley area (La Manna et al., 2008b). This map was constructed from field samples, satellite images and a digital elevation model, using a standard protocol for the Andean Region (Irisarri et al., 1995; Ferrer et al., 2006). Soil classes were previously separated in phases according to slope (flat/wavy/sloping/steep) and 17 types of soils were identified and classified up to the Great Group level, according to USDA (Soil Survey Staff, 1999). Mean values of pH NaF and texture for each soil class were extracted from this map, considering only those profiles that had been described in areas with *A. chilensis* forests. The pH in NaF allows detecting amorphous constituents (i.e., allophane, imogolite) from volcanic ash (Irisarri, 2000).

2.3. Data analyses

2.3.1. Contingency analysis

In order to identify the association between the incidence of the disease and site features in the study area, site variables were categorized. The areas of diseased and asymptomatic forests for each variable were determined with the Tabulate Area tool of Arc View software, for each site attribute layer. This tool enables to calculate the number of pixels corresponding to the intersection of layer categories (i.e., *A. chilensis* class and site class). Histograms were built from these data.

In order to analyze these data with statistical tests, 5000 points were drawn at random on the total area. Under the condition that points were separated from each other >79 m, a sub sampling of 4757 points was obtained with 274 of these points being included within patches of *A. chilensis*. These 274 points were considered for statistical analysis. This threshold distance (i.e., 79 m buffer) reduced problems of spatial autocorrelation because it assured that 95% of the points corresponded to different forest patches and avoided misinterpretations resulting from extremely large sample size (Ramsey and Schafer, 1997). Based on contingency tables the association between each site variable and the disease was evaluated with Chi square analysis and the Cramer's V statistic. Both statistics compare the observed frequency distribution with the expected distribution using a Pearson's goodness of fit test (Ramsey and Schafer, 1997; Reich and Lundquist, 2005). Cramer's V presents values between 0 and 1. The greater the statistics value, the greater the association between the site feature and the disease. For ordinal variables Goodman & Kruskal's gamma statistic was also calculated. This statistic provides information about the correlation strength and the direction of the relationship, presenting values between -1 and 1 .

2.3.2. Multivariate analysis

1200 patches were randomly selected from the *A. chilensis* map of the study area. The selection included 400 patches of each

category identified in the original map: *A. chilensis* affected by the disease, asymptomatic dense, and asymptomatic thin patches. The random selection was carried out with the extension Table Select deluxe tools v.1.0 of Arc View software. The site layers were converted to grids with $10\text{ m} \times 10\text{ m}$ cells. The mean values of each site attributes layer was extracted for each selected patch by the Zonal attributes tool of ERDAS software. This tool enables to extract the zonal statistics (mean, standard deviation, minimum and maximum) from a vector coverage and save them as polygon attributes. The data were tabulated for the statistical analysis.

The site variables associated with the disease were identified through a discriminant analysis, considering three groups (i.e., dependent variables): diseased, asymptomatic dense and asymptomatic thin patches. The independent variables were: mean annual precipitation, slope, elevation, relative south aspect, relative east aspect, distance to streams, soil clay content at 60–80 cm depth, soil loam content at 60–80 cm depth and pH NaF of soil at 0–20 cm depth. Variables were transformed to comply with the statistical techniques assumptions (Williams, 1983). Elevation was log-transformed $[\ln(x)]$ and clay content was transformed according to Box and Cox (1964) $\{[(x+10) - 0.19 - 1]/(-0.19)\}$. A stepwise procedure was used to retain the most significant variables for discrimination. Stepwise discriminant analysis is an efficient procedure for removing redundant variables and selecting those of greatest discrimination capacity (Afifi and Clark, 1984). The classification rates were assessed by means of a cross-validation procedure.

In order to generate a predictive model for the *A. chilensis* disease syndrome occurrence, logistic regression was applied. The binary dependent variable was disease occurrence (i.e., diseased patch) and disease absence (i.e., asymptomatic dense patch). Asymptomatic thin patches were excluded from the model on the basis of the discriminant analysis results. The independent variables were the same ordinal variables used for the discriminant analysis: mean annual precipitation, slope, elevation (log-transform), relative south aspect, relative east aspect, distance to streams, soil clay content (Box and Cox (1964)—transform), soil loam content and pH NaF. Three categorical variables were also considered: soil classes (17 categories), soil phases (4 categories), and geomorphology (8 categories). The models evaluated included only one categorical variable, and when soil classes or soil phases were included in the model, soil variables (texture and pH NaF) were excluded.

The logistic regression presents the following formula:

$$\text{Logit}(P) = \beta_0 + \beta_1 \times V_1 + \beta_2 \times V_2 + \dots + \beta_n \times V_n$$

where P is the probability of the *A. chilensis* disease syndrome occurrence; β_0 is the Y -intercept; and $\beta_1 \dots \beta_n$ are the coefficients assigned to each of the independent variables during regression. The V letters represent the various independent variables. Probability values can be calculated based on the equation below, where e is the natural exponent:

$$P = \frac{e^{\text{logit}(P)}}{1 + e^{\text{logit}(P)}}$$

The variables for the model were chosen with the best subsets selection technique (Hosmer and Lemeshow, 1989). The final model was selected according to the lowest Akaike information criterion (AIC) (Burnham and Anderson, 1998), the greatest sensitivity (i.e., proportion of correctly predicted the *A. chilensis* disease syndrome occurrences) and the model fit according to Hosmer-Lemeshow test (Hosmer and Lemeshow, 1989). The Wald statistics was used to assess the significance of the coefficients in the models. The prediction accuracy of the final model was assessed with a Receiver Operating Characteristic (ROC) plot

(Marsden and Fielding, 1999; Schadt et al., 2002). This plot was obtained by plotting all sensitivity values (true positive fraction) on the y axis against their equivalent (1–specificity) values (false positive fraction) on the x axis [specificity of a model refers to the proportion of correctly predicted absences]. The area under the ROC curve is used as an index of prediction accuracy. Values between 0.7 and 0.9 indicate reasonable discrimination ability. For example, a value of 0.8 for the area under the ROC curve indicates that in 80% of all cases for a randomly chosen area with presence, a greater presence probability is being calculated than for a randomly chosen area with non-presence (Marsden and Fielding, 1999; Schadt et al., 2002).

Statistical analyses were carried out with SPSS for Windows and Box and Cox (1964) variables transformation was done with the free software Wessa (2007).

3. Results

3.1. Contingency analysis

Classification criteria used for crosstabs analysis (i.e., disease syndrome incidence and site attributes) were not independent for slope, geomorphology, soil phases, soil classes, allophanization degree and textural classes ($p < 0.05$) (Fig. 1). The percentage of affected surface tended to be greater in the flat and wavy phase soils (Fig. 1, Table 1). These soil classes corresponded to non-allophanized, moderately well to poorly drained soils, and mostly fine textured (Table 1). According to the gamma statistic, the disease incidence was negatively associated with allophanization degree and coarser textures (Fig. 1). The soil classes with the maximum disease incidence were FP1, FP2, FP3, WP1 and WP5 (Fig. 1). These soil classes also corresponded with low total area of *A. chilensis* forests (Fig. 2). The area of *A. chilensis* corresponding to FP1, FP2, FP3, WP1 and WP5 was 13, 166, 33, 22 and 39 ha, respectively, whereas the mean area of *A. chilensis* in the other soil classes was greater than 300 ha. The area of forest with disease symptoms was negatively correlated with the total area of *A. chilensis* ($r^2 = -0.704$; $p = 0.002$).

The percentage of affected area was greater in geomorphologies associated with alluvial processes: floodplains, alluvial terraces and alluvial fans (Fig. 1). However, no clear relation was found between the disease and the distance to rivers or lakes. The affected forest area reached high values even at large distance to streams (Fig. 1).

Slope and relative south aspect were negatively related with the disease incidence, according to gamma statistics. The incidence of the disease was greater at gentler slopes and north aspects (i.e., low values of South variable) (Fig. 1). It also tended to be greater at low elevations ($p < 0.1$). No clear relations were found between the disease and precipitation, nor between disease and relative east aspect (Fig. 1).

3.2. Discriminant analysis between diseased, asymptomatic dense and asymptomatic thin patches

The within patch variation of the site variables was low. Since the mean size of *A. chilensis* patches was low (0.2 ha for diseased patches, 0.29 ha for asymptomatic thin patches and 0.49 ha for asymptomatic dense ones) in most of the cases the within standard deviation was close to zero for the site variables. Thus, the site variables mean for each patch, which was used for the statistical analysis, was robust.

pH NaF, elevation (log-transformed [$\ln(x)$]) and relative south aspect were identified by discriminant analysis as the key variables to differentiate *A. chilensis* patch classes. The model created two functions but only the first function allowed a good differentiation of groups (Wilks's $\lambda = 0.851$, $p < 0.001$). This function was positively associated with pH NaF, elevation and relative south aspect. Fig. 3 shows the relationship between variables and group centroids in the canonical axes space. *A. chilensis* diseased patches were negatively related to the function while dense asymptomatic *A. chilensis* patches were positively related. The centroid of thin asymptomatic *A. chilensis* patches was positive, but close to zero (Fig. 3). Diseased patches were associated with non-allophanized soils, low elevations and north aspect, whereas asymptomatic dense patches were related to allophanized soils, higher elevations and south aspect. The soil clay content was negatively related to the discriminant function ($r = -0.664$), i.e., diseased patches were associated with fine texture soils whereas asymptomatic dense patches were related to coarse textures (Fig. 3).

This discriminant model could accurately discriminate between diseased and asymptomatic dense patches, but it did not discriminate asymptomatic thin patches. According to cross-validation results, 65% of diseased patches and 69% of asymptomatic dense patches were well classified, but only 10% of asymptomatic thin patches were correctly classified. 39% of asymptomatic thin patches were classified as diseased patches, and 51% as asymptomatic dense patches.

Table 1
Characteristics of soil classes in "16 de Octubre" Valley, Argentina (La Manna et al., 2008b)

	Code	Drainage	Depth	Texture class	Allophanization
Flat phase. Slope <5%	FP1	Moderately well drained	Deep	FI	None
	FP2	Poorly to Moderately well drained	Deep	F	None
	FP3	Poorly drained	Moderately deep	FA	None
Wavy phase. Slopes <5% and <30% intermingled	WP1	Moderately well to poorly drained	Deep	FI	None
	WP2	Poorly to Moderately well drained	Moderately deep	FA	None
	WP3	Poorly drained	Shallow to Moderately deep	a	None
	WP4	Poorly to Moderately well drained	Shallow to Moderately deep	a	None
	WP5	Poorly to Moderately well drained	Shallow to Moderately deep	FaA	None
	WP6	Moderately well drained	Moderately deep to Deep	FA	Imogolite
Sloping phase. Slope: 5–30%	SP1	Well to moderately well drained	Deep to moderately deep	FA	Imogolite
	SP2	Moderately well drained	Deep to moderately deep	FA	Allophane
	SP3	Moderately well drained	Deep	FaA	Imogolite
	SP4	Well drained	Moderately deep	FA	Allophane
Steep phase. Slope >30%	STP1	Well drained	Shallow to moderately deep	FA	Allophane
	STP2	Well drained	Deep to moderately deep	FA	Allophane
	STP3	Well drained	Deep to moderately deep	FA	Allophane
	STP4	Well drained	Moderately deep	FA	None to Allophane

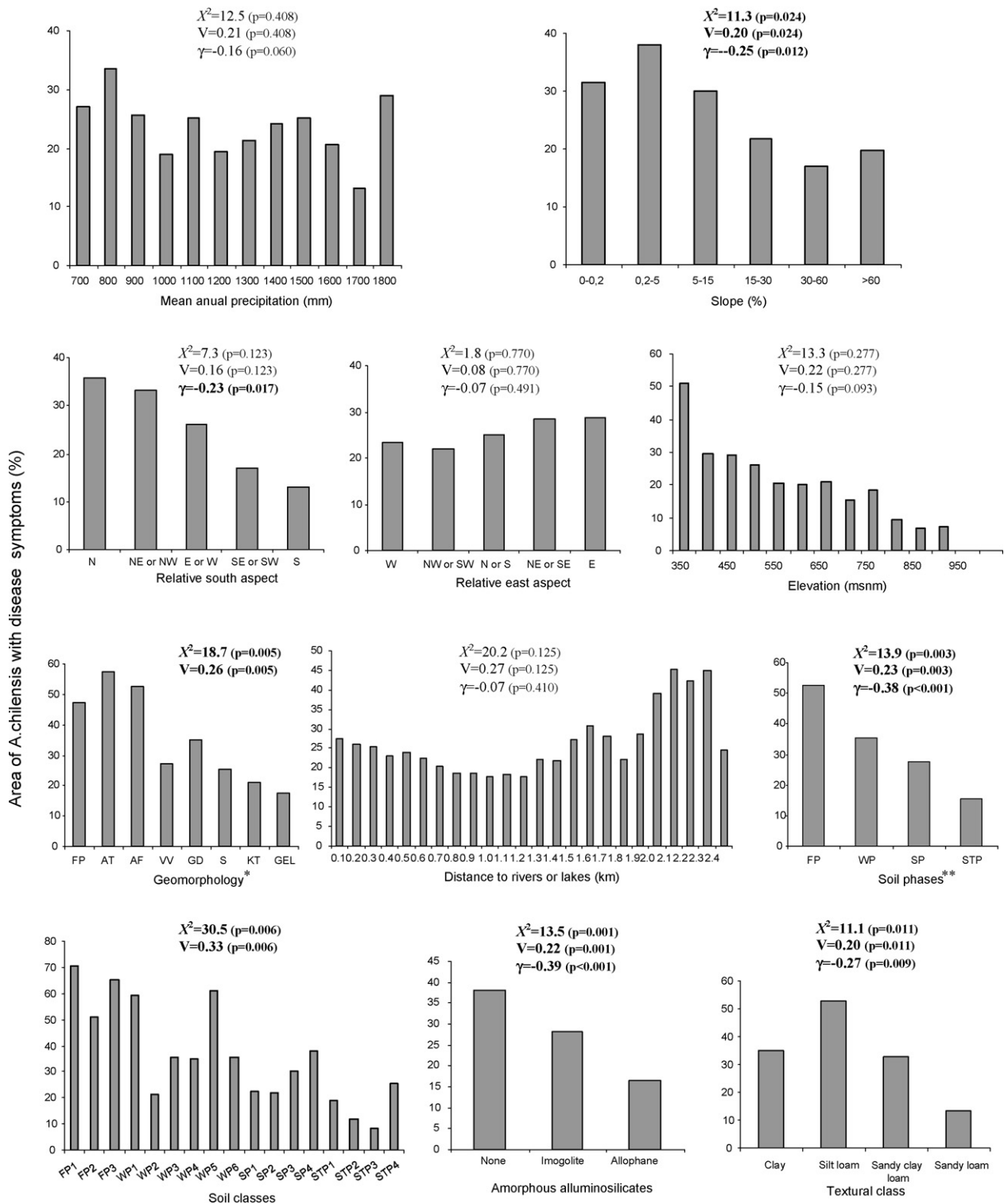


Fig. 1. Incidence of *A. chilensis* disease according to site features. Results of the contingency analysis of asymptomatic and diseased *A. chilensis* forest areas and its association with site variables are shown for each histogram. Chi square (χ^2) and Cramer's V statistic (V) were evaluated for all the variables. Goodman and Kruskal's gamma statistic (γ) was evaluated for ordinal variables. Statistical significance is highlighted in boldtype.

*Geomorphology classes: FD = floodplains; AT = alluvial terraces; AF = alluvial fans; VV = V valleys; GD = glacial deposits; S = slidings; KT = Kneading trough; GEL = glacial eroded landscape.

**Soil phases and soil classes: detailed in Table 2.

In order to assess the influence of the classification error in the original map of *A. chilensis* patch classes (La Manna et al., 2008a) on the discriminant analysis, 40 patches were randomly selected from the 400 patches of asymptomatic thin forest used for the

discriminant analysis. These patches were surveyed in the field for their health condition, density and site features. The classification was proved correct, since all the patches corresponded to asymptomatic thin forests. Two contrasting site

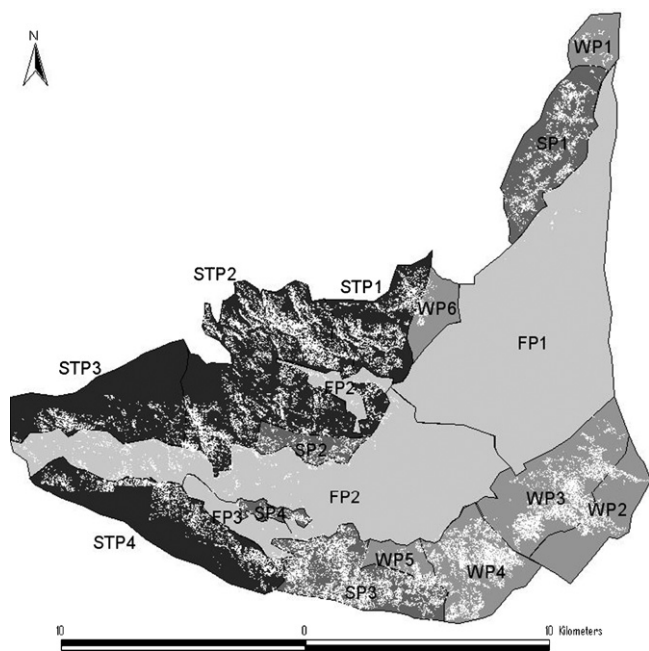


Fig. 2. Soil map of *A. chilensis* distribution area in the "16 de Octubre" Valley (La Manna et al., 2008b) and *A. chilensis* distribution (in white) according to La Manna et al. (2008a). Soil phases and classes are detailed in Table 2.

conditions were found: thin patches corresponding to regeneration forests located on gentle slopes with clayey soils; and thin forest with adult trees on steep slopes with superficial rocks. These field observations agree with the discriminant analysis results.

3.3. Logistic regression

Given the discriminant analysis results, a logistic regression model was generated discarding the asymptomatic thin patches; thus, the logistic regression was carried out considering two groups: diseased patches and asymptomatic dense patches. Four models were developed according to best subsets selection process (Table 2). The first model was chosen for assessing *A. chilensis* disease syndrome occurrence, since it presented the lowest AIC and the greatest sensitivity. The Hosmer-Lemeshow goodness of fit test indicates that this model fitted quite well (Hosmer and Lemeshow, 1989). The second model was discarded because of the greatest AIC. The third and fourth models were discarded since they did not fit well (Table 2).

The selected model parameters are shown in Table 3. According to *p* values, relative south aspect, elevation and soil phases showed the highest relative importance in the model ($p < 0.001$). The probability of *A. chilensis* disease syndrome occurrence increases as relative south aspect values and elevations decrease, and in soils corresponding to flat and wavy phases (Table 3, Fig. 4). These soil phases, with flat sites and slopes lower than 5% and lower than 30%

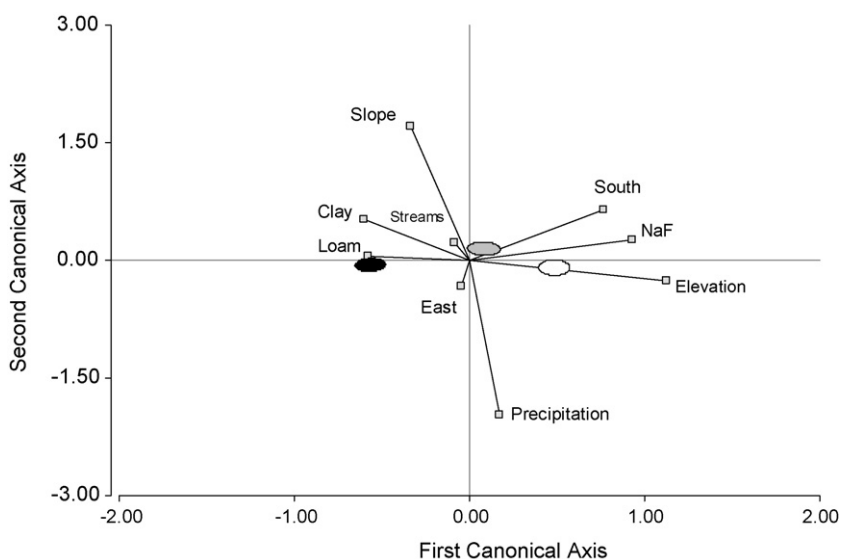


Fig. 3. Discriminant analysis biplot showing variables (squares) and group centroids (ellipses) for *A. chilensis* diseased patches (black); *A. chilensis* thin asymptomatic patches (grey); *A. chilensis* asymptomatic dense patches (white).

Table 2
Logistic regression models selected by the best subsets selection process

Variables in the model	AIC ^a	Hosmer-Lemeshow goodness of fit	Sensitivity ^b	Specificity ^c
Slope, South, Elevation, Precipitation, Soil phases (4 categories) ^d	901.1	$X^2 = 5.8$ ($p = 0.674$)	73	73
South, Elevation, Soil phases (4 categories)	947.5	$X^2 = 5.2$ ($p = 0.740$)	70	74
Slope, South, Elevation, Precipitation, Clay content, Geomorphology (8 categories)	904.4	$X^2 = 16.5$ ($p = 0.036$)	69	75
Slope, South, Elevation, Precipitation, pH NaF, Clay content, Geomorphology (8 categories)	915.9	$X^2 = 16.9$ ($p = 0.031$)	71	75

Sensitivity and specificity refer to the percentage of correctly classified *A. chilensis* disease occurrences and non-occurrences, respectively (both at $P = 0.5$).

^a Akaike information criterion.

^b Proportion of correctly predicted *A. chilensis* disease syndrome occurrences.

^c Proportion of correctly predicted absences.

^d Indicates the final model chosen for assessing *A. chilensis* disease syndrome occurrence.

Table 3

Parameters of the logistic regression model chosen for assessing *A. chilensis* disease occurrence in "16 de Octubre" Valley, Chubut Province, Argentine

Variable	$\beta \pm$ standard error	Wald	<i>p</i>
Intercept	18.510 \pm 3.087	36.0	<0.001
Slope (°)	0.043 \pm 0.013	10.9	0.001
Relative south aspect (°)	-0.010 \pm 0.002	33.0	<0.001
Elevation (msnm) ^a	-2.897 \pm 0.498	33.0	<0.001
Precipitation (mm)	-0.001 \pm 0.000	4.7	0.030
Soil phase		68.6	<0.001
Flat phase	3.408 \pm 0.534	40.7	<0.001
Wavy phase	1.537 \pm 0.287	40.7	<0.001
Sloping phase	0.957 \pm 0.232	17.0	<0.001

^a Log-transformed.

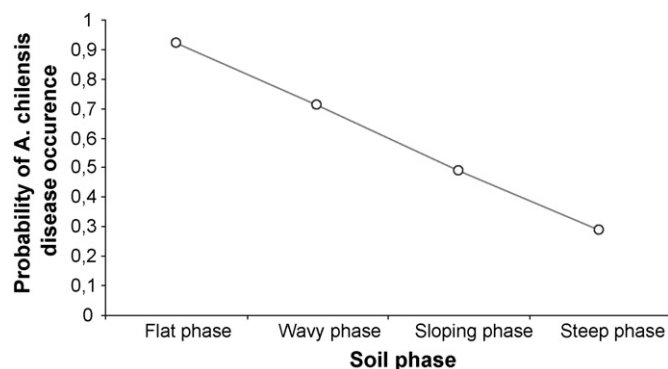


Fig. 4. Unweighted marginal means of the variable soil phases for the logistic regression model chosen for assessing *A. chilensis* disease occurrence in "16 de Octubre" Valley, Chubut Province, Argentine. Wald $\chi^2 = 68.61$ ($p < 0.001$).

intermingling, corresponded to non-allophanized, moderately well to poorly drained, and mostly fine textured soils (Table 1). These results suggested that disease occurrence is associated to gentle slopes, however the variable slope presented a positive coefficient in the model. Precipitation presented a negative coefficient suggesting that the probability of disease occurrence increases in lower precipitation sites (Table 3).

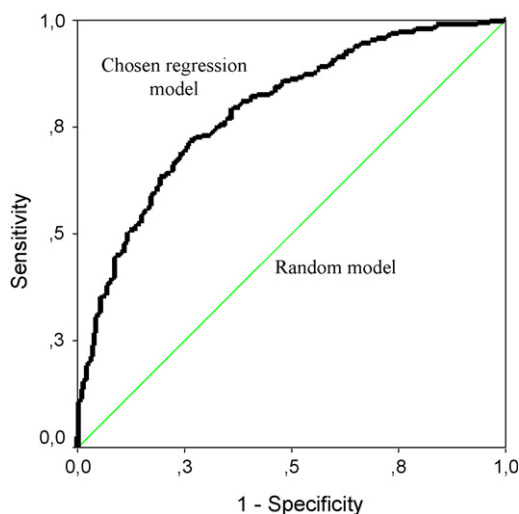


Fig. 5. Receiver Operating Characteristic (ROC) plot for the logistic regression model chosen for assessing *A. chilensis* disease occurrence in "16 de Octubre" Valley, Chubut Province, Argentine.

The ROC plot had an area under the curve of 0.790 ± 0.016 , indicating reasonable discrimination (Fig. 5). It resulted significantly greater than the area under the random model ($p < 0.001$).

4. Discussion

This work revealed a strong relationship at the landscape scale in the incidence of the *A. chilensis* disease syndrome and site variables related to poor soil drainage. The landscape corresponding to non-allophanized soils with fine textures, geomorphologies associated to alluvial process, and low elevations and gentle slopes was positively related to the incidence of the disease. These results agree with previous studies carried out at microsite level (La Manna and Rajchenberg, 2004a,b). The relationship between the disease and soil drainage found at a detailed scale, was confirmed at a landscape scale. The spatial distribution of the *A. chilensis* disease syndrome at a landscape scale is associated with topographic and edaphic features that affect drainage.

Impeded drainage reduces oxygen level in soils, which retards root growth, reduces water and mineral absorption and modifies the soil microorganism community (Manion, 1991). Poor drained soils are probably the most important factor that increases the severity and spread of *Phytophthora*. Poor soil aeration and prolonged soil saturation promote sporangia formation and zoospore release required for growth, reproduction and dissemination of *Phytophthora* (Erwin and Ribeiro, 1996). Although the degree of aggressiveness of *P. austrocedrae* is still unknown (Greslebin and Hansen, 2007), it is expected that the severity of the attack is greater in sites favoring the development of the pathogen. Many studies have shown an association between *Phytophthora* attacks and wet soils (Jung et al., 2000; Rhoades et al., 2003; Jung and Blaschke, 2004; Jönsson et al., 2005). Thomas et al. (2002) suggested that in hydromorphic soils with fluctuating water tables the intermittent soil moisture conditions may increase the oak trees susceptibility to *Phytophthora*. Clayey soils, where the rooting in the subsoil is impaired, are more disease-prone for oak decline (Jung et al., 2000; Jönsson et al., 2005). During dry periods in the growing season, fine roots are restricted to the superficial soil layers, and the rather negative soil matric potentials in the clay-rich subsoil increase the risk of severe drought stress in the trees. The hypothesis proposed by Thomas et al. (2002) could be true for *A. chilensis*, since the disease incidence was greater in shallow to moderately deep soils with fine textures, as those of the wavy phase.

Most of the predictions posed in this study were confirmed: the incidence of the disease was greater in gentle slopes, and non-allophanized soils with fine textures. The disease was also associated with low elevations, probably due to the fact that in the study area low elevation areas overlap with flat and gently sloping sites.

Two predictions were not confirmed. There was not enough evidence to support the association of disease incidence with high precipitation or with the stream neighborhood. The relationship between the disease symptoms and precipitation did not show a clear pattern and in the regression model it was negatively related to the incidence of the disease. These results could be explained by the overriding effects of edaphic and topographic conditions. In fact, the distribution of edaphic and topographic conditions promoting disease incidence in the study area does not overlap with high rainfall. Large areas with steep slopes and well drained soils (both characteristics associated to asymptomatic forests) prevail in the west portion of the study area, where mean annual precipitation is greater than 1000 mm. On the contrary, in the east portion of the study area, precipitation is lower but probably enough for soil water accumulation in the large areas with low

slope and poorly drained soils (both characteristics associated to diseased forests). Our results disagree with those described for Nahuel Huapi National Park (Argentina), where disease incidence increased with precipitation (Bacalá et al., 1998).

A relationship between disease and distance from streams was not found. These results disagree with previous field surveys in the same study area which showed that patches affected by the *A. chilensis* disease syndrome were strongly associated to temporary and permanent water streams, whether natural (streams, rivers) or artificial (canals) (La Manna et al., 2008b; Greslebin et al., 2005; La Manna, 2006). The water courses layer used for this study included all the rivers and streams detected by the satellite image (with 10 m resolution). However, in the study area, there are many small canals and narrow and temporary streams (La Manna, 2006), undetected by the satellite image. The incidence of the disease was greater in geomorphologies associated with alluvial processes: floodplains, alluvial terraces and alluvial fans, suggesting the importance of water courses as a factor also related to the disease. The proximity to watercourses should not be discarded as a variable in a risk map. The sites along main rivers and streams should be considered as high risk areas since many *Phytophthora* species around the world spread along water courses (Jung and Blaschke, 2004; Meentemeyer et al., 2004).

The association between north aspect and the disease was unexpected, since south aspect is coincident with more humid sites in this area. However, this result could be influenced by the distribution of soil types according to aspect. The study area can be divided in two sub areas. The south portion has predominantly north aspect (the 55% of it presenting N, NE or NW aspect and only the 24% with S, SE or SW aspect) and 35% of the area corresponds to fine texture soils of the wavy phase. On the contrary, the north portion of the study area has predominantly south aspect (56% of it presenting S, SE or SW aspect and only the 25% with N, NE or NW aspect) and 90% of it corresponds to coarse texture soils of the sloping and steep phase. These percentages were calculated taking into consideration only the areas covered by the *A. chilensis* forest. On the other hand, north aspect is also warmer, and temperature could affect *P. austrocedrae* growth as occurs with other *Phytophthora* species (Venette and Cohen, 2006). In *Alnus* sp. forests it was shown that warmer aspects favor the growth of *P. alni* and thus the invasion of alder bark after infection (Jung et al., 2007).

A. chilensis forests are frequently used as cattle foraging area along its entire distributional area (Veblen et al., 1995), which could affect the spread of *Phytophthora* by soil clinging to the feet of cattle (Goheen et al., 2005). In particular, in “16 de Octubre” Valley both symptomatic and asymptomatic stands are affected by strong cattle use (La Manna et al., 2008c). The 230 forest patches used as training areas for building the distributional map of *A. chilensis* disease syndrome in the study area corresponded to different geomorphologies, slopes, elevations and soil types (La Manna et al., 2008a) and most of them evidenced cattle use. The lack of sites without grazing does not allow a good control of this variable, impeding to determine the role of grazing on the distribution of *A. chilensis* disease syndrome. However, this is an issue that should be explored in future works together with investigations that could clarify whether *P. austrocedrae* could be spread by cattle.

The soil classes in which the disease incidence was greater corresponded to the soil classes with smaller forest area. This result suggests that disease-prone sites are those of lower aptitude for *A. chilensis* development. Colmet Dâage (1992) hypothesized that “mal del ciprés” appears when *A. chilensis* colonizes inappropriate sites, where a higher risk of becoming diseased exists. Our results seem to agree with this hypothesis.

Even when asymptomatic thin patches were excluded from the logistic regression, the predictive model is valid for the study area

in order to construct risk maps. Most of these patches corresponded to thin forest with adult trees in sites with steep slopes and superficial rocks; that is, with similar site conditions as those of the asymptomatic dense patches. On the contrary, asymptomatic thin patches whose site features were similar to those of the diseased patches corresponded to young forests and regeneration patches located on poor drained soils, susceptible to the disease. These forests seemed to be high risk sites, where the trees may not have reached the susceptible age, which is still unknown. The tree age could be a determinant factor for disease predisposition (Manion, 1991; Jung and Dobler, 2002; Goheen et al., 2005).

The predictive model could be used to generate risk maps, at a landscape scale, according to site variables shown to be associated with the disease (Meentemeyer et al., 2004; Van Staden et al., 2004; Fernández and Solla, 2006). This type of map could be a good tool for determining forest management and planning criteria, both for facilitating plant disease monitoring and for preventing restock in areas where the risk is greatest (Fernández and Solla, 2006). The predictive model obtained is only valid for “16 de Octubre Valley” and it should not be extrapolated outside the study area. The relationship between the disease and north aspect, and also the negative relation between the disease occurrence and precipitation, seemed both related to the particular distribution of soils in the study area. However, the variables shown to be associated with the disease provide hypotheses about the *A. chilensis* disease syndrome occurrence that should be tested by further field-work in other areas.

5. Conclusions

This work revealed that the incidence of the *A. chilensis* disease syndrome at a landscape scale is associated with topographic and edaphic features that affect drainage. Non-allophanized soils with fine textures from flat and wavy soil phases, geomorphologies associated to alluvial process, and low elevations and gentle slopes are disease-prone sites.

These results should be considered in forest management and planning criteria. Current silvicultural management allows cutting *A. chilensis* dead trees regardless of site and season. Disease-prone sites should be more protected from intervention in order to avoid the increase of the disease. Forest harvesting, cattle and humans could encourage the spread of *Phytophthora* by soil clinging to feet and equipment (Goheen et al., 2005). Disease-prone sites should be enclosed, at least during the wet season. The relationship between the disease and site conditions should also be considered for plant disease monitoring planning and for preventing restock in areas where the risk is greatest.

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