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Structural and Functional Properties of *Araucaria araucana* and *Araucaria angustifolia* Seed Proteins as a Plant-Based Food Source

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ABSTRACT

This study compares the morphological, compositional, and protein characteristics of seed flours from *Araucaria angustifolia* and *A. araucana*. Morphologically, *A. angustifolia* seeds were significantly larger, while *A. araucana* exhibited more regular, triangular shapes. Proximate composition revealed a carbohydrate-rich profile in both species, with a significantly higher lipid content in *A. araucana*. Amino acid analysis showed similar profiles, with high levels of aspartic and glutamic acids. Both flours had favorable essential amino acid scores, suggesting good protein quality. Kjeldahl conversion factors (5.95 for *A. angustifolia* and 6.32 for *A. araucana*) differed from commonly used estimates. Protein solubility increased under alkaline conditions and was significantly higher for *A. araucana* at neutral to acidic pH. Water-extractable albumins were the predominant protein fraction. FTIR analysis confirmed the presence of proteins, lipids, and carbohydrates, and secondary structure analysis indicated random coil and β-sheet dominance. Starch analysis by deconvolution suggested a predominance of amorphous over ordered regions. Overall, both seed flours demonstrate valuable nutritional and functional properties, with *A. araucana* offering slightly enhanced solubility and lipid content.

1 | Introduction

Before European colonization, the diet of Indigenous people in southern South America was predominantly plant-based. Meat consumption was infrequent and largely dependent on the occasional hunting of wild species such as guanacos. Besides, various native plants were consumed, including squash, quinoa, and various fruits such as those from the algarrobo (*Prosopis chilensis*), arrayán (*Luma apiculata*), maqui (*Aristotelia chilensis*), quilo (*Muehlenbeckia hastulata*), and the seeds of the *Araucaria* genus (chilena 2024).

Araucaria trees are distributed across the Southern Hemisphere, with three species producing edible nuts. *Araucaria angustifolia*, or pinheiro-do-paraná, is found in Brazil, Paraguay, and northeastern Argentina, between 18° S and 30° S (dos Reis et al. 2014). *Araucaria araucana*, or pehuén, grows between 37°30′ S and 40°10′ S on both sides of the Andes (Bernal et al. 2024), while *Araucaria bidwillii*, or bunya pine, is native to Australia (Nadolny et al. 2023). The seeds are commonly referred to as pine nuts (*A. araucana*), piñones (*A. angustifolia*), and bunya nuts (*A. bidwillii*).

Araucaria araucana forests are ecologically unique and dominated by a species often considered a "living fossil". *A. araucana* can reach heights of up to 30 m and live for over a thousand years. Historical accounts highlight the cultural and subsistence

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significance of piñones for the Indigenous communities (Cortés et al. 2019). *A. araucana* was a vital dietary component for the Mapuche people. These seeds were used in a variety of traditional preparations such as soups, flatbreads, and beverages (chilena 2024).

The seeds (displayed in Figure 1) are typically boiled or roasted prior to peeling, a process that facilitates the transfer of phenolic compounds from the husk to the seed, thereby enhancing its nutritional profile (Cordenunsi et al. 2004).

Despite their high initial moisture content (over 40%), in dry mass they are primarily composed of starch, with approximately 7% protein, 2% lipids, and 4% ash, and minor compositional differences exist between species, as reported by Nadolny et al. (2023), Cordenunsi et al. (2004), and Conforti and Lupano (2011).

The seed of *Araucaria angustifolia* is a seasonal product harvested between April and August. Historically, it served as a significant source of carbohydrates for native populations in southern Brazil. Today, the seeds are typically consumed after boiling or baking, followed by dehulling. They are also used to produce a type of flour commonly incorporated into regional dishes. Nutritionally, the seeds are low in lipids (less than 2%) and proteins (less than 3%), with starch being the predominant component, accounting for approximately 36% (Cordenunsi et al. 2004). Despite its traditional importance, there is limited literature on the nutritional profile of *A. angustifolia* flour (Goncalves et al. 2014).

To date, the structural characterization of proteins from *A. araucana* and *A. angustifolia* remains unexplored. Therefore, the objectives of this study were to (i) compile and analyze data on the chemical composition of these seeds, (ii) assess their potential dietary benefits and functional characteristics, and (iii) contribute to the structural and nutritional characterization of their seed proteins.

2 | Experimental Procedures

2.1 | Materials

The seeds of *Araucaria araucana* were obtained from local shops in the province of Neuquén, Argentina, while the seeds of *Araucaria angustifolia w*ere obtained in San Antonio, province of Misiones, Argentina, in 2024. Samples were stored under appropriate conditions until analysis.

2.2 | Morphology

A total of 75 seeds from each species (*A. araucana* and *A. angustifolia*) were randomly selected, and their width, length, and thickness were measured using a caliper. In addition, photographs were taken to document morphological characteristics.

2.3 | Raw Seed Flour

The seeds were dried at 65°C ± 5°C for 4 h to reduce the moisture content and milled (flour passed through a 0.500-mm sieve). The moisture content before milling and after milling was > 45% and < 10%, respectively.

2.4 | Chemical Composition

The chemical composition of each flour was determined by the AACC Official Methods (2000) and expressed as g per 100 g of dry flour. Protein was determined by Kjeldahl, while the Soxhlet method was used for lipid quantification (Methods 46-12.01 and 30-25.01 respectively). Moisture content was determined by drying in an oven at 105°C ± 5°C until constant weight (Method 44-19), while the ash content was determined in a muffle at 550°C by the direct method (Method 08-01). The crude fiber content was measured according to AOAC (1984).

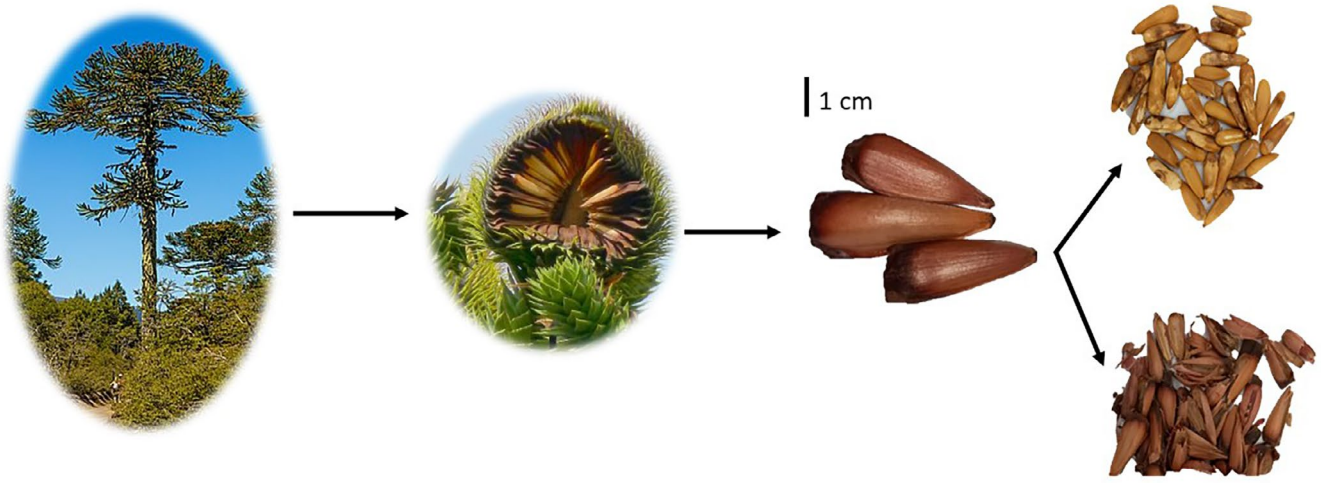


FIGURE 1 | Processing of *Araucaria* seeds: From the tree and to the whole seeds, and their separation into kernel (top) and seed coat (bottom). Scale bar represents 1 cm.

2.5 | Determination of Extinction Coefficient (E280)

The apparent E280 (L = 1 cm) was determined by measuring the absorbance at 280 nm of protein extracts obtained from *A. araucana* and *A. angustifolia* flours. Samples were weighed, and protein extraction was carried out using either distilled water or water adjusted to pH 8 with NaOH. The mixtures were centrifuged (30 min at 15,800 × g, 10°C), and the resulting supernatants were collected and diluted (1:6). Absorbance at 280 nm was recorded, and protein content was quantified using the Kjeldahl method, as previously described. The E280 value was calculated as the ratio of absorbance to protein concentration (g/100 mL), based on the Beer–Lambert law. A total of at least five determinations were performed with distilled water and with the pH 8 solution.

2.6 | Protein Solubility at Different pH

The Nitrogen Solubility Index was determined following the AACC Method 46-23 (1983), with slight modifications. Two grams of sample (*A. angustifolia* or *A. araucana* flour) were accurately weighed into an Erlenmeyer flask. Then, 40 mL of distilled water at 30°C was gradually added, and the mixture was dispersed. The pH was adjusted using NaOH or HCl. The assay was conducted on sieved raw seed flours (0.5 mm mesh). Dispersions were prepared at pH values of 2, 4, 6, 8, and 10, and stirred for 2 h using a magnetic stirrer at 120 rpm. The suspensions were transferred to 100 mL volumetric flasks, filtered through cotton in a funnel, and brought to volume with distilled water. Samples were then centrifuged for 15 min at 15,800 × g and 10°C (Sorvall RC SB Plus centrifuge, Wilmington, USA). Protein content in the supernatants was determined in duplicate using the Kjeldahl method.

2.7 | Protein Solubility According to Osborne Classification

Proteins from *A. angustifolia* and *A. araucana* seed flours were sequentially extracted following the classical Osborne method (1907). For each extraction, 4.8 g of each seed flour were treated sequentially with 30 mL of the following solvents: distilled water (albumins), 5% NaCl (globulins), 70% ethanol (prolamins), and 0.1 M borate buffer at pH 10 (glutelins). Each step involved homogenization using an Ultra-Turrax T25 for 3 min, followed by centrifugation at 11,000 × g for 20 min. The residues were re-extracted with the same solvent, and the recovered filtrate was combined. Total nitrogen content was determined via the Kjeldahl method in each fraction. Reported values represent the mean of two independent extractions.

2.8 | Amino Acid Analysis and Kjeladhl Factor Determination

The acid content was determined according to AOAC (1995) from a 0.1 g sample hydrolyzed with 6 N HCl at 110°C for 24 h. Cys and Met were analyzed after oxidation with performic acid, and Trp was determined from a separate sample treated with 4.2 N NaOH at 110°C for 22 h. All hydrolysates were filtered, derivatized with OPA/FMOC in borate buffer (pH 9.9), and analyzed using HPLC with a Hypersyl column and fluorescent detection. Measures were performed in duplicate with external standards (Sigma-Aldrich, Steinhein, Germany). The amino acid content was expressed as milligrams of amino acid per gram protein.

The amino acid score (AAS) was calculated for each essential amino acid as: AAS = (mg of amino acid per g of sample protein)/(mg of amino acid per g of reference protein) × 100, using the FAO/WHO reference pattern for human nutrition. AAS values equal to or greater than 1 (≥ 1) indicate that the amino acid content is sufficient to meet human dietary requirements according to FAO/WHO recommendations. The lowest amino acid score predicted the first–limiting amino acid. The reference protein used was that established by FAO/WHO.

The corresponding Kjeldahl conversion factors (Kj factors) were calculated mathematically according to Mossé (1990), as the ratio of the sum of the anhydrous amino acids (AAA) to the sum of the nitrogen content of each of the AA residues including ammonia released during hydrolysis, assuming that all measured nitrogen comes from the protein Templeton and Laurens (2015).

2.9 | Protein and Starch Characterization by Fourier-Transform Infrared Spectroscopy (FTIR)

FTIR *A. araucana* flour was performed according to Salinas et al. (2021). Analysis of spectra and spectral deconvolution of peaks within the region 1580–1710 cm^{-1} (amide I-protein secondary structure) and 1065–950 cm^{-1} (starch structure) was performed using curve fitting algorithms (OMNIC PeakFit 4.12 software, SPSS Inc., Chicago, IL, USA).

2.10 | Statistics

All analyses were run in duplicate, unless otherwise stated, and results were expressed as mean values. In order to compare data of *A. angustifolia* and *A. Araucana* flour, a test for equality of variances was first conducted, followed by a two-sample t-test for comparing means ($p \leq 0.05$).

3 | Results and Discussion

3.1 | Composition and Morphological Characteristics of the Seeds

Figure 2 compares the morphological and compositional characteristics of seeds from *Araucaria angustifolia* and *A. araucana*. Figure 2 shows representative images of seeds from both species, highlighting their size and shape differences. Moreover, the seeds of *A. araucana* exhibit a regular shape with a triangular appearance, whereas those of *A. angustifolia* are more variable and display a more rounded shape at one end. Besides, the average values for seed length, width, and thickness are also displayed. *A. angustifolia* seeds were significantly larger, with mean values of 5.16 cm (length), 1.75 cm (width), and 1.51 cm

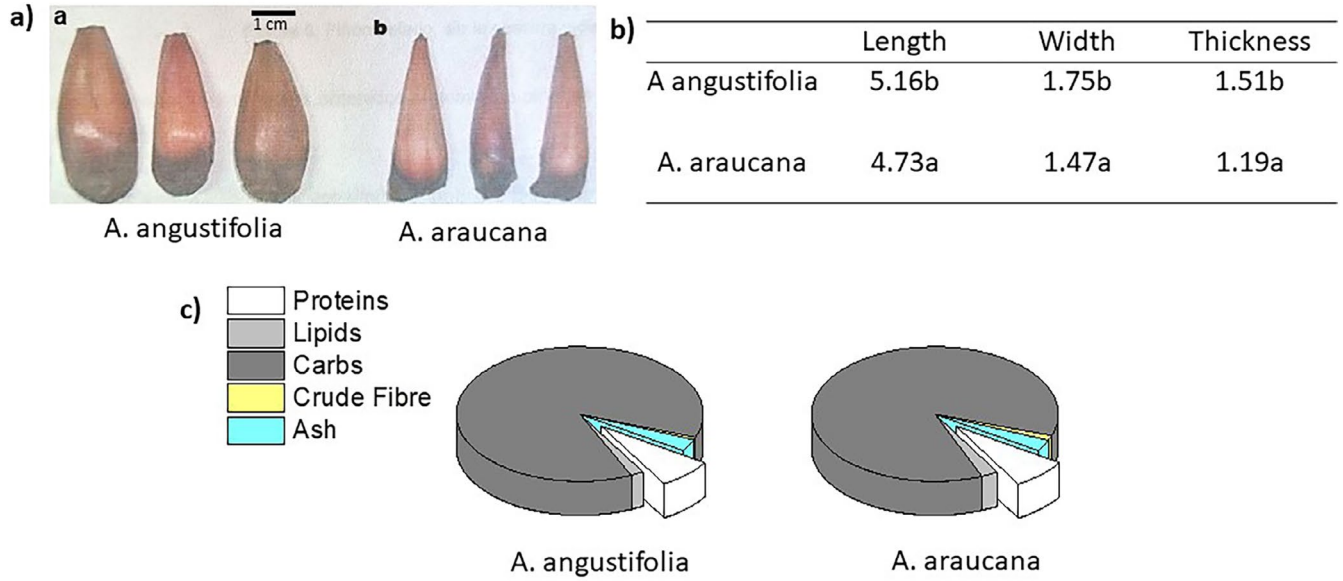


FIGURE 2 | Morphological and compositional comparison of *Araucaria angustifolia* and *A. araucana* seeds. (a) Representative images of seeds from both species. (b) Mean values (± standard deviation) for seed length, width, and thickness; different letters indicate statistically significant differences ($p < 0.05$). (c) Proximate composition of seeds represented as pie charts, showing the relative proportions of proteins, lipids, carbohydrates (carbs), crude fiber, and ash.

(thickness), compared to 4.73, 1.47, and 1.19 cm, respectively, for *A. araucana* ($p < 0.05$). Henríquez et al. (2008) evaluated *A. araucana* seeds and found that their dimensions ranged from 3.5 to 4.5 cm in length and around 2 cm in width, making them slightly shorter and wider than those evaluated in the present study. Moreover, both seed types exhibited a reddish color, with *A. angustifolia* being slightly darker. This coloration is likely due to the presence of phenolic compounds, including benzoic acid derivatives, procyanidins, and flavonoids (Schmeda-Hirschmann et al. 2021). Besides, some of these compounds have been shown to reduce glycemia in rats following starch administration (Schmeda-Hirschmann et al. 2021).

Figure 2c shows the proximate composition of the flours as pie charts. Both species exhibit similar profiles, with carbohydrates as the major component, followed by proteins, while crude fiber and ash were present in lower proportions. The overall composition was similar between species, with significant differences observed only in lipid content, which was higher in *A. araucana* (2.2%) than in *A. angustifolia* (1.7%) ($p < 0.05$). The proximate composition of these seeds closely resembles that of chestnuts (*Castanea sativa*), which are also rich in carbohydrates (≈80%, mainly starch, ranging from 42% to 66% on a dry weight basis), followed by moderate amounts of protein (4.5%–7.4%) and low levels of lipids and fiber (both below 4%) (Pereira-Lorenzo et al. 2006). During flour production, the average yield was calculated as grams of flour per 100 g of whole seed. *A. angustifolia* showed a total yield of 34.4%, while *A. araucana* yielded a higher value of 39.8% (data not shown).

3.2 | Protein Solubility in Different Extraction Medias and at Different pH

The protein solubility of *A. Araucana* and *A. angustifolia* flour was evaluated at different pH values. As shown in Figure 3a, the solubility remained relatively low and stable at acidic pH values (pH 3–4), with approximately 15%–19% of proteins remaining soluble. A gradual increase in solubility was observed from pH 6 onward, reaching the highest value at pH 10, with over 35% soluble protein in both cases. Similar results were found by Walters et al. (2018) who indicated that the solubility of oat proteins was low between pH 3 and 5, while the maximum solubility was observed at pH ≥ 9.0 due to the increased net charge of proteins and availability of attractive forces with water. This behavior suggests that solubility improves under alkaline conditions, likely due to the increased ionization of acidic amino acid side chains, which enhances protein–water interactions and prevents aggregation. The high solubility at alkaline pH in the present results may also indicate a substantial presence of negatively charged residues, such as glutamic and aspartic acid, which contribute to greater protein dispersion and stability in solution. These amino acids are present in a high proportion in both flours (see following section). Moreover, the protein solubility of *A. araucana* seed flour was higher than that of *A. angustifolia* flour at both acidic and near-neutral pH values ($p \leq 0.05$), whereas no significant differences were observed at strongly alkaline pH levels (above 9.5) ($p > 0.05$).

Figure 3b presents the soluble protein content (%) of both flours sequentially extracted using different solvents: water, saline solution, ethanol, and borate buffer, along with the final residue. Water extraction yielded the highest amount of soluble proteins, approximately 35% in *A. araucana* and 19% in *A. angustifolia*, indicating that a significant proportion of the proteins are water-soluble albumins. In contrast, the saline solution, ethanol, and borate buffer extracted considerably lower amounts, all below 5%, suggesting that the globulin, prolamin, and glutelin fractions are present in much smaller quantities. Notably, the residue retained around 35% of the protein content, indicating that a substantial fraction of the proteins remained insoluble throughout the extraction process. When the percentages of protein

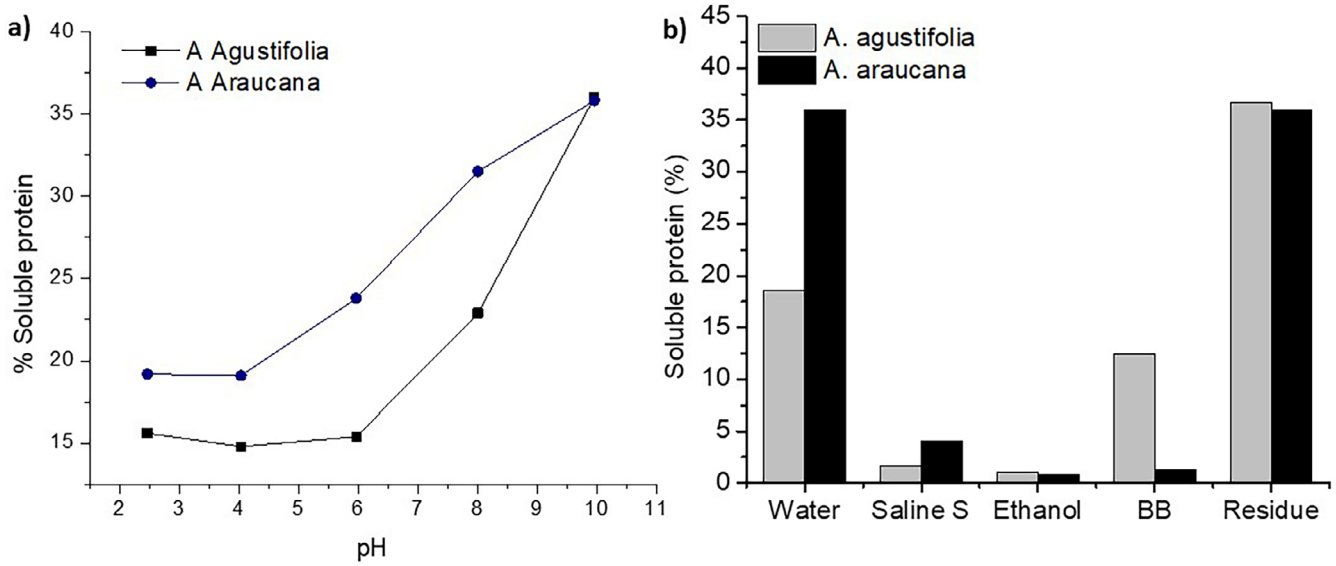


FIGURE 3 | Protein solubility in seeds of *Araucaria angustifolia* and *A. araucana*. (a) Soluble protein (%) as a function of pH. (b) Soluble protein extracted with different solvents: Water, saline solution (Saline S), ethanol, borate buffer (BB), and the insoluble residue.

solubilized in the different solvents and the fraction remaining in the residue are added together, the total falls short of 100%. This discrepancy may be attributed to cumulative sample losses during the extraction and centrifugation steps, as well as during the transfer of material from centrifuge tubes to aluminum foil for drying. Additionally, random experimental errors inherent to the analytical procedures may have contributed to the observed difference. These results highlight the predominance of water-soluble proteins in both flours. Moreover, when comparing the soluble protein fractions displayed in Figure 3b with reference values, the protein profile closely resembles that of chestnut. According to Yang et al. (2018), Osborne solubility-based fractionation revealed that albumins were the predominant proteins in Chinese chestnut (71.62% of total soluble protein), followed by glutelins (28.38%), while globulins and prolamins were not detected in any of the samples.

3.3 | Determination of Kj Factor and Aminoacid Analysis

The amino acid composition was similar in both species, with significant differences observed only for alanine, leucine, methionine, phenylalanine, and tyrosine. The respective contents (mg/g protein) in *A. angustifolia* were 48.3, 71.5, 24.0, 60.9, and 44.9, while in *A. araucana* they were 60.5, 67.9, 26.8, 55.9, and 67.0. Among the non-essential amino acids, aspartic acid and glutamic acid were the most abundant in both species, each exceeding 100 mg/g protein. A similar trend was reported for *A. bidwillii* (Nadolny et al. 2023). Regarding essential amino acids, both flours showed high levels of aromatic amino acids (AAA: Phe + Tyr) and sulfur-containing amino acids (SAA: Met + Cys).

The essential amino acid score (AAS) for each flour is shown in Figure 4. The lowest score (0.93) was found for tryptophan in *A. araucana*, indicating it as the limiting amino acid, while in *A. angustifolia* the score was 1.04. Overall, the AAS values suggest that both flours are excellent protein sources with a balanced amino acid profile.

Based on the molecular weight of individual amino acids, the proximate molar composition of the proteins was estimated. The corresponding Kjeldahl conversion factors (Kj factors) calculated were 5.95 for *A. angustifolia* and 6.32 for *A. araucana*. The differences in Kjeldahl conversion factors were associated with the amino acid composition of *A. angustifolia* and *A. araucana*. *A. araucana* presented lower levels of histidine and lysine than *A. angustifolia*; therefore, a higher Kjeldahl factor was observed for *A. araucana*. The factor for *A. angustifolia* differs from the commonly used 6.25 value applied in previous studies on Araucaria species (Cordenunsi et al. 2004; Henríquez et al. 2008; Conforti and Lupano 2011).

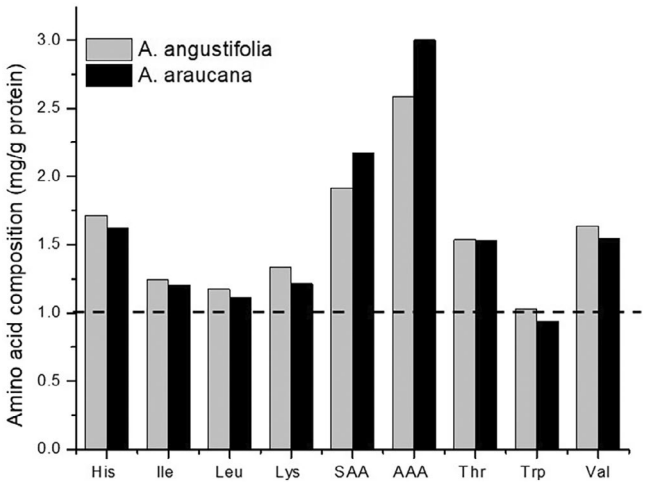


FIGURE 4 | Essential amino acid composition of proteins from *Araucaria angustifolia* and *A. araucana* seeds, expressed as mg amino acid per g of protein. Values above the dash line (≥ 1) indicate sufficient content to meet human dietary requirements according to FAO/WHO recommendations.

3.4 | Determination of E280

The absorbance at 280 nm of a protein solution can be used to calculate its concentration if the extinction coefficient (E280) is known. Another option is to compare the absorption to a calibration curve made with a standard protein that has similar aromatic amino acids' content to ensure an accurate result (Simonian 2002).

The obtained results of E280 of both samples indicate that the E280 values were not significantly influenced by the pH of the medium. However, significant differences between species were observed ($p < 0.05$), with *A. angustifolia* exhibiting a higher E280 (1 cm) value (63.3 ± 3.0) compared to *A. araucana* (46.6 ± 2.8). The differences could be explained by taking into account the different aromatic amino acids, phenylalanine, tryptophan, and tyrosine, which have appreciable absorbance near 280 nm. The content of these amino acids was 60.9, 7.8, and 44.9 in *A. angustifolia* and 55.9, 6.2, and 67.1 in *A. araucana*, respectively. These coefficients enable the estimation of protein concentration via spectrophotometry. They are especially useful when Kjeldahl analysis cannot be used due to interference from non-protein nitrogen sources.

3.5 | FTIR Analysis

FTIR analysis is useful to study the main functional groups, molecular interactions, and conformational aspects of the sample/flour. Figure 5 shows the original spectrum of the sample subjected to FTIR analysis and the major peaks. A broad peak is observed at 3282 cm^{-1} which corresponds to O—H stretching in water molecules and also in the amylose and amylopectin of the starch. In addition, two peaks were found at 2929 and 2855 cm^{-1} in the 3100 to 2800 cm^{-1} region, associated with asymmetric and symmetric stretching vibrations of the CH_2 aliphatic of the saturated fatty acid (Guillén and Cabo 2000). In the next region, there is a small peak at 1742 cm^{-1} due to the vibration of the ester group/bond C═O of fatty acids (Resende et al. 2020; Barraza-Garza et al. 2013). Then, in the 1700 to 1500 cm^{-1} region, two bands are observed at 1639 and 1547 cm^{-1} associated with amide I and amide II structures of the protein, product of C═O binding tension of the peptide bond of proteins, C—N bond tension, and N—H bond bending.

The significant band/peak found at 1639 cm^{-1} was deconvoluted for the purpose of studying the primary structure of the proteins in the sample. After that, it was possible to resolve bands associated with different secondary structures of proteins in *A. araucana* flour. These peaks were found at 1613, 1628, 1641, 1655, 1668, and 1681 cm^{-1} and associated with secondary protein structure, as shown in the table displayed in Figure 5. The predominant secondary structure with major relative contribution was random coil (23.8%), followed by parallel β sheet intramolecular (22.1%), α-helix (21.8%), parallel β sheet intermolecular (12.8%), β-turns (11.7%), while the minority corresponds to antiparallel β-sheet (7.7%).

Weak bands were identified at 1409, 1367, and 1242 cm^{-1} corresponding to the presence of CH bending vibrations in CH_2 and CH_3 groups from lipids (Guillén and Cabo 2000; Barraza-Garza et al. 2013). Finally, the wavelength range from 800 to 1200 cm^{-1} corresponds mainly to C—O and C—C stretching vibrations of polysaccharides. In this range, bands at 1149, 1077, and 993 cm^{-1} were observed. Resende et al. (2020) associated 1149 and 1077 cm^{-1} bands with vibration of molecular bonds present in dietary fiber, attributing it to pectins and hemicellulose molecules. The high intensity of the 993 cm^{-1} band could be associated with water content and starch conformation (Htoon et al. 2009; Monroy et al. 2018).

The region of the FTIR spectrum 1070 to 950 cm^{-1} contains useful information to describe the starch structure of the sample. By the deconvolution of this region, three characteristic peaks

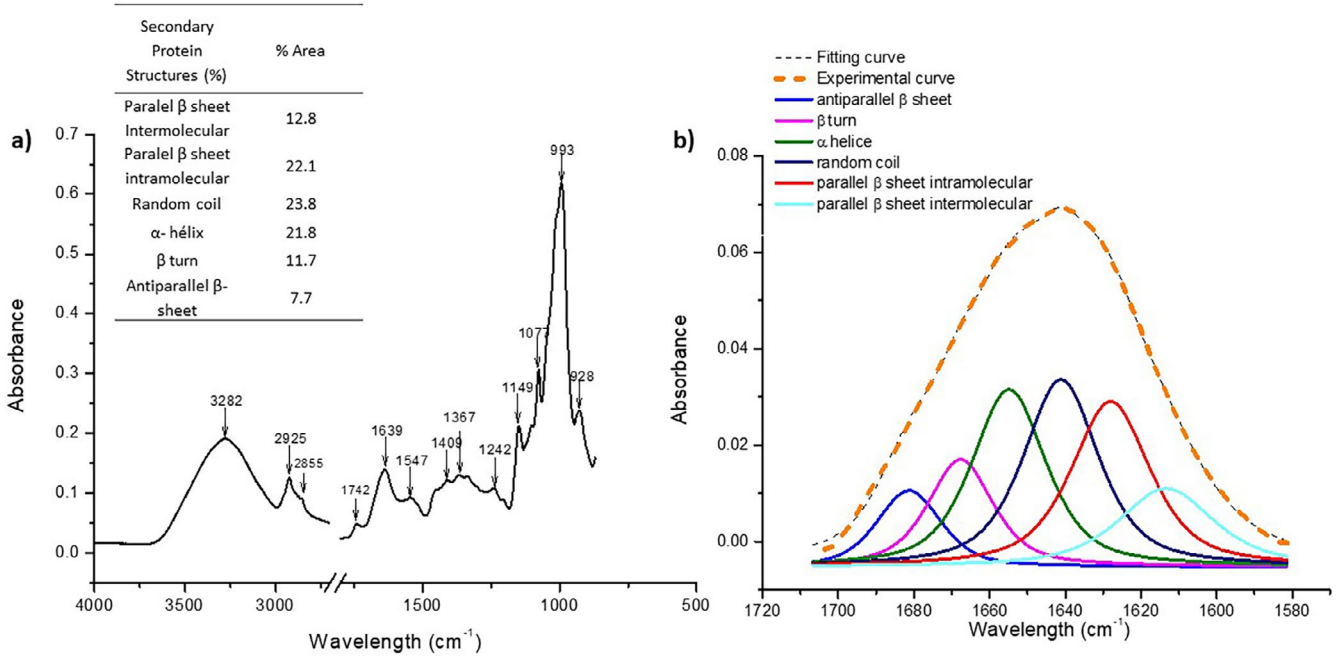


FIGURE 5 | (a) ATR-FTIR whole spectra of the *A. araucana* flour and (b) deconvolved amide I band of *A. araucana* flour.

of starch are found near 1045, 1022, and 996 cm^{-1} (Monroy et al. 2018). The deconvolution of *Araucaria araucana* flour revealed three peaks near the above mentioned: 1044, 1016, and 990 cm $^{-1}$. The band at 1045 cm^{-1} is attributed to the ordered regions of starch, while the band at 1022 cm^{-1} represents absorption by stretching modes in the amorphous region of starch. The band at 996 cm^{-1} reflects the hydration of the starch helices. The relationship between the absorbance intensities of bands at 1045/1022 and 1022/996 allows us to know the conformation of the starch in the sample and reflects the state of the crystalline and amorphous regions, respectively (Htoon et al. 2009; Monroy et al. 2018). *Araucaria araucana* flour presented a 1045/1022 ratio of 0.36 and 1022/995 ratio of 0.72. In this case, the starch had a higher ratio of 1022/995, indicating a predominance of the disordered structure or amorphous over the ordered starch structure.

4 | Conclusions

This study provides a comprehensive characterization of seed flours from *Araucaria angustifolia* and *A. araucana*, highlighting their potential as novel plant-based protein sources. Both species exhibited high carbohydrate content, moderate protein levels, and low lipid and fiber content, resembling chestnut composition. Amino acid analysis revealed a balanced profile with essential amino acid scores above 0.9, confirming their high nutritional quality. Solubility assays indicated good protein extractability, especially under alkaline conditions, with albumins as the predominant fraction. FTIR analysis confirmed the presence of key functional groups and a predominance of random coil and β-sheet structures in proteins, while starch conformation showed a predominance of amorphous regions. These findings support the nutritional and functional value of Araucaria seed flours and encourage further research into their use in food formulations, particularly for plant-based or gluten-free applications.

Author Contributions

Juliana Ripari Garrido performed the formal analysis and investigation. Mariela Patrignani and Paula A. Conforti conceived and designed the study, and wrote the first draft of the manuscript. All authors contributed to and approved the final draft of the manuscript.

Ethics Statement

No human or animal subjects were used in this research.

Conflicts of Interest

The authors declare no conflicts of interest.

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