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Maqui (*Aristotelia chilensis* [Mol.] Stuntz) morphological and phenolic traits associated with forests type and latitudinal gradient in natural populations of Patagonia Argentina

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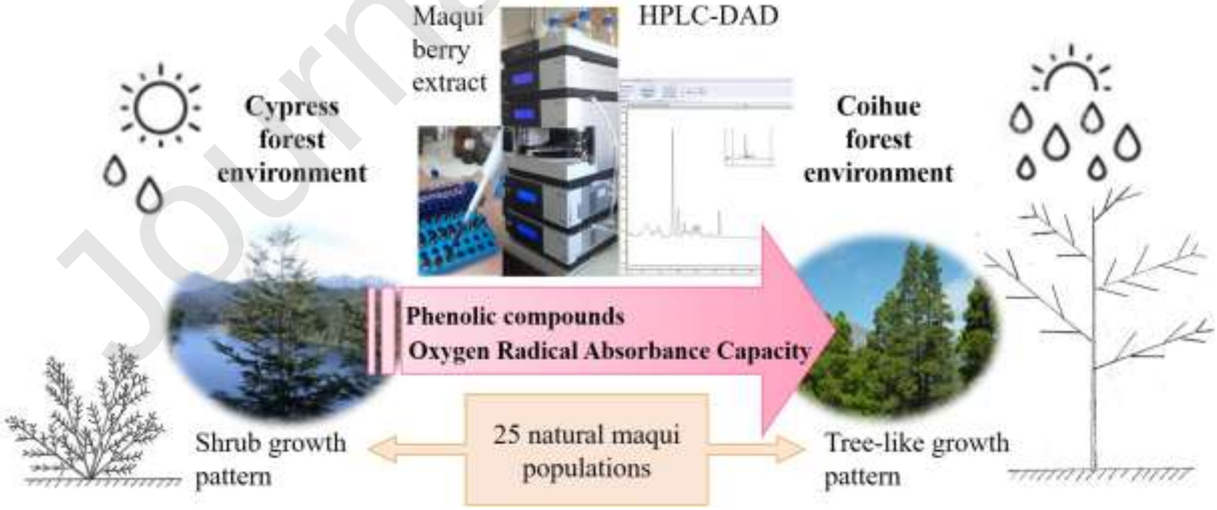
Graphical abstract



Abstract

Maqui (*Aristotelia chilensis* [Mol.] Stuntz) is a native berry of the Patagonia Andean forests, which has one of the highest antioxidant levels currently known. This biochemical characteristic strongly depends on the phenolic profile and is highly influenced by the growing environment. The objective of this study was to characterize natural maqui populations in the immediate lee (Argentina) of the Northern Patagonian Andes, distributed in a latitudinal gradient and associated with coihue (*Nothofagus dombeyi*) and cypress (*Austrocedrus chilensis*) forests, humid and xeric environments, respectively. Twenty-five natural populations that spanned the geographical distribution of the species in Argentina, were identified. The sites were associated with two forests (coihue and cypress) and three latitudinal groups (north, center and south). Canopy cover and light interception were measured in the selected sites, as well as plant morphology, fruit yield components, phenolic profiles and oxygen radical absorbance capacity (ORAC) of mature berries. Maqui populations associated to cypress are exposed to greater incident total solar radiation and lesser rainfalls, and showed shorter plants with several main stems, multiple branching and smaller specific leaf area (SLA) as compared to those of coihue forest. Maqui populations associated to coihue presented an increase in the number of berries per bunch, and also in the accumulation of phenols and ORAC. The evaluation of the acclimation responses of the natural populations by different environments can contribute to the development of high-yield and quality maqui crops as source of bioactive compounds.

Keywords: Environment acclimation, native berry, ORAC, phenolic compounds

1. Introduction

The Andean Patagonian forests of Argentina and Chile have a wide variety of native berries, which can be endemic, such as *Ugni molianae* (Myrtaceae), *Berberis darwinii, B. mycrophylla* (Berberidaceae), *Ribes magellanicum* (Grossulariaceae) and *Aristotelia chilensis* [Mol.] Stuntz (Elaeocarpaceae). The latter, known as maqui, is an endemic small evergreen berry-tree (4 to 5 m in height) that can be found in Argentina from parallel 38° to 43° S (SIB, 2002), whereas in Chile, it has a wider distribution (30º to 45º S; Fredes *et al.*, 2014). Berries and leaves of maqui are characterized by high polyphenol contents (Misle *et al.*, 2011; Fredes *et al.*, 2012; González *et al.*, 2015), and it is known as the berry with the “greatest” antioxidant activity when compared to different commercial berries (Miranda-Rottmann *et al.*, 2002). Maqui has been used by the native Patagonians as food and medicine for over 14,000 years (Schmeda-Hirschmann *et al.*, 2019). Actually, the nutraceutical properties of the berry (Céspedes *et al.*, 2008; 2010) have prompted the development of functional foods, cosmetic and pharmaceutical products (Gironés-Vilaplana *et al.*, 2012).

In Argentina, the Andean Patagonian forests are located between the parallels 35º and 54º S, from the provinces of Neuquén to Tierra del Fuego, distributed along a narrow strip of land of about 80 km wide, between the Andes and the Eastern plains, with a marked environmental heterogeneity. In cross-barrier direction, the annual climatological precipitation varies largely from about 2000 mm near the Andes crest (i.e., roughly the Argentina and Chile border) to less than 400 mm farther east on the dry Patagonian steppe (Viale *et al.*, 2019), and so this heterogeneity comprises different types of forest. In along-barrier direction, the precipitation varies slightly in the study area, increasing southward in extratropics where the storm tracks maximize (Viale *et al.*, 2019). The humid forest near the crest of the Andes is dominated by coihue (*Nothofagus dombeyi* (Mirb.) Oerst), an evergreen broadleaf tree, whereas farther East in the forest-steppe ecotone, the dominant species is cypress (*Austrocedrus chilensis* (D. Don) Pic.Serm. & Bizzarri), a conifer tree. There are also mixed forests where coihue and cypress are codominant species (Pastorino & Gallo, 2002). Likewise, climatic variation by latitude and altitude (Ignazi *et al.*, 2019) are evidenced. Maqui plants can grow in the understory of forests or in open areas (Faggi and Cagnoni, 1996; Misle *et al.*, 2011), possibly due to a high acclimation capacity, thrivering in diverse environments (Lusk, 2002). Accordingly, the natural maqui populations are exposed to variable climate signals/stressful conditions, changing phenotypic characteristics, including fruit yield, which is of great interest in domestication programs. There are no reports on the fruit yield of maqui plants due to their distribution in Argentina, or of other native species. In Chile, Vogel *et al.* (2014) found 68% higher fruit set of maqui in a coastal population (with maritime influence) than in a population at the Andes foothills, with larger thermal amplitudes. In other study at the Alps, Barizza *et al.* (2013) found higher productivity of blueberry *(Vaccinium myrtillus* L.) in an open forest, without light limitation. Plants have developed throughout their evolution various protection mechanisms, as well as morphogenic responses (He *et al.*, 2018; Potters *et al.*, 2007). Among these mechanisms, the production of secondary metabolites plays an important role in the adaptation of plants to different stressful conditions (Akula and Ravishankar, 2011). Phenolic compounds are a large variety of secondary metabolites that have diverse biological functions in plants. Many serve as attractants for pollinators and seed dispersers, or act as defense compounds against herbivores and pathogens (Harborne and Williams, 2000). Others play a protective role against stress by absorbing potentially harmful radiation and possessing antioxidant activity (Balasundram *et al.*, 2006; Dixon and Pavia, 1995; Xu *et al.*, 2014). The capacity of biosynthesis of phenolic compounds is determined by genetic factors, but environmental conditions influence phenolics composition and concentration, especially when those conditions cause some kind of stress on the plant (Akula and Ravishankar, 2011). Alfaro *et al.* (2013) found that the total polyphenol content and antioxidant activity in murtilla berries (*Ugni molinae*) was influenced by genotype and harvest years, and relates with rainfall and frost. Mariangel *et al.* (2013) showed that calafate berries (*Berberis mycrophylla*) varied their phenolic content and antioxidant activity according to their location in Chile, with higher values towards the south. In addition, a latitudinal variation of anthocyanins was found for wild bilberries of European forests, with higher contents towards the north (Zoratti *et al*., 2015). Maqui is able to show variation in the content of anthocyanins and other polyphenols in fruit according to its geographical distribution, as demonstrated in Chile by Fredes *et al.* (2014), which is the only precedent found for this species.

This work aims to evaluate the effect of different types of environments by forest and latitudes on maqui plant morphological characteristics, fruit yield and phenolic composition of the mature berries, in natural populations of Argentina.

2. Materials and methods

2.1. Plant material and study design

Twenty-five natural maqui populations, and thereby study sites, were identified in a distribution area corresponding to the Patagonian Andes of the Argentinian provinces of Neuquén, Río Negro and Chubut. The study area stretches from Huechulafquen Lake as the northern boundary (39º46’40” S) to Futalaufquen Lake (42º48’30” S) in the South. Maqui populations were defined as a copse of 20 plants and were classified according to forest type (coihue or cypress) and latitudinal group represented by the North (Neuquén province, mean latitude: 40°), the Center (Río Negro province, mean latitude: 41º), and South (Chubut province, mean latitude: 42º). Table 1S and Maps 1-3 in Supplementary Material show the study sites characteristics and location. The minimum distance between maqui populations was 30 km.

Table1

2.2. Climatic conditions

The air temperatures and rainfall in the study area were recorded by 11 weather stations distributed within each of the three latitudinal groups with plants sampling. Daily mean, maximum and minimum air temperatures and the rainfall data were considered from September to April during 2016-2019.The percentage of solar radiation transmissivity though the forest canopy was estimated for each study site using hemispherical photographs, based on Promis and Cruz (2009). Three photographs for each study site, spatially separated 25 m, were taken on a cloudy day during the fruit harvest period (February to March). Photographs were analysed with Gap Light Analyzer Software V 2.0. Maps 1-3 in Supplementary Material show the location of the weather stations.

2.3. Morphological characterization and berry sampling

Within each maqui population, 20 plants separated at least 3 m apart from each other were selected and marked with plastic tags. During the flowering period of the first season (October to December 2017), five female maqui plants per study site were recognized according to their floral morphology, as a dioecious cross-pollinated species (Vogel *et al.*, 2014).

All the plants (female and male) were used to evaluate morphological traits. The total height of the plants was measured with a telescopic rod. The number of main stems per plant were counted and the main stems diameter (0.3 m above the ground) of all the main stems per plant were measured with a caliper.

The fruits maturation progress was visually followed in female plants from January to March until berries ripped (epicarp coloration turns to bright black/dark purple) based on González *et al.* (2015). Then, two reproductive branches per plant were sampled and used to evaluate: branch length, basal diameter of the branch, number of berries per bunch, number of bunches per branch, number of berries per branch and specific leaf area (SLA) of mature leaves from the middle section, drying leaf discs to constant weight at 40 ºC. Only plants with intact leaves were selected for this sampling.

Samples of ca. 500 g of mature berries per plant were randomly taken, frozen at -80 ºC and then lyophilized at a temperature of -54 ºC and at an atmospheric pression of 0.056 mm Hg for 7 days. Fruit’s sampling and biochemical analysis were done for the 25 maqui populations during season 1 and for 14 populations during season 2 (Table 1).

2.4. Biochemical analyses

Fifty lyophilized berries per sample were randomly taken and ground to powder with an analytical mill (IKA A11, Staufen, Germany). Then, 0.5 g of powder were placed in 15 mL tubes containing 12 mL of methanol:water:HCl (50:49:1), as described by Connor *et al.* (2002), and extracted at 4 °C for 24 h. Supernatants were transferred into 1.5 mL tubes and centrifuged 5 min at 10,000 rcf. The phenolic compounds (anthocyanins and low molecular weight polyphenols) were determined using high-performance liquid chromatography equipment with a photodiode array detector (HPLC-DAD; Dionex UltiMate 3000, Thermo Fisher Scientific Inc., Germany) as described by Fontana *et al.* (2016, 2014). The oxygen radical absorbance capacity (ORAC) was evaluated with a microplate fluorometer (Fluoroskan Ascent FL; Thermo Fisher Scientific, Wilmington, DE, USA) as described by Berli *et al.* (2014), with extract dilutions of 1:1000 (v/v).

2.5. Statistical analysis

Factorial analysis of variance (ANOVA) was used to evaluate effects of forest type (FT), latitudinal group (LG) and their interactions (FTxLG). The statistical analysis was carried out using R (R Core Team, 2019; https://www.R-project.org/) by using *lm* and *glm* for continuous or discrete quantitative variables, respectively. Significant differences between means were determined by Tukey Test and accepted if $p \leq 0.05$ and the results were expressed as mean ± standard error of mean (SEM).

3. Results

3.1. Climatic conditions

For all the latitudinal groups (Figure 1 A), the accumulated rainfall was markedly higher for the sites located closer to the Andes crest, with mean values of 839.5 ± 93.9 mm as compared to those farther East (162.6 ± 23.5 mm). There are no differences in recorded rainfall between latitudinal groups but there are differences between longitude groups, being significantly higher towards the West than towards the East. Figure 1 B shows daily mean minimum air temperatures increased from North to South in the study sites at the West longitude, but did not vary with latitude at the East. In the Center and South groups, the minimum temperatures were higher closer to the Andes than those farther East on the steppe, although these cross-barrier differences were not distinguishable in the North group (Figure 1 B). Maximum temperatures only showed differences at Center group, with higher values in the East longitude than the West longitude (Figure 1 C). Mean temperatures showed no differences in both longitudes and latitudinal groups (Figure 1 D).

Figure 1

The total radiation transmissivity of the trees canopy differed stronger between different forest types, than between different latitudinal groups (Figure 2 A). The coihue forest had canopy transmissivity mean values of 19.58 ± 0.68%, while the cypress forest had 56.9 ± 2.3%. The canopy transmissivity differences between forest types were greater in the North (42.64 ± 0.9 %.) and in the South (42.82 ± 2.2 %) than in the Center (24.89 ± 1.2 %), with significant interaction for forest type and latitude (Table S1).

3.2. Morphological characteristics

The maqui plants height is affected by forest type, without significant interactions between both factors (Figure 2 B; Table S1). The maqui plants were taller when associated with coihue than cypress only for the Center latitudinal group. The lowest maqui plants reached 3.4 ± 0.1 m and were found in association with cypress forest at the Center, while the tallest maqui plants reached 5.1 ± 0.1 m and were found in the coihue forest from the North.

Regarding the number of main stems per plant, there were differences for forest types and latitudinal groups (Figure 2 C). Maqui plants in cypress forest had a greater number of stems than maqui plants in coihue forest, for each latitude groups. The highest stem number per maqui plant was obtained in the populations of the North associated with cypress. Maqui plants associated with cypress forest showed no differences between Center and South groups for number of main stems, and were significantly lower than those from the North. The total area of main stems was calculated as the sum of the sectional area of the stems. It showed differences between forest type at North latitude and at South latitude, being higher for cypress forest, significant interaction (Figure 2 D; Table S1).

Figure 2

The morphological characteristics of the fruitful branches are presented in Figure 3. The length of the fruitful branch was greater in coihue forest with a mean value of 0.42 ± 0.02 m, with respect to the cypress forest (0.36 ± 0.02 m), only for the North group.

The basal diameter of the fruitful branches showed no statistically significant differences, between forest types and latitude (Figure 3 B). Significant factors interaction was found for SLA (Figure 3 C). Maqui populations associated to coihue forests have higher SLA than those associated to cypress forests, in the North and Center latitudinal group. There were no statistically significant differences for SLA between forest type in the South.

Figure 3

The fruit yield characteristics are shown in Figure 4. At North and South latitudes, the number of berries per bunch was higher in maqui plants associated to coihue forest than those associated to cypress forest (Figure 4 A). At the Center, the berries per bunch were not significantly affected by forest type. The maqui in coihue forest and in the North had the highest quantity of berries per bunch (7.2 ± 0.4 berries/bunch), while those in cypress forest at the South had de lesser (4.6 ± 0.4 berries/bunch. No differences were observed for the number of bunches per fruitful branch between forest type at any latitude (Figure 4 B).

Figure 4

3.3. Biochemical characteristics of mature maqui berries

ORAC values for maqui populations in coihue forest type were higher than those values found in populations associated with cypress forest, for the Center latitude (significant factors interaction; Figure 5 and Table 1). There were no differences between forest types at the North or the South. Mean ORAC value for all maqui populations was 33,475 ± 1129 mM TE/ g dw and the highest was 60.483 mM TE/ g dw and it was found in a coihue forest population in the South.

Figure 5

Five different anthocyanins were identified and quantified for both sampling seasons in mature maqui berries, two cyanidine derivatives and three delphinidine derivatives (Figure 6). The anthocyanins profile coincided for both seasons, but there was a signifficant difference in the anthocyanins concentrations (p(season*compound)=0.0026).

Delphinidin-3,5-diglucoside was the only anthocyanin that differed between maqui populations during the season 2018, with a concentration of 344 ± 24 mg/100 g dw in coihue forest, and 254 ± 28 mg/100 g dw in cypress forest (Figure 6 A). In addition to delphinidin-3,5-diglucoside, in 2019 the delphinidin-3-glucoside also showed variation in populations located in coihue forest and in cypress forest. It was higher for coihue forest (379 ± 39 mg/100 g dw) than for cypress forest (280 ± 48 mg/100 g dw; Figure 6 B). Delphinidin-3-sambubioside-5-glucoside, cianidin-3-sambubioside, and cianidin-3-glucoside showed no differences between forest types for both sampling seasons.

Figure 6

The concentrations of low molecular weight polyphenols are shown in Table 2. The quercetin-3-galactoside had the higher concentration for both seasons (2018 and 2019) and increased for cypress forest type (p(forest type*compound)=0.0024). Quercetin-3-glucoside and (-)-epicatechin were identified only in the first season, and also increased for Cypress. Other differences were found between seasons with (+)-catechin, caftaric acid, procyanidins and pterostilbene which were identified only in the first season, while p-coumaric acid and (-)-epigallocatechin gallate were found only in season 2019.

The (-)-epigallocatechin gallate was the most abundant compound in season 2019 and had major concentration in coihue forest.

Table 2

4. Discussion

In this work, maqui populations in their natural environment in the Northern Andean Patagonian forests of Argentina were phenotypically described, with emphasis on some morphological and biochemical aspects. The largest climatic variation within the distribution and sampling area was the variation of rainfall in cross-barrier direction, with a greater accumulation closer to the crest of the Andes than farther east on the steppe as a result of a strong rain shadow effect to the lee of the Andes (Viale *et al.*, 2019). In second order of variation, rainfall decreases from South to North due to the location of the storm tracks in the extratropics (Viale *et al.*, 2019). The differences in altitude of the climatic stations and the density of the surrounding forests have also influences on temperatures in different latitudinal groups analyzed here.

Therefore, the maqui plants in the coihue forest possibly grow in a less stressful environment in terms of water availability, but with sunlight limitations in a dense forest (transmissivity of the canopy *ca.* 20% of the total radiation). Notable morphological differences were observed between the maqui plants of the coihue and cypress forests in terms of the main stems. Maqui plants in cypress forest were more branched, generating a bush-like architecture, compared to those growing in coihue forest, which had a tree-like morphology. Misle *et al.* (2011) described this species in Chilean cypress forests, and characterized it as a shrub with the trunk divided into numerous stems. We also found that the fruit branches in the coihue forest were 16% longer with a greater SLA than those of the cypress forest, for North and Center populations. A higher SLA indicates that the plant builds a larger leaf area with a given amount of leaf biomass and these characteristics are typical of species adapted to shady environments to maximizes the collection of light energy (Damascos and Prado, 2001).

The fruit yield of maqui plants was estimated by the number of berries per bunch and by the quantity of bunches per branch. There was no evidence of variation across the latitudinal range, but variation across the contrasting environments of coihue and cypress forest for some latitudinal groups were observed. In this regard, rainfall due to the longitudinal location and transmissivity of sunlight by the forest type were the variables that showed marked differences. In this regard, Moya *et al.* (2019) also found differences in maqui clones in relation to different light conditions. They demonstrated that in all the clones studied, the shaded plants (50% of the solar radiation; black net-covering) grew taller and decreased their flowering capacity than those exposed to full sunlight (without coverage). In our study, we did not evaluate the flowering capacity, but we found that maqui plants from coihue forest in the North and South produced more berries per bunch than those from cypress forest, without differences in the number of bunches per branch. The total number of fruit-bearing branches per plant was not measured and should be considered to correctly evaluate the effects on fruit yield. Maqui plants in the cypress forest have a greater number of main stems than those in the coihue forest, possibly with a major capacity to sustain higher fruit production, as shown by Tustin *et al.*, (2001). Costa *et al.*, (2016) and Leduc *et al.*, (2014) also showed that the branching is related to fruit yields.

Maqui structure is formed by long shoots or sprouts with an apical vegetative bud and axillary buds that develop the fruit branches. The sprouts of the season are formed from the vegetative buds at the end of the branch developed the previous year. When monopodial growth is disrupted, e.g. the apical bud freezes, dies or is removed, one to four apical buds will continue to sprout (Vogel *et al.*, 2014). Thus, the maqui fruit production would be optimized by pruning management, as proposed by Doll *et al.* (2017).

Antioxidant activity from maqui populations in Chile was assessed in dried and unseeded berries (Céspedes *et al.*, 2008). They also prepared the extraction solution with methanol containing 0.1% HCl v/v and reached an ORAC of 29,689 ± 120 mM of TE/100 g dw. This is an ORAC value lesser to that of our study with extraction from lyophilized whole berries, including seeds (33,475 ± 898 mM of TE/100 g dw). Céspedes *et al.* (2008) also evaluated 2,2-diphenyl-1-picrylhydrazyl radical scavenging (DPPH) and ferric reducing antioxidant power (FRAP) and conclude that maqui berries MeOH extracts were strongly related with total polyphenol content.

Miranda-Rottmann *et al.* (2002) reported that maqui berry juice extracts have exceptionally high phenolic content and score better for total radical trapping potential and total antioxidant reactivity compared to different commercial berries. Brauch *et al.* (2016) also carried out extractions with acidified methanol (0.1% HCl, v/v) using powders from whole maqui berries. They found a higher total anthocyanin content compared to other anthocyanin-rich fruits and with more significant antioxidant activities than other "superfruits".

We found a high relative amount of delphinidin derivatives (90.7%), higher than the 70-80% reported by Escribano-Bailón *et al.*, (2006) and Fredes *et al.* (2014). Consistently with those authors, only glycosylated derivatives of delphinidins and cyanidins have been reported for maqui berries. Brauch *et al.* (2017) used HPLC-DAD-MS and Two-Dimensional Nuclear Magnetic Resonance (2D-NMR) spectroscopy, and showed that the relative proportions of diglycosylated anthocyanins were 84% of total anthocyanins, exceeding those of mono-substituted anthocyanins in maqui berries. The anthocyanin antioxidant properties are modulated by glycosylation, hydroxylation and methoxylation (Sroka, 2005; Wang *et al.*, 1997). The methoxylated and trihydroxylated anthocyanins are characterized by a lesser antioxidant activity, but are more stable to oxidation, relevant for assessing color stability of maqui anthocyanins in future food applications (Brauch *et al.*, 2017). Within the metabolic pathway, delphinidins and cyanidins are in a prior stage to O-methyl transferase (OMT), and do not have methyl groups. It is known that O-methylation reduces the chemical reactivity of phenolic hydroxyl groups (Hugueney *et al.*, 2009; Zhang *et al.*, 2014), therefore the anthocyanin profile of maqui berries increase its antioxidant activity, as compared to other berries.

In the present study, we found traces of caftaric acid, a combination of caffeic acid and tartaric acid, which had not been reported before for maqui species but which is common for other berries such as grapevines (Berli *et al.*, 2011). A wide variety of flavonoids, such as kaempferol, and several glycosylated derivatives of quercetin and myricetin have been determined in maqui berries (Céspedes *et al.*, 2010; Genskowsky et al., 2016; Ruiz *et al.*, 2016; Li *et al.*, 2017). In addition, phenolic acids such as sinapic, gentisic, ferulic and ellagic have also been identified in maqui berries (Céspedes *et al.*, 2010; Genskowsky *et al.*, 2016). These compounds are typical of seeds. The (-)-epigallocatechin gallate was the most abundant compound found in our samples, a flavanol compound that was only identified in the second season of sampling and that has not been previously reported in maqui berries. In addition, traces of a pterostilbene were identified only in the first season, and there are no previous reports of this compound in maqui.

Plants have evolved different response mechanisms to an environmental signal such as acclimation or response to an evoked damage (Valladares et al., 2007). Maqui plants in cypress forest can be adapted to the higher radiation levels, especially by triggering morphogenic responses, and possibly increasing fruit yield per plant, at the expense of the accumulation of phenolic compounds and the increase of antioxidant activity in berries. Besides the higher percentage of solar radiation interception by the tree canopy in coihue forest, different microclimatic differences as light qualities and air relative humidity are expected, possibly affecting the cryptogamic parasites incidence. The extent of phenotypic change in response to a signal is its phenotypic plasticity and results from both genetic and environmental influences (Nicotra *et al.*, 2010). Therefore, variability in phenolic compounds between sampled populations and also between years in natural populations of maqui was expected, especially as a dioecious cross-pollinated species (Vogel *et al.*, 2014). Phenolic compounds are induced in response to multiple environmental factors, such as cold, drought, ultraviolet radiation and pathogens (Akula and Ravishankar, 2011; War *et al.*, 2012). *Aristotelia chilensis* is a pioneer species that colonizes and grows in stressed and disturbed environments. González-Villagra *et al.* (2018) found that maqui plants subjected to severe drought increased their levels of abscisic acid (ABA) and reduced their relative growth rate. In addition, maqui plants increased the anthocyanin accumulation by upregulation of the gene expression of UDP glucose: flavonoid-3-O-glucosyltransferase (UFGT).

5. Conclusions

The first phenotypic description of maqui populations in the Andean-Patagonian forests was made, covering a wide range of the species in Argentina. Contrary to our expectations, we did not find a clear pattern of biochemical changes. Only the populations in the centre of the distribution revealed changes of biochemical variables, which possibly responded to punctual situations of temperature and precipitation. Morphologically, we found changes associated with growth under shade. Maqui plants present morphological and phenolic traits characterized mainly by forest type, but also some latitudinal effects.

The high levels of phenolic compounds and antioxidant activities obtained in the different environments give an important clue to the potential of maqui as a source of bioactive compounds. Furthermore, understanding acclimation responses is crucial for predicting and managing the effects of climate change on native species, as well as a basis for proposals for high-yielding cultivation techniques.

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author contribution statement

CSR: sample collection, data curation, methodology and analysis. AF: funding acquisition and HPLC-DAD methodology. GC: project conception, funding acquisition, methodology and supervision. MV: climatic data collection. FJB: project conception, funding acquisition, methodology, analysis and supervision. CSR and FB prepared the draft manuscript. All authors reviewed, edited and approved the final version of the manuscript.

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Figure captions

Figure 1. Climate characterization of study sites based on their location at three latitudinal groups (North, Center and South) and two longitudes (West and East). Accumulated rainfall (A), daily minimum air temperature (B), maximum air temperature (C) and mean air temperature (D). Data from September to April during 2016-2019 were considered and different letters indicate significant differences (Tukey Test; $p \leq 0.05$).

Figure 2. Environmental and morphological characteristics of maqui plants for two forest types (Coihue and Cypress) and three latitudinal groups (North, Center and South). Total radiation transmissivity of the forest tree canopy (A), maqui plant height (B), maqui plant main stems number (C), and maqui plant total area of main stems (D).

Figure 3. Morphological characteristics of fruitful branches of maqui plants from two types of forest (Coihue and Cypress), and three latitudinal groups (North, Center, and South). Branch length (A), basal diameter of the branch (B), and Specific Leaf Area (C).

Figure 4. Fruit yield traits of maqui plants from two forest types (Coihue and Cypress), and three latitudinal groups (North, Center, and South). Number of berries per bunch (A) and number of bunches per branch (B).

Figure 5. ORAC of mature maqui berries from two types of forest (Coihue and Cypress), and three latitudinal groups (North, Center, and South).

Figure 6. Quantitative results of anthocyanins of mature maqui berries from two sampled season. Season 1, 2018 (A) and Season 2, 2019 (B) for two forest types (Coihue and Cypress). Compound: 1., Delphinidine-3-sambubioside-5-glucoside; 2., Delphinidine-3,5-diglucoside; 3., Delphinidine-3-glucoside; 4., Cyanidine-3-sambubioside; 5., Cyanidine-3-glucoside. Different letters for the same compound and for each season indicate significant differences, $p \leq 0.05$.

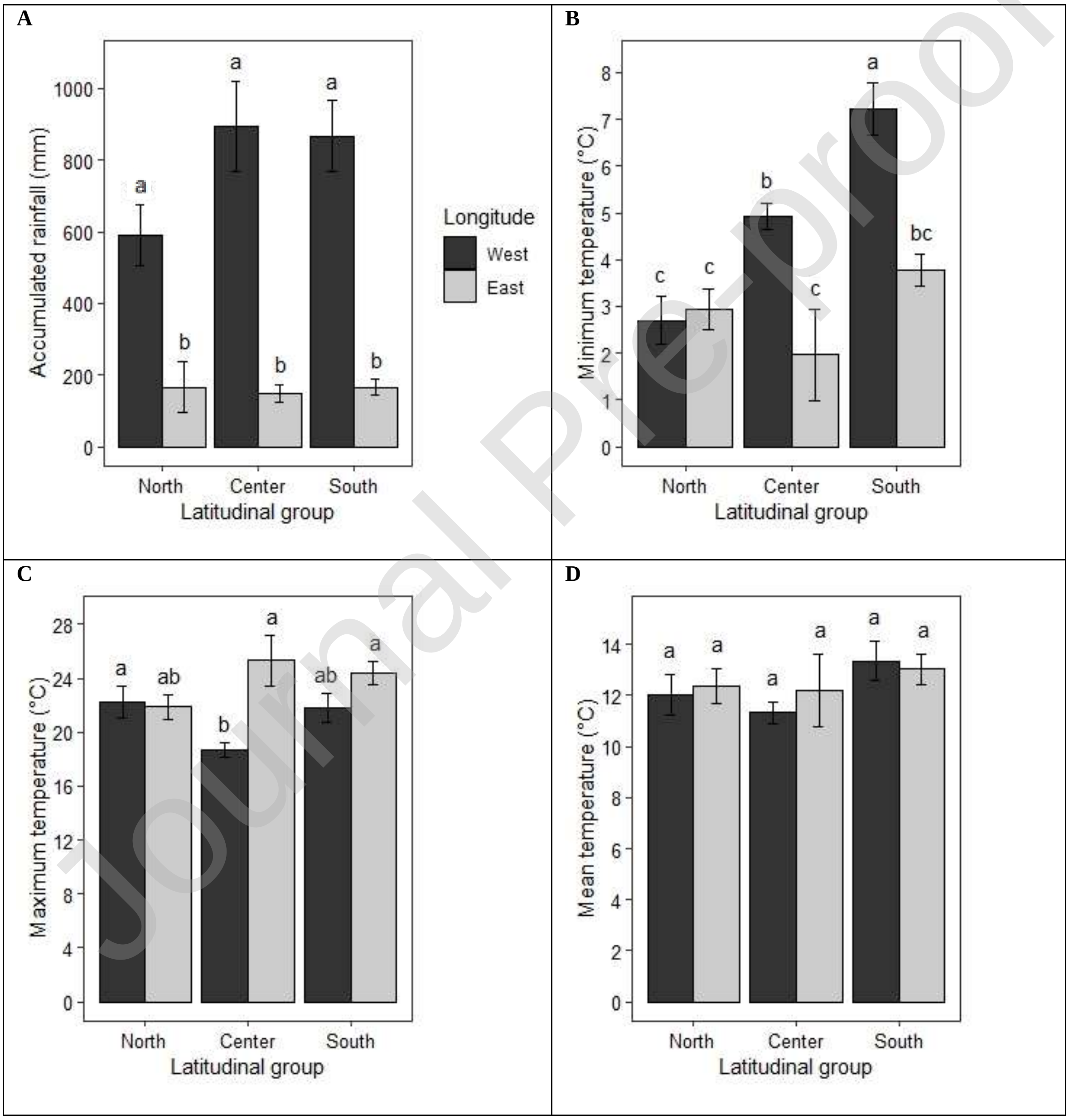

Figure 1.

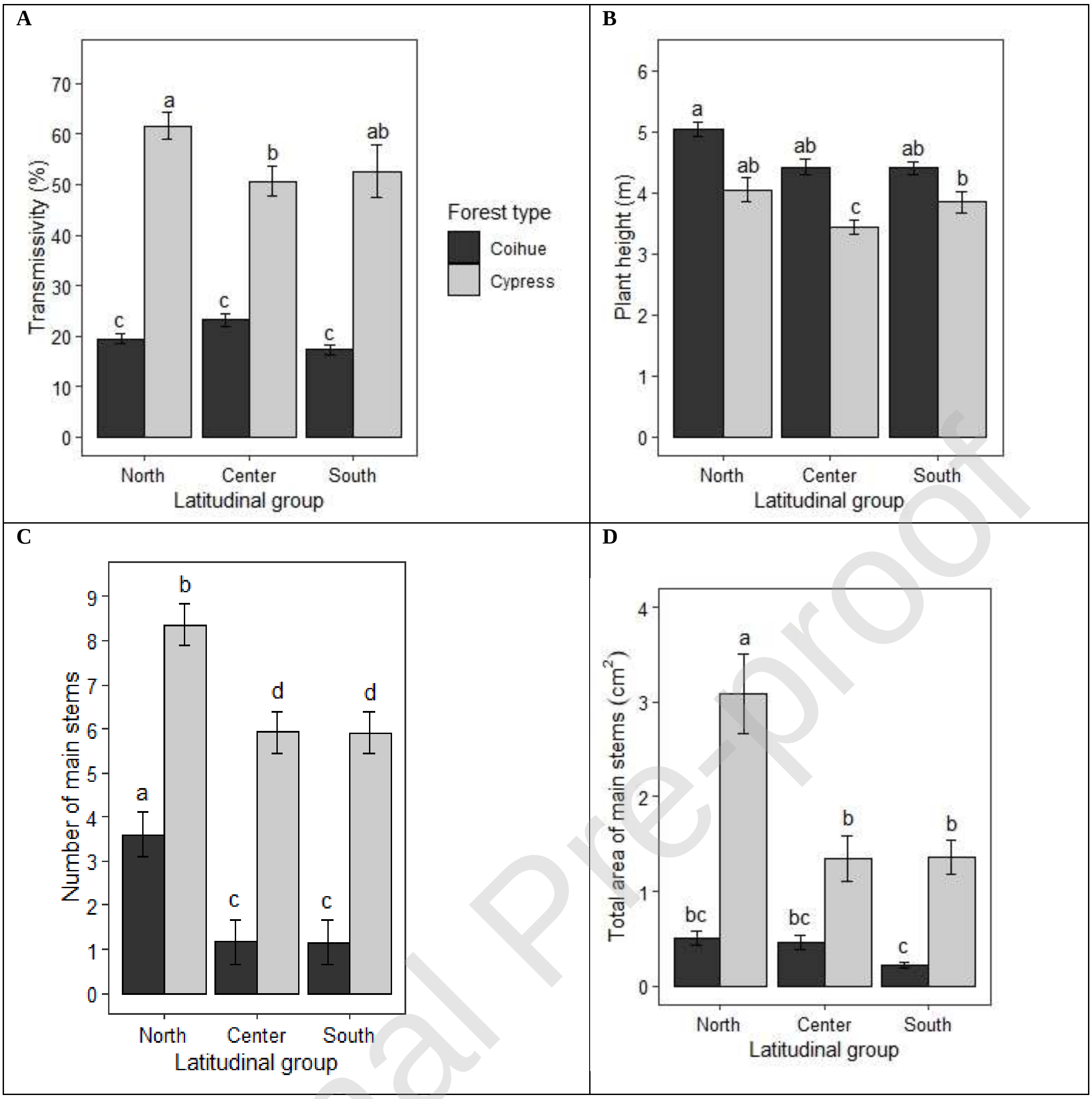
A
Transmissivity (%)
0
10
20
30
40
50
60
70
c
a
c
b
c
ab
North
Center
South
Latitudinal group
Forest type
Coihue
Cypress
B
Plant height (m)
0
1
2
3
4
5
6
a
ab
ab
c
ab
b
North
Center
South
Latitudinal group
C
Number of main stems
0
1
2
3
4
5
6
7
8
9
a
b
c
d
c
d
North
Center
South
Latitudinal group
D
Total area of main stems (cm^2)
0
1
2
3
4
bc
a
bc
b
c
b
North
Center
South
Latitudinal group

Figure 2.

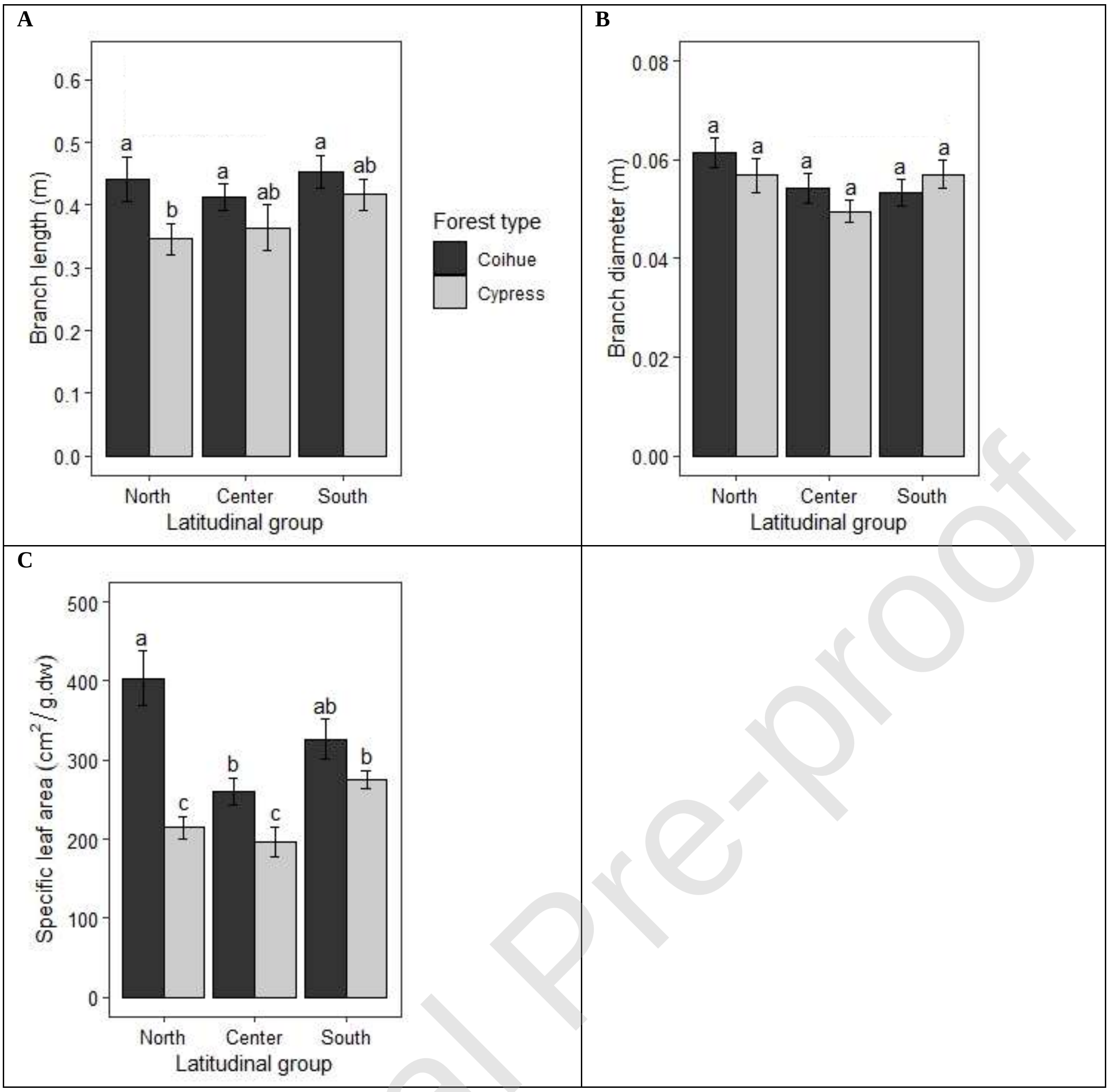
A
Branch length (m)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
a
b
a
ab
a
ab
North
Center
South
Latitudinal group
Forest type
Coihue
Cypress
B
Branch diameter (m)
0.00
0.02
0.04
0.06
0.08
a
a
a
a
a
a
North
Center
South
Latitudinal group
C
Specific leaf area (cm2 / g.dw)
0
100
200
300
400
500
a
c
b
c
ab
b
North
Center
South
Latitudinal group

Figure 3.

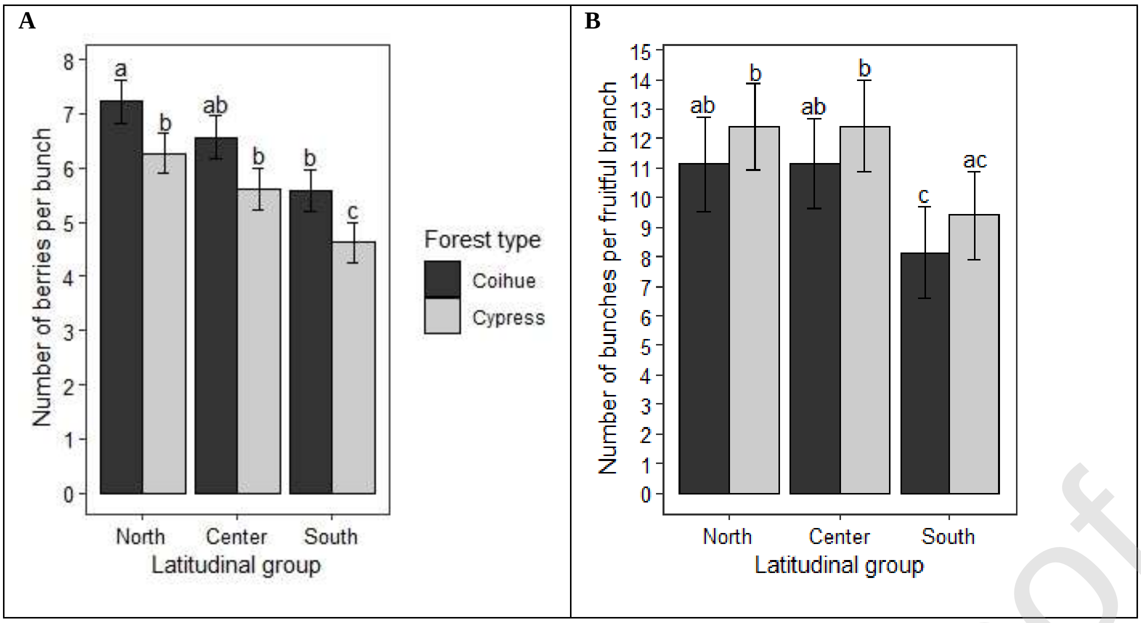
A
Number of berries per bunch
0
1
2
3
4
5
6
7
8
a
b
ab
b
b
c
North
Center
South
Latitudinal group
Forest type
Coihue
Cypress
B
Number of bunches per fruitful branch
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
ab
b
ab
b
c
ac
North
Center
South
Latitudinal group

Figure 4.

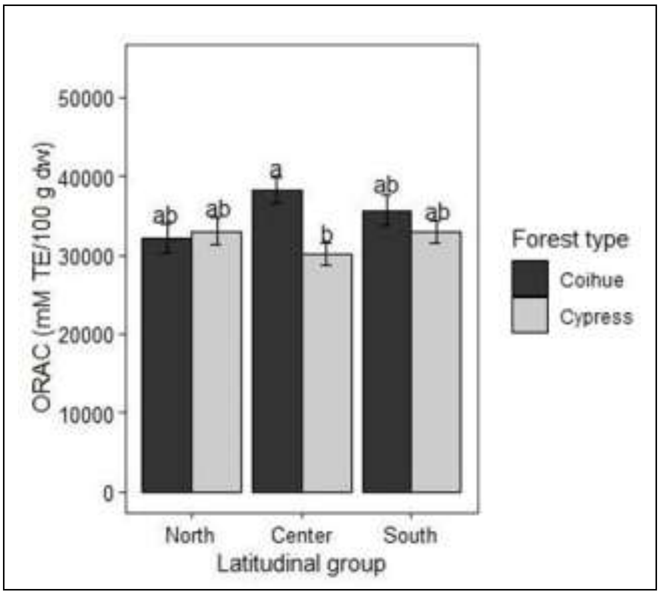
50000
40000
30000
20000
10000
0
ORAC (mM TE/100 g dw)
ab
ab
a
b
ab
ab
North
Center
South
Latitudinal group
Forest type
Coihue
Cypress

Figure 5.

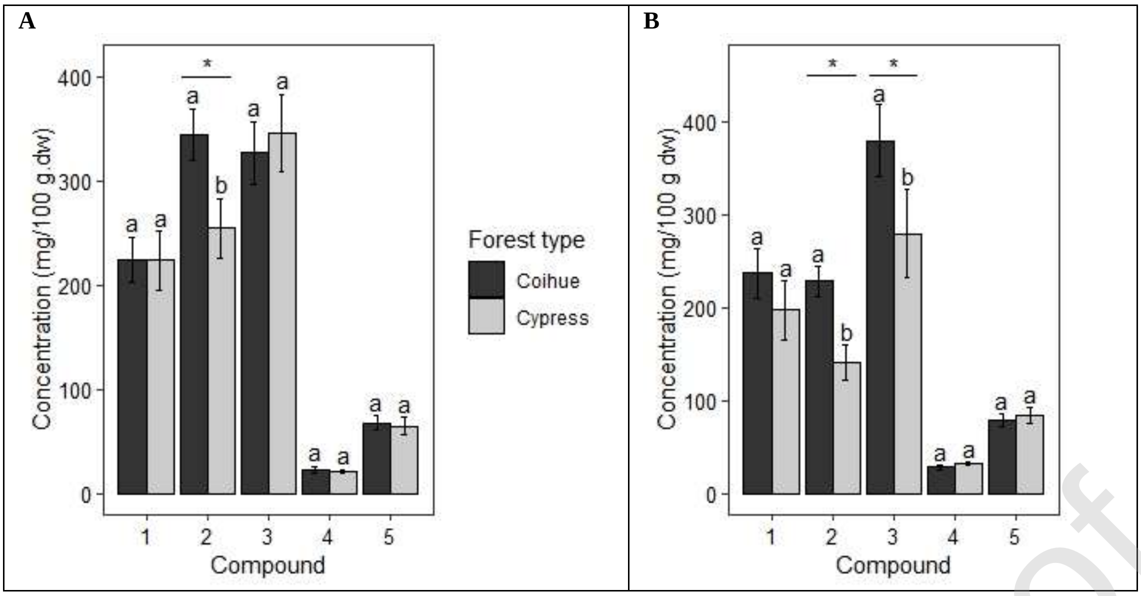

Figure 6.

Table 1. Maqui populations distributed by forest type and latitudinal group. Coordinates, altitude, and sampling dates.

Site	Forest type	Latitudinal Group	Latitude	Longitude	Altitude (m a.s.l.)	Sampling date	
						Season 1	Season 2
L.Huechulafquen (Nqn)	Cypress	North	39°46'40.4"	71°14'19.8"	917	6 Feb	12 Feb
Yuco (Nqn)	Coihue	North	40°8'35.20”	71°28'49.2"	661	6 Mar	26 Feb
Quila Quina (Nqn)	Cypress	North	40°10'25.6”	71°21'44.47"	710	6 Mar	12 Feb
L. Filo Hua Hum (Nqn)	Cypress	North	40°30'9.30"	71°18'30.50"	857	20 Feb	12 Feb
Portezuelo (Nqn)	Coihue	North	40°36'11.9"	71°37'40.30"	933	28 Feb	26 Feb
Ea. 7 Cóndores (Nqn)	Cypress	North	40°42'56.80”	71° 7'19.70"	599	20 Feb	12 Feb
Paso Samoré (Nqn)	Coihue	North	40°40'30.60"	71°43'51.80"	855	21 Feb	26 Feb
Va. La Angostura (Nqn)	Cypress	North	40°55'19.4"	71°26'14"	859	19 Feb	6 Feb
Tom Weasley (RN)	Coihue	Centre	41°5'6.98"	71°27'53.97"	823	15 Feb	-
Co. Otto (RN)	Cypress	Centre	41°8'24.6”	71°20'12"	978	12 Feb	21 Feb
L. Gutiérrez (RN)	Coihue	Centre	41°10'51.10"	71°24'57.80"	750	6 Mar	21 Feb
Co. Ventana (RN)	Cypress	Centre	41°12'13.40"	71°23'56.90"	833	12 Feb	19 Feb
Pampa Linda (RN)	Coihue	Centre	41°16'32.70"	71°37'36.80"	834	27 Feb	-
Baqueanos (RN)	Cypress	Centre	41°15'4.90"	71°27'15.40"	835	12 Feb	19 Feb
B. Suegra (RN)	Coihue	Centre	41°21'2.40"	71°36'20.50"	850	27 Feb	-
Va. Mascardi (RN)	Cypress	Centre	41°20'45.60"	71°30'24.60"	824	7 Feb	19 Feb
RN 40 Gpq (RN)	Cypress	South	41°32'45.70"	71°27'52.20"	1025	7 Feb	-
El Manso (RN)	Coihue	South	41°36'9.07"	71°43'47.91"	729	1 Mar	-
R. Azul (RN)	Coihue	South	41°56'29.60"	71°33'22.90"	776	7 Feb	-
Cuesta Ternero (RN)	Cypress	South	41°52'43.0"	71°26'31.6"	727	8 Feb	19 Feb
Pto. Patriada (Ch)	Coihue	South	42°9'37.40"	71°30'58.80"	336	12 Mar	-
Epuyén (Ch)	Cypress	South	42°15'34.70"	71°21'29.60"	592	12 Feb	-

L. Rivadavia (Ch)	Coihue	South	42°36'9.40"	71°38'37.60"	543	11 Mar	-
Pq. Los Alerces (Ch)	Cypress	South	42°45'33.34"	71°44'37.65"	581	11 Mar	-
L. Futalaufquen (Ch)	Coihue	South	42°49'0.67"	71°42'54.98"	535	11 Mar	-

§ Nqn: Neuquén Province, RN: Río Negro Province, Ch: Chubut Province.

Table 2. Quantitative results of low molecular weight polyphenols of mature maqui berries from two sampled season (Season 1, 2018; Season 2, 2019) and two forest types (Coihue and Cypress). Statistical significance is indicated by different letters for each compound and season (Fisher LSD; p≤0.05).

Compound		**2018**			**2019**		
		Conc	**± SEM**		**Conc**	**± SEM**	
Kaempferol-3-galactoside	Coihue	12.35	1.74	a	7.41	0.58	a
	Cypress	11.14	1.32	a	7.92	0.65	a
Quercetin	Coihue	5.06	0.30	a	3.29	0.04	a
	Cypress	6.14	0.32	a	3.33	0.03	a
Quercetin-3-galactoside	Coihue	11.13	3.31	a	18.39	2.45	a
	Cypress	24.43	3.99	b	30.74	4.96	b
Quercetin-3-glucoside	Coihue	3.35	1.61	a	nd	nd	-
	Cypress	7.04	2.04	a	nd	nd	-
(-)-Epicatechin	Coihue	38.92	7.08	a	nd	nd	-
	Cypress	56.44	9.41	b	nd	nd	-
Gallic acid	Coihue	8.85	2.94	a	14.48	2.62	a
	Cypress	5.66	1.64	b	14.56	2.16	a
p-coumaric acid	Coihue	nd	nd	-	100.17	13.52	a
	Cypress	nd	nd	-	90.50	9.79	b
(-)-Epigallocatechin gallate	Coihue	nd	nd	-	1555.84	205.00	a
	Cypress	nd	nd	-	1392.91	151.79	b
(-)-Gallocatechin gallate	Coihue	778.80	179.88	a	785.81	109.64	a
	Cypress	663.04	87.06	b	633.45	77.56	b
(+)-Catechin	Coihue	93.61	21.61	a	nd	nd	-
	Cypress	104.69	19.38	b	nd	nd	-
Astilbin	Coihue	6.06	1.99	a	0.44	0.24	a
	Cypress	3.00	0.83	b	0.09	0.01	b
Caftaric acid	Coihue	1.00	0.14	a	nd	nd	-
	Cypress	0.90	0.09	a	nd	nd	-
Procyanidin B1	Coihue	0.12	0.12	-	nd	nd	-
	Cypress	nd	nd	-	nd	nd	-
Procyanidin B2	Coihue	9.18	1.24	a	nd	nd	-
	Cypress	6.22	0.75	b	nd	nd	-
Pterostilbene	Coihue	0.23	0.04	a	nd	nd	-
	Cypress	0.29	0.04	a	nd	nd	-