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Comparative analyses of the nutritional and antinutritional composition of pod flours from *Neltuma* spp. (Fabaceae, Caesalpinioideae) species from drylands of Mexico, Kenya and Tanzania

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A B S T R A C T

Identifying novel risk-resilient diets is urgent to address food insecurity and tackle global hunger and malnutrition. This study evaluated the suitability of mesquite (*Neltuma* spp.) pod flours as food staples for human nourishment and compared nutritional properties of mesquites growing natively or as introduced species in the drylands of Mexico, Kenya and Tanzania. Using gas chromatography and mass spectrometry, we analysed chemical composition, dietary fibre, antinutrients, amino acids and fatty acids of pod flours from *Neltuma laevigata, N. laevigata* × *N. odorata* and *N. velutina* (abundant native species of Northern Mexico). We also studied the introduced *N. juliflora* from Kenya, and *N. pallida* from Tanzania which have become invasive. This research demonstrates that mesquite flour contains all the essential amino acids, with the highest being valine, leucine and lysine. The most abundant non-essential amino acids are aspartate, glutamate and proline. Mesquite flours are rich in palmitic, oleic and linolenic acids. Besides this, mesquite flour is abundant in phenols and contains less gallic and phytic acids than wheat. We show that nutritionally, mesquite flours are comparable to wheat flour. These findings demonstrate that *Neltuma* pod flours are excellent candidates to reduce malnutrition and hunger for the poorest people of the world.

1. Introduction

Out of the 25,000 edible species consumed by humanity throughout history, today we rely on only 30 plant species to obtain food (Muthamilarasan and Prasad, 2021). Of those, just six of them -rice, wheat, maize, potato, soybeans, and sugarcane- account for over 75% of the energy we obtain from plants (Singh et al., 2022). Pandemics, global conflicts and extreme climate events have exposed the vulnerability of current global agri-food systems (Tzachor et al., 2021), which are incapable of reducing the hunger that 820 million people in the world

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are experiencing (Hannah, 2024). Therefore, it is urgent to find new food staples that help reduce food insecurity, global hunger and malnutrition.

A good nutritional food source should contain sufficient calories, be a good source of proteins and micronutrients and contain little or no amounts of antinutritional components (Mallick et al., 2013). Legumes are good candidates to improve nutrition as they are rich in high quality proteins and micronutrients, although they also contain antinutrients (Lisciani et al., 2024). Antinutritional factors are chemical compounds that interfere with the digestion and absorption of food nutrients; for example, trypsin inhibitors can alter digestive enzymes in charge of digesting proteins from food (Kårlund et al., 2021). In some instances, antinutrients can cause adverse biochemical and/or physiological changes, becoming toxic (Gómez et al., 1998; Samtiya et al., 2020) or have estrogenic effects (Rizzo and Baroni, 2018). Plant lectins protect plants from pathogens. If consumed, these can adhere to carbohydrates on the intestinal surface, damaging it and reducing absorption and transportation of nutrients (De Hoff et al., 2009). To reduce the impact of antinutrients in legumin-derived products, thermic treatments have been successfully used (Chiou and Cheng, 2001; Lisciani et al., 2024; Samtiya et al., 2020; Sharma, 2021). On the other hand, there is compelling evidence demonstrating that antinutrients improve health, as they can reduce the risk of diabetes, metabolic syndrome and cancer, to mention a few (Iwai et al., 2006; Kårlund et al., 2021; Nath et al., 2022).

A solution to address food insecurity is presented in the leguminous trees or shrubs from the genus *Prosopis* L. s.l. (mesquites) which are well adapted to the extreme conditions of the drylands (Tebboth et al., 2020). As well as fixing nitrogen and reducing soil erosion and desertification, the pods of mesquite trees are potential food and feed alternatives and have industrial applications (de Lemos et al., 2023; Palacios, 2006; Trenchard et al., 2008). Recently, *Prosopis* has been reclassified by Hughes et al.(2022) into four separate genera: *Anonychium* (Benth.) Schweinf*., Neltuma* Raf*., Strombocarpa* (Benth.) Englem. & A. Gary and *Prosopis;* we adopt the new nomenclature in this paper.

Independent nutritional studies for different species of *Neltuma* pod flours have reported them to be rich in sugars and fibre, relatively rich in protein and lipids, and gluten-free (Bodoira et al., 2023; Cittadini et al., 2024; García-Azpeitia et al., 2022; Gonzales-Barron et al., 2020; Grados and Cruz, 1996). The results of these analyses are dependent on the extraction methods, the *Neltuma* species, and the geographic location of the trees; for example, pods from *N. laevigata* collected from Oaxaca Mexico, contain 11.77 to 12.4% of crude protein (Sandoval-Torres et al., 2022), while flour from seeds (without the mesocarp) from the same specie collected from Hidalgo Mexico contains 36.51% (Díaz-Batalla et al., 2018). This is also true for other mesquite flour components such as fats, ranging from 2.8 to 3.2% (Gonzales-Barron et al., 2020); crude fibre, which ranges from 21.3 to 32.22 % DW (García-Azpeitia et al., 2022; Grados and Cruz, 1996), and energy, ranging from 7.15 to 30.3 MJ/kg (Armijo-Nájera et al., 2019; Becker and Grosjean, 1980; Del Valle et al., 1983; Marangoni and Alli, 1988; Montañez-Valdez et al., 2021). Mesquite flours have also been reported to contain antinutrients, including total phenolics (3.4 to 3.9 mg TAE/g), gallic acid (123.37 mg/g) (García-Azpeitia et al., 2022; Gonzales-Barron et al., 2020), and Trypsin Inhibitor Units 0.932 TIU (mg/g) (González Galán et al., 2008). It has also been reported that *Neltuma juliflora* flour contains values of histidine of 10.8 g/kg DW, isoleucine of 26.5 g/kg DW and leucine of 42.5 g/kg DW (Marangoni and Alli, 1988). Analyses of *Neltuma* flours completeness through the Amino Acid Score (AAS) indicator of the completeness of a protein (a value of 1 is considered complete) have been reported, and it has been suggested that these flours are short in meeting the FAO recommended intake levels for valine, methionine and leucine with score values of 0.64, 0.95 and 0.92, respectively (Cittadini et al., 2024). The highest fatty acids reported to be present in *Neltuma* flours include linoleic, oleic and palmitic acids (Cittadini et al., 2024; Cruz-Gracida et al., 2019). However, comparative analyses of the nutritional properties of pods from different mesquite species growing natively or as introduced species in the drylands of different continents, and against reported values of wheat and soybean flours are missing.

Drylands are home to around 25% of the global population, including the most marginalised and poorest, and cover over 41% of the Earth's land (Decade, 2010-2020). About 44% of the cultivated areas of the world are located in these regions, moreover, increased droughts and flash floods, compromise food supplies which increase hunger and malnutrition deaths (Oxfam, 2021). Additionally, every year, drylands are extending due to land degradation caused by climate change and unsustainable use (Feng and Fu, 2013). Besides, when irrigation is used in these areas, more than 50% of the total water supply is consumed, exacerbating water shortages, reduction of groundwater, and impacting the ecology and local communities (Zhu et al., 2022).

Archaeological evidence shows that *Neltuma* seeds were consumed by American peoples since 9,000 BC (Flannery, 1986). Historically, mesquite has been a major food staple and a source of wood, medicines, energy and economic income for indigenous peoples of the American continent, mainly in the drylands (Montaño-Arango et al., 2021). In Mexico, twelve species of mesquite have been identified (Palacios, 2006), with the recent reclassification of *Prosopis*, eleven correspond to *Neltuma* and one to *Strmbocarpa* genera (Hughes et al., 2022). According to the International Union for Conservation of Nature, mesquite species present in Mexico are considered stable (IUCN, 2024). Moreover, the Mexican government social programme 'Sowing Life' (which aims to reduce poverty and environmental degradation), includes mesquite as one of the tree species that could stimulate sustainable development (Diario de la Federación, 2024; Gastélum, 2024; Navarro, 2022), supporting the viability of this resource as a food staple in this country.

To solve problems of desertification and provide a source of animal feed and income to communities in other continents, including Africa, *N. juliflora* was introduced, but it has become highly invasive and continues spreading (Eckert et al., 2020; Kilawe et al., 2017; Malila et al., 2023; Tebboth et al., 2020). In Eastern Africa, the areas with high presence of *N. juliflora* include Kasalla in Sudan, Hargeisa in Somalia, Afar in Ethiopia, Arusha, Kilimanjaro and Manyara in Tanzania and Baringo, Turkana and Bura (Tana River) in Kenya (Kamiri et al., 2024; Paliwal et al., 2024). Specifically, in Tanzania, *Neltuma* is also present in Mara, Simiyu, Mwanza, Tanga, Morogoro and Dodoma, and continues spreading (Eckert et al., 2020; Kilawe et al., 2017). In Kenya, *Neltuma* is also present in other 24 other counties, including West Pokot, Marsabit, Isiolo, Mandera and Wajir (Maundu et al., 2009; Ng et al., 2018; The BORESHA Consortium, 2022). In addition to *N. juliflora*, the presence of *N. chilensis* is distributed in Baringo, Wajir, Magadi, Mandera and Turkana (Maundu and Tengnas, 2005); *N. pallida* have also been reported in Kenya (Castillo et al., 2021; Pasiecznik et al., 2001). The extension of the distribution of these trees highlights the importance of understanding and comparing the nutritional properties of pods from mesquites growing natively or in an introduced way and their relevance to reduce hunger, which has been addressed in this study.

In an effort to manage *N. juliflora*, African governments have developed National Strategies and plans for its management and control (Choge et al., 2022; Kamiri et al., 2024). Projections show that 9.65% of the Earth's surface is vulnerable to the spreading of *N. juliflora* (Pasha and Reddy, 2024), illustrating the high availability of this resource for the future, and its potential for sustainable development. These projections also highlight not only the importance of considering *Neltuma* spp. management strategies, but their potential to reduce hunger and poverty. It is imperative, however, to engage primary stakeholders affected or benefited by its presence during management decision taking, and to consider that values and views can be highly contrasting and may change over time (Tebboth et al., 2020).

To find safe alternative and sustainable food staples derived from plants adapted to extreme temperatures and to address food insecurity in the drylands, we identified *Neltuma* species from Mexico (native), Kenya and Tanzania (introduced). We collected and prepared pod flours from these species to study their protein, fat, fibre, energy, amino acids and fatty acids content. We also determined the phenolic content, phytic and gallic acids, and trypsin inhibitors of pod flours from *Neltuma* species identified.

We hypothesised that the nutritional and antinutritional properties of *Neltuma* pods are comparable to those of wheat and soybean, and that significant variability between pods collected from trees growing in the drylands of Mexico, Kenya and Tanzania is present.

2. Materials and methods

2.1. Species identification

Using community participatory approaches, pods, leaves, branches and flowers from native *Neltuma* species (growing naturally in four Mexican localities) and from two introduced *Neltuma* species (growing naturally in Kenyan and Tanzanian localities) were collected and used for species identification (Fig. 1, Table 1). Samples were prepared and photographed for curation (Lot and Chiang, 1990; Sánchez-González et al., 2007) and the vouchers were deposited in herbaria from participant research institutions. Mexican, Kenyan and Tanzanian samples were stored at CIIDIR (Instituto Politécnico Nacional, CIIDIR Durango), University of Nairobi (NAI), and Sokoine University of Agriculture (SUA) respectively (acronyms according to Thiers (2024)). Mesquite species were identified using the taxonomic criteria of Rzedowski (1988), Pasiecznik et al. (2004), and Palacios and Bravo (1981). The terminology was based on Moreno (1984) and Harris and Harris (1994) and the new nomenclature proposed by Hughes et al. (2022) is used in this paper.

2.2. *Neltuma* pod plant material

About 1 kg of mature pods from 45 *Neltuma* trees (four to twelve biological replicates per species) growing in the selected localities were collected and the growing conditions recorded. The selected localities for sample collection include, in Mexico:- El Mezquital ($23^{\circ}17'58.2''N$, $104^{\circ}30'38.5''W$), Lerdo ($25^{\circ}16'2.0''N$, $-103^{\circ}44'44.1''W$) and San Juan de Guadalupe ($24^{\circ}37'57''N, 102^{\circ}46'41''O$) in Durango, and Estación Doctor in Sonora ($31^{\circ}55'59.88''N, 114^{\circ}42'00''W$). In Kenya: the Ngambo Area ($0^{\circ}29'6''N$, $36^{\circ}3'30''E; 0^{\circ}26'57''N$, $36^{\circ}0'30''E$), in Baringo. In Tanzania: Lang'ata Bora ($3^{\circ}39'27''S$, $37^{\circ}26'29''E$) in the Kilimanjaro region (Table 1).

Table 1
Identified species and regions where *Neltuma* samples were collected.

Species	Region/ Country/ Date of collection	Locality	Tree sample number	Community
Neltuma laevigata	Durango, Mexico. June 2019	San Juan de Guadalupe and El Mezquital	7	Rural
Hybrid of *Neltuma laevigata* × *Neltuma odorata*	Durango, Mexico. June 2019	Lerdo	4	Rural
Neltuma velutina	Sonora, Mexico. November 2019	Estacion Doctor	10	Rural/Yaqui peoples
Neltuma juliflora	Ngambo Area, Kenya. November 2019	Baringo Area	12	Il Chamus and, Tugen peoples
Neltuma pallida	Kilimanjaro, Tanzania. November 2019	Lang'ata Bora	12	Lang'ata Bora rural

Mature *Neltuma* pods were collected using a tarpaulin sheet avoiding pod contamination with soil, damaged pods were discarded. Samples were sun dried and stored in bags containing 1 kg of calcium oxide per 20 kg of pods to avoid insect damage and stored in a dry place until used. Pod samples were weighted and washed for 15 min by covering them with water added with 1 mL of sodium hypochlorite at 5% per L to remove the calcium oxide, kill bacteria and sanitize the pods prior to processing. Whole pods were dried in an oven at 65∘C per 1 h and ground using an industrial blender (Tapisa #125). Flour was packaged and

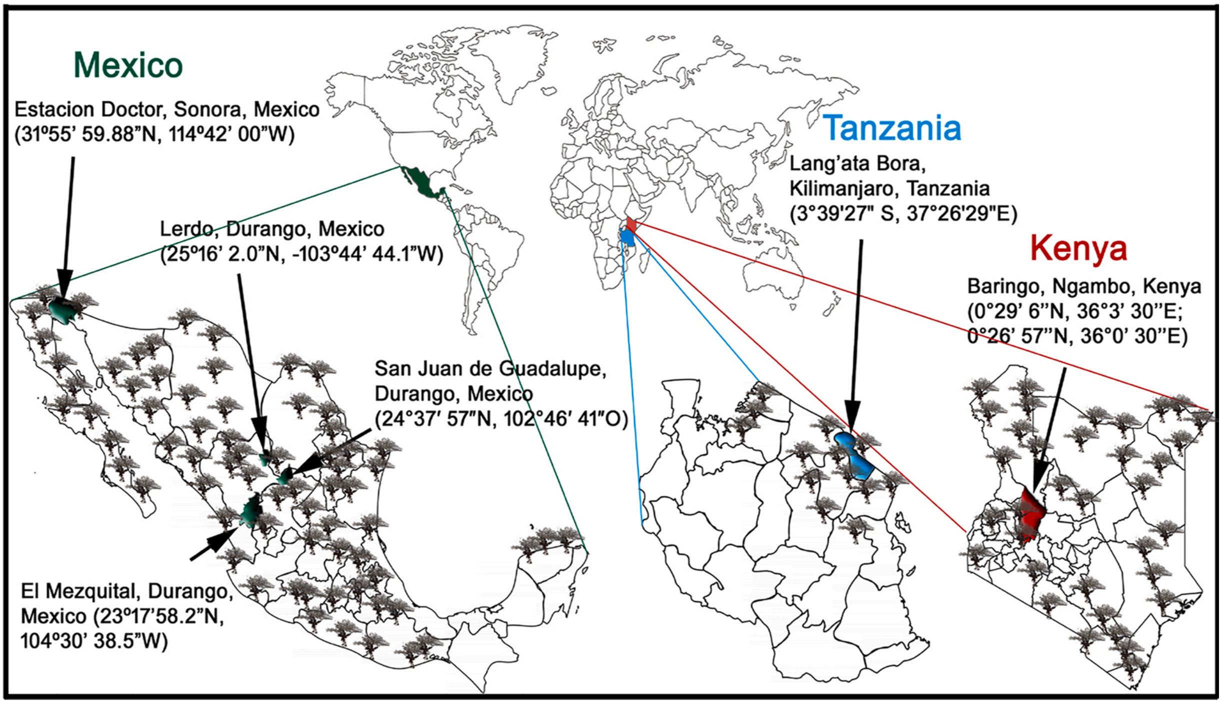

Fig. 1. Locations and geographic coordinates of areas where *Neltuma* spp. samples were collected. Distribution of *Neltuma* spp. are indicated in the map, this information has been adapted from Palacios (2006), Hughes et al. (2022) and (2022) (Mexico), Eckert et al. (2020) and Kilawe et al. (2017) (Tanzania), Maundu et al. (2009), Ng et al. (2018), and The BORESHA Consortium (2022) (Kenya).

shipped for analyses to UK and/or Mexico.

2.3. Proximate analysis

Samples were freeze-dried using a Christ^{TM} Freeze Dryer. The samples were ground to a fine powder in a liquid nitrogen cooled pestle and mortar and stored in a desiccator until analysed. Moisture content was estimated using the method No. 926.07 (AOAC, 2000).

2.4. Protein analysis

Crude protein content was determined using the Dumas method (Shea and Watts, 1939); briefly, the nitrogen content of 50 mg freeze-dried mesquite powder was determined using an EA 1112 elemental analyser (Thermo Scientific, UK) (International Organisation for Standardisation, 2008) and compared to an aspartic acid standard (10.52 (w/w) N%) (D5055, Elemental Microanalysis). A standard conversion factor of 6.25 was used to convert nitrogen quantities into total protein.

2.5. Fat analysis

Total fat content was determined through extraction using 1g freeze-dried mesquite powder in Gerhardt's Soxtherm system (Gerhardt Analytical Systems, Germany) (Palmquist and Jenkins, 2003). In brief, in the Soxtherm system, the sample was boiled in petroleum at 150 °C for 30 min followed by refluxing for 90 min to ensure all fat was collected. The solvent was reduced to dryness and weight of fat determined. Fat samples were resuspended in hexane and kept at -20°C until analysis. To determine fatty acid content, triacylglycerol (TAG) was hydrolysed followed by fatty acid methyl esterification (FAME) according to Lock et al. (2005). Samples were stored in hexane at -20°C before analysis using gas chromatography mass spectrometry (GCMS) ISQ7000 (GC: Thermo Scientific Trace 1300, MS: Thermo Scientific ISQ 7000) according to previously described methodology (Gedi et al., 2017).

2.6. Fibre analysis

Neutral Detergent Fibre (NDF), Acid Detergent Fibre (ADF) and Acid Detergent Lignin (ADL) (non-digestive carbohydrates) were determined using the Van Soest detergent procedure (Van Soest et al., 1991). Hemicellulose content (HC) was calculated using the equation HC=NDF-ADF whilst cellulose content (CC) was calculated using the equation CC=ADF-ADL.

2.7. Energy analysis

Gross energy was determined using 1g freeze-dried sample powder in an Oxygen Bomb Calorimeter (Parr 6300 calorimeter, Parr Instrument company, USA) using standard calorific grade benzoic acid (Part No. 3415) following the protocol proposed by Zhang et al., (2020).

2.8. Antinutrient analysis

Total phenolic content was quantified as described in Gallegos-Infante et al. (2010, 2013) using the Folin-Ciocalteu method. Trypsin inhibitors were analysed following the protocol described in Chen et al. (2014). Phytic acid was quantified using the protocol published by McKie and MccleAry, (2016) and gallic acid was quantified as described in Blainski et al. (2013). Trypsin inhibitors were calculated using the Ba 12-75 AOAC method (AOAC, 2000).

2.9. Amino acid analysis

Amino acid composition was determined on freeze-dried mesquite powder, using 30 mg ($>$ 60% (w/w) crude protein content) or 50 mg ($<$ 60% (w/w) crude protein content) to obtain approximately 5 mg nitrogen content. For every 10 samples, a standard of 30 mg of soy flour (Standard Reference Material® 3234 Soy Flour, National Institute of Standards and Technology) was used. Samples were first oxidised in performic acid (10% hydrogen peroxide in formic acid) at 4^{o}C for 18 h followed by acid hydrolysis in 6 M HCl at 110^{o}C for 24 h. Samples were analysed with a Vanquish uHPLC, and an Altis Triple Quadrapole Mass Spectrometer with an Opta-Max NG ion source. An Acclaim^{TM} Trinity P1 mixed-mode column, controlled by TSQ Altis Tune Application XCalibration software was used. Data integration and extraction was carried out using TraceFinder 4.1 software (Thermo Scientific^{TM}) according to a method established in our laboratories (Muleya et al., 2023). The amino acid score (AAS) of each flour sample was determined to predict the completeness of the proteins present in *Neltuma* flour. The AAS was established by assessing amino acid proportions of each amino acid compared to the reference protein, as provided by the Food and Agriculture Organization (FAO, 2013) and based on the amino acid requirement of a child (6 months to 3 years): AAS = Amino acid in test protein (g) /Amino Acid in reference protein (g) × 100.

2.10. Data analysis

Data were analysed by one-way ANOVA using Genstat statistical software (21st Edition) with significant differences accepted at $P < 0.001$, except for fatty acids, where P values are shown. This was followed by *post hoc* Tukey test, with significant differences accepted at $P < 0.05$. Data are presented as the means ± standard error of the mean. Figures were created using Adobe Photoshop V7.0.1 (Systems, 2019).

3. Results and discussion

3.1. Species identification

Hybridization between mesquite species occurs frequently which causes species misidentification (Foroughbakhch et al., 2024; Galindo-Almanza et al., 1992; Hughes et al., 2022; Palacios and Bravo, 1981). This problem is exacerbated when confusing synonyms of mesquite species are used (Foroughbakhch et al., 2024; Pasiecznik et al., 2004). Thus, it is crucial to correctly identify mesquite species and its hybrids to provide a solid base when reporting their nutritional properties, and to increase our understanding of the impact of hybridisation among mesquite species on pod quality.

In this study, taxonomical identification revealed the presence of *Neltuma laevigata* (Humb. & Bonpl. ex Willd.) Britton & Rose in the localities of Mezquital and San Juan de Guadalupe in Durango; the hybrid *N. laevigata* × *N. odorata* (Torr. & Frém.) C.E. Hughes & G.P. Lewis in Lerdo, Durango; and *N. velutina* (Wooton) Britton & Rose in Sonora, Mexico. *N. juliflora* was identified in Kenya, while *N. pallida* (Humb. & Bonpl. ex Willd.) C.E. Hughes & G.P. Lewis was identified in Tanzania (Figs. 1, 2 A–E, Table 1).

These results confirm the distribution described for these species in Mexico (Foroughbakhch et al., 2024; Palacios, 2006) and Kenya (Kamiri et al., 2024; Pasiecznik et al., 2004). For Tanzania, however, this is the first time *N. pallida* is confirmed to be present, as this species has not been previously recorded for this country (Castillo et al., 2021; Pasha and Reddy, 2024).

3.1. Proximate chemical composition and fibre analysis

Analysis of the nutritional composition of pod flours prepared from the identified *Neltuma* species revealed statistically significant differences among the *Neltuma* flours ($P < 0.001$) (Table 2).

The chemical composition of *Neltuma* flours from the five species studied show variability in macro nutrient parameters studied. *Neltuma laevigata* shows the highest content of protein (%DW) (13.87%), which along with *N. juliflora* (13.72%) was significantly ($P < 0.05$) higher than

Fig. 2. Species identified in Mexican, Kenyan and Tanzanian localities. A) *Neltuma laevigata*, collected in San Juan de Guadalupe, Durango, Mexico. B) Hybrid *Neltuma laevigata* × *Neltuma odorata*, from Lerdo, Durango, Mexico. C) *Neltuma velutina*, from Estacion Doctor, Sonora, Mexico. D) *Neltuma juliflora*, collected in the Ngambo Area, Baringo, Kenya. E) *Neltuma pallida*, collected in Lang'ata Bora, Kilimanjaro region, Tanzania. Bars indicate a scale of 3 cm.

Table 2
Proximate chemical composition of whole *Neltuma* pods from Mexico, Kenya and Tanzania.

Proximate chemical composition (%DW)	*N. laevigata Durango, Mexico*	*N. laevigata* × *N. odorata Durango, Mexico*	*N. velutina* Sonora, Mexico	*N. juliflora Ngambo, Kenya*	*N. pallida Kilimanjaro, Tanzania*	Wheat bran	Whole soybean
Protein	13.87 ± 1.63 b	13.12 ± 1.81 ab	10.78 ± 1.60 a	13.72 ± 1.50 b	11.01 ± 1.52 a	9.32 - 12.6[1]	40.2[3]
Fat	1.37 ± 0.35 ab	2.45 ± 0.64 b	1.44 ± 0.68 ab	2.35 ± 0.67 b	0.73 ± 0.26 a	0.91 - 1.38[1]	20.5[3]
Neutral Detergent Fibre	30.76 ± 2.80 b	24.40 ± 2.97 a	25.53 ± 2.28 a	32.11 ± 3.63 b	22.21 ± 2.30 a	45.6[3]	13.4[3]
Acid Detergent Fibre	20.68 ± 2.89 bcd	17.32 ± 1.55 ab	17.60 ± 2.16 abc	21.69 ± 2.48bd	14.92 ± 1.89 a	13.5[3]	7.8[3]
Acid Detergent Lignin	5.48 ± 0.68 b	4.39 ± 0.29 ab	4.42 ± 0.72 b	5.47 ± 1.46 b	3.08 ± 0.48 a	3.9[3]	1[3]
Hemi-cellulose	10.24 ± 1.16 c	6.90 ± 1.32 a	8.23 ± 1.80 ab	10.19 ± 1.71 c	7.26 ± 0.93 a	31.60 ± 1.58[2]	50[4]
Cellulose	15.01 ± 2.81 bc	13.10 ± 1.63 abc	12.89 ± 1.71 ab	16.24 ± 1.95 c	11.85 ± 1.50 a	9.60 ± 0.48[2]	20[4]
Total Energy (MJ/kg)	17.78 ± 0.54 ab	17.94 ± 0.05 ab	17.60 ± 0.44 a	18.16 ± 0.37 b	17.60 ± 0.42 a	18.5[3]	20.8[3]

Where one-way ANOVA was significant ($P < 0.001$), a Tukey test was carried out. Means with different letters are significantly different ($P < 0.05$). *N. laevigata* n=7, *N. laevigata* × *N. odorata* n=3, *N. velutina* n=12, *N. juliflora* n=12, *N. pallida* n=12. For comparison, previously reported nutritional data for wheat and soybean is included ([1]Siddiqi et al., 2020; [2]Ghodrat et al., 2017; [3]Noblet et al., 2002; [4]Snyder and Kwon, 1987).

N. pallida (11.01%) and *N. velutina* (10.78%). The flours with the highest and lowest values were from Mexico. Protein content of *Neltuma* flours is slightly higher than reported for wheat and about 2.9-fold lower than soybean. Fat content (%DW) of the hybrid *N. laevigata* × *N. odorata* (2.45%) and *N. juliflora* (2.35%), were significantly higher ($P < 0.05$) than *N. pallida* (0.73%). Fat content of *Neltuma* flours is higher than reported for wheat, except for *N. pallida,* and lower than soybean by about 8.4-fold. Based on this analysis *N. pallida* flour from Tanzania had the lowest macronutrient content.

Food energy is crucial for human survival, as it provides energy to cover the basic metabolism, physical activities, growth, pregnancy and production of milk (FAO, 2004). Total energy analyses from *Neltuma* flours studied here show that *N. juliflora* has the highest level of energy (18.16 MJ/kg), while *N. velutina* and *N. pallida* have the lowest level of energy (17.6 MJ/kg) (Table 2). This is probably a reflection of the *N. juliflora* having highest fat and fibre contents. The energy content of *Neltuma* flours is similar to those reported for wheat (18.5 MJ/kg) and slightly lower than those of soybean (20.8 MJ/kg) (Noblet et al., 2002).

Reported values for proximal analyses performed on pod flour for *Neltuma* species collected from drylands vary among species. For example, Sandoval-Torres et al., (2022) for *N. laevigata* reported a protein content, dependant on the blending method to extract the flour, of between 11.77 and 12.4%; a fat content between 2.16 and 2.90% and energy levels between 7.15 and 8.33 MJ/kg. For *N. juliflora*, depending on the geographic location of the trees, the reported values for proteins range between 10.1 and 14.7%, for fats between 2.8 and 3.2%; reported energy levels were 14.6 MJ/kg (Del Valle et al., 1983; Marangoni and Alli, 1988). The reported values for *N. velutina* were, for proteins 11.81%, for fat 2.36%, and for energy 18.9 MJ/kg (Becker and Grosjean, 1980). For *N. pallida,* the values reported for protein content were 9.5%, for fat 1%, and for energy 16.3 MJ/kg (Gonzales-Barron et al., 2020). Other values where the *Neltuma* species have not been declared show energy levels between 14.82 and 30.3 MJ/kg (Armijo-Nájera et al., 2019; Montañez-Valdez et al., 2021). Remarkably, the protein and fat levels of *Neltuma* flours, are higher than those reported in wheat, but have similar energy levels. Compared to soybean, *Neltuma* flours have about half of the protein levels, 10-fold less fat than soybean and slightly lower levels of energy (Noblet et al., 2002; Siddiqi et al., 2020).

Reported values for crude fibre on pods for *Neltuma* species found in the American drylands ranges from 21.3 to 32.22 %DW (Becker and Grosjean, 1980; Del Valle et al., 1983; García-Azpeitia et al., 2022; Grados and Cruz, 1996), However, comparative detailed analyses regarding cellulose, hemicellulose, NDF, ACD and ADL for species growing in Mexico, Kenya and Tanzania are missing. In this study we determined these subcomponents of fibre across the *Neltuma* species identified. The NDF in *Neltuma juliflora* (32.11%) and *N. laevigata* (30.76%) was significantly ($P < 0.05$) higher than all the other flours. The content of Acid Detergent Fibre (ADF) is highest in *N. juliflora* (21.69%) and lowest in *N. pallida* (14.92%), with this difference being significant ($P < 0.05$). Acid Detergent Lignin (ADL) content is highest in *N. juliflora* (5.47%) and *N. laevigata* (5.48%), while *N. pallida* shows the lowest (3.08%), with this difference being significant ($P < 0.05$). In comparison wheat has about 1.5-fold more NDF and soybean has around 2.4-fold less than *Neltuma* flours. The reported content of ADF is lower in wheat and soybean by about 0.9 and 3-fold respectively. However, ADL is not different in wheat, but soybean has about 2 to 5-fold less ADL compared to *Neltuma* flours.

We found that the content of hemicellulose (10.24 and 10.19%) and cellulose (15.01 and 16.24%) are significantly higher ($P < 0.05$) in *N. laevigata* and *N. juliflora* than in *N. pallida* which has the lowest content of hemicellulose (7.26%) and cellulose (11:85%). Previous studies show that *N. laevigata* has hemicellulose and cellulose content of

16 and 20.8% respectively (Zapata-Campos et al., 2020). The reported content of hemicellulose and cellulose for *N. juliflora* rank from 6.6 to 30.9% and 5 to 26.6% respectively (Gayathri and Uppuluri, 2022; Morán-Guillén et al., 2017; Sarasvati et al., 2014). The great variability maybe due to extraction methods in each study, the geographic location of trees or the stress and climatic conditions where these samples were collected. For instance, Zapata-Campos et al. (2020) collected their samples in Tamaulipas Mexico, in 2017 and during the rainy season. Morán-Guillén et al. (2017) collected their material in Venezuela, while the samples used by Gayathri and Uppuluri (2022) were collected in India. The hemicellulose content in wheat is 3-fold higher than *Neltuma* flours, whilst *Neltuma* flours contain more cellulose compared with wheat (9.6%). However, soybean shows higher content of cellulose and hemicellulose by about 1.2 and 4.9-fold respectively.

Dietary fibre is important as it contributes to good cardiovascular and gastrointestinal health in humans. The recommended daily intake of dietary fibre in adults is 25-38 g /day (King et al., 2012). Therefore, *Neltuma* flours appear to be able to provide a meaningful proportion of the recommended daily intake, especially *N. laevigata* and *N. juliflora* which are within this range when considering the NDF. Generally, it appears that the NDF component of *Neltuma* flours is between wheat and soya, but *Neltuma* ADF is higher than both, which results in the derived value for hemicellulose in *Neltuma* being three times lower than wheat and five times lower than soya bean (Campos-Zapata et al., 2020; Noblet et al., 2002; Snyder and Kwon, 1987). Cellulose is predominantly composed of glucose. Hemicellulose has a more diverse composition of a range of monosaccharides such pentose, xylose and arabinose; it also has hexose, glucose, mannose and galactose. The hemicellulose oligosaccharide derivatives have potential prebiotic effects (Davani-Davari et al., 2019). Interestingly, it has been reported that hemicellulose could improve the weakened intestinal mucosal barrier, lower systemic inflammation and control blood sugar levels in mice with potential therapeutic properties to treat type 2 diabetes mellitus (Liu et al., 2023). It remains to be determined what the impact of this fibre type composition from *Neltuma* flours has on human gastrointestinal health.

Nutritional contents of *Neltuma* flours analysed in this study show variability between species. Differences to values previously reported in the literature for the corresponding *Neltuma* species were also observed. For example, *N. laevigata* flour (pods collected in Durango in June 2019, Mexico) shows higher content of protein and energy, but less amount of fat than the reported by Sandoval-Torres et al. (2022) (pods collected in Oaxaca, Mexico on 2016). Similarly, the values we obtained for *N. juliflora* (pods collected in Kenya in June 2019) are within or lower than those reported by Marangoni and Alli (1988) (pods collected in Ecuador in December 1985) and by Del Valle et al. (1983) (pods collected in Chihuahua, Mexico). These differences demonstrate that *Neltuma* flours' nutritional content is dependent on the geographic location and environmental conditions that the mesquite trees are exposed to, the handling and pod storage prior to analysis and utilization and the flour extraction methods.

Underutilised species, such as mesquites, which comprise 44 leguminous species (Hughes et al., 2022; Hunziker et al., 1986) can improve diets for marginalised communities (Talabi et al., 2022); however, their nutritional content studies tend to focus on the most popular species (Bodoira et al., 2023; González Galán et al., 2008). Frequently, the taxonomic characterisation of the material analysed, and the growing conditions of trees are overlooked (Castillo et al., 2021). Here we have presented the nutritional characterisation of pod flours from four species and a hybrid. The nutritional content of a *Neltuma* hybrid shows differences with the species studied, in particular one of the parental lines of this hybrid. Mesquites have a high tendency to hybridise (Foroughbakhch et al., 2024; Hughes et al., 2022; Hunziker et al., 1986). Hybridisation happens when two different species cross to generate a progeny which usually shows improved features compared to that of their parents (Miyaji and Fujimoto, 2018). For this reason, many plant hybrids are used in modern agriculture, which usually are obtained through breeding techniques (Ter Steeg et al., 2022). As opposed to plant hybrids used in agriculture, mesquite hybrids occur naturally. They represent a potential source of food to address food insecurity. Our results highlight the importance of identifying *Neltuma* species and analysing the impact of plant hybridizations on the quality of pod flours. To untap the potential of this resource as a solution to malnutrition and hunger in the drylands, a systematic characterisation of the other 44 species and its hybrids is necessary. Moreover, it is important to taxonomically identify these species, recognise the eco-geographical growing conditions of the trees, and to define the handling and preparation of flours prior to their nutritional characterisation to maximise the benefits of this resource.

3.2. *Antinutrient analysis*

Although legumes are a good source of proteins, fibre, carbohydrates, and minerals, they also contain antinutritional factors that can reduce nutrient absorption and transport (Elizalde et al., 2009). However, antinutrients can also reduce the risk of diabetes and cancer (López-Moreno et al., 2022; Shukla et al., 2023). Here we establish the phenolic content, trypsin inhibitors, and phytic and gallic acids of pod flours from *Neltuma laevigata, N. laevigata* × *N. odorata, N. velutina, N. juliflora*, and *N. pallida*.

Comparative analysis shows statistically significant differences ($P < 0.001$) in the antinutritional constituents analysed in pod flours of the five species of *Neltuma*. For analogy, we included antinutrient composition previously reported for wheat flour (Mallick et al., 2013; Miladinović et al., 2020; Nikolić et al., 2019) and soybean flour (El-Shemy et al., 2000; Sharma et al., 2014; Zhang et al., 2012) (Table 3).

The lowest amount of phenolics (total content) in the flours from *Neltuma* species studied is 5.75 mg TAE/g and 6.36 mg TAE/g in *N. pallida* and *N. juliflora* respectively. The highest amount of 8.98 mg TAE/g was in *N. velutina*. The total phenolic content in *Neltuma* flours are slightly higher than those reported in wheat (3.88 to 5.14 mg TAE/g) and higher than soybean flour (1 to 1.5 mg TAE/g).

The amount of trypsin inhibitors units (TIU) in *Neltuma* flours is statistically different among the species studied with the lowest amount (0.333 TIU mg/g) of TIU present in *N. velutina.* Amounts of between 0.488 and 0.650 mg/g of TIU were observed in flours of the other *Neltuma* species studied. In contrast, the amount of trypsin inhibitors that are present in wheat and soybean flours range between 66 to 394 mg/g TIU and 41.5 to 858 TIU mg/g respectively.

The levels of phytic acid in *Neltuma* flour do not show statistically significant differences, varying from 99 to 168 mg/g. Levels of phytic acid in *Neltuma* flours are lower than wheat flour by 2 to 10-fold, and higher than soybean flour by 3 to 4-fold.

The content of gallic acid is highest in *N. velutina* (1101mg/g), which was significantly different ($P < 0.05$) from the lowest amounts detected in the hybrid *N. laevigata* × *N. odorata* (254 mg/g), *N. pallida* (256 mg/g), and *N. laevigata* (336 mg/g). The gallic acid levels in wheat and soybean vary from 705 mg/g to 2380 mg/g respectively; *Neltuma* flours levels are in the range of those reported for soybean. It is noticeable that *N. velutina* also had the highest total phenolic content but had the lowest crude protein and fat content (though compared to wheat, its crude protein and fat content is higher), while TIU was lowest. This suggests that *N. velutina* flour nutritional value is potentially compromised. Mesquite trees survive in difficult climatic conditions, particularly high temperatures. The year 2019 presented droughts in Sonora, therefore, it is important to repeat these analyses to compare the proximal and antinutrient content of *N. velutina* and include a processing step before ruling it out as a potential nutritional source.

Reported values of antinutrients for *Neltuma* species in the literature are limited. For instance, for *N. laevigata* total phenolics are reported as 3.94± 5.7 mg TAE/g, and gallic acid as 123.37 mg/g (García-Azpeitia et al., 2022), lower than what we observed in this study. For *N. juliflora*

Table 3
Anti-nutrient composition of flours from whole *Neltuma* pods from Mexico, Kenya and Tanzania compared with wheat and soybean flours.

Anti-nutrient composition	*N. laevigata* Durango, Mexico	*N. laevigata* × *N. odorata* Durango, Mexico	*N. velutina* Sonora, Mexico	*N. juliflora* Ngambo, Kenya	*N. pallida* Kilimanjaro, Tanzania	Wheat bran	Whole soybean
Total phenolic content (mg TAE/g)	7.72 ± 2.80 ab	6.88 ± 0.73 ab	8.98 ± 2.69 b	6.36 ± 2.45 a	5.75 ± 0.98 a	3.88 to 5.14[6]	1.0 to 1.5[8]
Trypsin Inhibitor Units (TIU mg/g)	0.579 ± 190.36 b	0.650 ± 207.40 b	0.333 ± 90.42 a	0.488 ± 105.25 b	0.500 ± 81.17 b	66.33 to 394.09[6]	41.5 to 858[8]
Phytic acid (mg/g)	99 ± 88.61	126 ± 93.91	160 ± 109.26	168 ± 114.56	160 ± 73.13	350 to 1200[6]	25 to 56[8]
Gallic acid (mg/g)	336 ± 61.92 ac	254 ± 58.84 a	1101 ± 40.20 d	352 ± 37.99 c	256 ± 39.13 ab	705.60 ± 82.78[5]	850 to 2380[7]

Where one-way ANOVA was significant ($P < 0.001$), a Tukey test was carried out. Means with different letters are significantly different ($P < 0.05$). Where there are no letters, no significant differences were noted for the one-way ANOVA. *N. laevigata* n=7, *N. laevigata* × *N. odorata* n=3, *N. velutina* n=12, *N. juliflora* n=12, *N. pallida* n=12. For comparison, previously reported antinutritional data for wheat and soybean is included: [5]Nikolić et al. (2019); [6]Mallick et al. (2013); [7]Zhang et al. (2012);[8]Sharma et al. (2014).

the reported values of Trypsin Inhibitor Units are 0.932 TIU (mg/g) (González Galán et al., 2008), double compared to those obtained in this study. For *N. pallida* the total phenolic content has been reported as 3.4 mg TAE/g (Gonzales-Barron et al., 2020). We were unable to find studies related to the trypsin inhibitors, phytic and gallic acids for *N. pallida* and *N. velutina,* for which total phenolic content has not been reported, suggesting this is the first study to report these compounds for these *Neltuma* species. The variability of our findings against the values reported for some of these antinutrients for *N. laevigata, N. juliflora* and *N. pallida* may be explained by the differences in geographical and environmental conditions where the trees were sampled, alongside the years of sample collection.

Neltuma is a leguminous tree, therefore, it is expected that antinutrients are present in the studied samples, moreover, samples used were unprocessed. Besides, effective processing of *Neltuma* dry pods and seeds before grinding may reduce antinutrient levels. These results suggest that *Neltuma* flour has comparable levels of antinutrients to those found in wheat and soybean and could be further reduced through processing. Moreover, Gonzales-Barron et al. (2020) performed cytotoxic activity assays on human tumour cell lines using *N. pallida* flour demonstrating no hepatotoxicity, and demonstrated that *N. pallida* has antimicrobial and antifungal properties. Considering the high incidence of waterborne and foodborne diseases in the drylands, the consumption of *Neltuma* flours could have a positive impact on health. However, more research and clinical studies are needed to confirm these benefits.

This makes *Neltuma* flour a potential alternative food staple for communities living in the drylands. Nath et al. (2022) suggest that optimal concentrations of antinutrients are necessary to observe their beneficial effects and they note that antinutrients are frequently present in different concentrations and combinations in foods. Analysis of the effects on health of antinutrients present in *Neltuma* pods, as well as the processing of mesquite flours to reduce their levels, is beyond the scope of this paper. These studies introduce future opportunities to investigate how different processing methods can reduce antinutrients in *Neltuma* flours, their antimicrobial and antifungal properties, and their impact on health and nutrition.

3.3. Amino acid content

Proteins are crucial for development and the existence of animals and humans. The essential amino acid content and their digestibility determine the nutritional quality of protein within a food staple (Hoffman and Falvo, 2004). Therefore, if essential amino acids are low in a food staple, this is a significant factor in considering it to be of poor quality. For instance, maize has low levels of tryptophan and lysine concentrations, wheat is low in lysine, and soybean is low in methionine (Friedman and Brandon, 2001). Additionally, when food is fermented spontaneously or through a planned process, the content of amino acids and other metabolites accountable for the aroma, quality and taste change (Balcázar-Zumaeta et al., 2023; Balcázar-Zumaeta et al., 2024).

To determine the amino-acid composition of pod flours from the *Neltuma* species identified in this study, we analysed the amount of eight essential, and nine non-essential amino-acids. In this study we have not performed digestibility analyses. Our results show statistically significant differences ($P < 0.001$, with differences between individual flours indicated by significant *post hoc* Tukey test $P < 0.05$) of the amino-acid composition analysed in flours from *Neltuma* species collected in Mexico, Kenya and Tanzania. We compared the obtained amounts to those reported for wheat (Abdel-Aal and Hucl, 2002) and soybean (Table 4) (Friedman and Brandon, 2001; Kudełka et al., 2021). We also calculated the Amino Acid Score (AAS) for essential amino-acids based on the amino-acid requirement of a child aged 6 months to 3 years, as indicated by FAO (2013), and compared this score to those reported for wheat and soybean (Table 5).

In general, flours of *N. laevigata, N. laevigata* × *N. odorata* and *N. juliflora* show the highest values for essential amino acids. The hybrid also has the highest amount of histidine, while *N. laevigata* shows the highest levels of isoleucine and leucine. *Neltuma juliflora* shows the highest levels of methionine. *N. laevigata* and *N. juliflora* show the highest levels of phenylalanine and *N. pallida* shows the highest amount of valine. Lysine is present in higher levels in *N. velutina, N. laevigata,N. laevigata* × *N. odorata,* and *N. juliflora* compared to *N. pallida. Neltuma pallida* shows the highest levels of valine. No statistically significant difference was detected in levels of threonine.

Compared to wheat, the essential amino-acid content of *Neltuma* flours is higher (lysine by about 1.4- to 1.8- fold), similar (threonine and valine), or lower (histidine; isoleucine, leucine, methionine sulfone and phenylalanine by about 1.2- and 2.9-fold), except for *N. pallida* that has similar amounts of lysine as wheat flour.

Compared with soybean the essential amino-acid content of *Neltuma* flours is higher for methionine, which is absent in soybean (Kudełka et al., 2021), histidine, leucine lysine, threonine and valine (by about 1.2- to 2.4-fold). An exception is *N. pallida* with similar levels of histidine and lower levels of lysine to soybean. Phenylalanine is higher in *N. laevigata* and *N. juliflora* compared to soybean, but the content is similar to those in *N. velutina, N. laevigata x N. odorata* and *N. pallida* (Table 4).

Leucine and valine play important roles in improving mitochondrial function and reducing or protecting against oxidative stress (Sharma et al., 2024), while threonine is involved in modulating nutritional metabolism, gut homeostasis and macromolecular biosynthesis (Tang et al., 2021). Lysine and methionine are amino acids of interest as in many cereals these are limited, especially wheat and soybean. Therefore, the higher content of these amino acids in *Neltuma* flours highlights

Table 4

Amino acid analyses for flours of whole *Neltuma* pods from Mexico, Kenya and Tanzania compared with wheat and soybean flours.

Essential (E)* and non-essential (N) Amino acids (g/kg DW)	*N. laevigata - Durango*	*N. laevigata × N. odorata - Durango*	*N. velutina - Sonora*	*N. juliflora - Kenya*	*N. pallida - Tanzania*	Wheat^{9} several varieties	Soybean
E-Histidine	16.79 ± 3.45 ac	18.85 ± 3.00 c	14.54 ± 4.26 abc	16.48 ± 3.64 ac	11.50 ± 1.73 ab	21–24	11.51^{10}
E-Isoleucine	17.59 ± 2.86 b	14.77 ± 2.51 ab	14.93 ± 3.19 ab	16.57 ± 2.58 b	12.00 ± 2.04 a	25–29	17.09^{10}
E-Leucine	47.48 ± 13.32 c	34.61 ± 1.18 abc	36.54 ± 8.24 bc	39.65 ± 9.58 bc	32.46 ± 4.75 ab	66–71	28.41^{10}
E-Lysine	31.16 ± 3.97 b	34.62 ± 6.01 b	28.05 ± 6.97 b	32.69 ± 6.27 b	20.65 ± 2.83 a	19–24	23.63^{10}
E-Methionine sulfone	8.61 ± 1.63 ab	8.94 ± 3.20 ab	8.12 ± 2.30 ab	9.29 ± 1.87 b	6.07 ± 0.85 a	14–18	0^{10}
E-Phenylalanine	25.71 ± 5.17 b	20.33 ± 1.28 ab	19.64 ± 5.35 ab	25.24 ± 4.79 b	16.65 ± 2.63 a	49–51	19.29^{10}
E-Threonine	25.78 ± 5.08	24.82 ± 9.18	25.09 ± 6.30	27.72 ± 4.09	24.30 ± 5.08	26–30	13.82^{10}
E-Valine	38.27 ± 5.72 ab	36.69 ± 7.11 ab	36.94 ± 8.81 ab	36.39 ± 4.18 ab	42.14 ± 9.72 b	37–44	17.34^{10}
N-Alanine	29.46 ± 4.10 c	28.86 ± 5.91 bc	26.17 ± 6.59 bc	30.70 ± 6.56 c	20.76 ± 3.52 ab	28–32	19.4-21.2^{11}
N-Arginine	58.63 ± 14.12 c	58.20 ± 5.84 bc	42.70 ± 18.19 bc	54.85 ± 12.25 c	33.27 ± 10.56 ab	39–44	33.3-37.2^{11}
N-Aspartate	104.22 ± 17.13 c	97.27 ± 19.33 ac	113.49 ± 32.79 c	115.44 ± 29.38 c	48.53 ± 17.74 a	43–46	51.9-56.7^{11}
N-Cysteic acid	8.13 ± 2.18	7.37 ± 1.33	7.48 ± 2.71	7.55 ± 2.57	6.41 ± 1.86	19–23	6.5-6.8^{11}
N-Glutamate	121.27 ± 21.04 b	119.65 ± 30.58 b	104.20 ± 36.57 b	115.41 ± 27.16 b	69.31 ± 15.02 a	337–370	87.7-97.2^{11}
N-Glycine	29.39 ± 5.09 abc	43.41 ± 18.58c	24.38 ± 7.70 ab	30.44 ± 7.71 bc	19.75 ± 6.98 a	31–39	19.3-20.9^{11}
N-Proline	69.78 ± 16.09 a	73.41 ± 18.46 a	79.10 ± 18.47 a	84.43 ± 13.97 a	145.39 ± 45.60 b	87–89	26.1-28^{11}
N- Serine	27.80 ± 4.19 ab	31.21 ± 11.07abc	26.53 ± 6.04 ab	30.32 ± 5.34 bc	20.65 ± 2.99 a	42–45	24.5-27^{11}
N- Tyrosine	18.95 ± 3.14 a	18.96 ± 3.73 ab	15.05 ± 3.88 a	16.58 ± 2.35 a	15.63 ± 2.74 a	25–29	17.5-19.1^{11}

Where one-way ANOVA was significant ($P < 0.001$), a Tukey test was carried out. Means with different letters are significantly different ($P < 0.05$). Where there are no letters, no significant differences were noted for the one-way ANOVA. *N. laevigata* n=7, *N. laevigata x N. odorata* n=3, *N. velutina* n=12, *N. juliflora* n=12, *N. pallida* n=12. *Tryptophan was not determined. For comparison, previously reported amino-acid composition data for wheat and soybean is included: [9]Abdel-Aal and Hucl (2002), [10]Kudełka et al. (2021), [11]Friedman and Brandon (2001).

Table 5

Total amino acid score (AAS) in flours of whole *Neltuma* pods from Mexico, Kenya and Tanzania, compared with AAS from wheat and soybean flours.

Amino acid	*N. laevigata*-Durango	*N. laevigata* × *N. odorata* -Durango	*N. velutina* -Sonora	*N. juliflora* -Kenya	*N. pallida* -Tanzania	Mean of *Neltuma* flours^{z}	Mean of Wheat varieties^{9}	Soy-bean ^{10,11}	FAO° (mg/kg/d)
Histidine	83.95 ± 17.25 ac	94.25 ± 15.00 c	72.70 ± 21.3 abc	82.40 ± 8.20 ac	57.50 ± 8.65 ab	**78.16 ± 16.08**	112.50	57.55	**20**
Isoleucine	54.97 ± 8.94 b	46.16 ± 7.84 ab	46.66 ± 9.97 ab	51.78 ± 8.06 b	37.50 ± 6.38 a	**47.41 ± 8.24**	84.38	53.41	**32**
Leucine	71.94 ± 20.18 c	52.44 ± 1.79 abc	55.36 ± 12.48 bc	60.08 ± 14.52 bc	49.18 ± 7.20 ab	**57.80 ± 11.23**	103.79	43.05	**66**
Lysine	54.67 ± 6.96 b	60.74 ± 10.54 b	49.21 ± 12.23 b	57.35 ± 11.00 b	36.23 ± 4.96 a	**51.64 ± 9.14**	37.72	41.46	**57**
Methionine sulfone	31.89 ± 6.04 ab	33.11 ± 11.85 ab	30.07 ± 8.52 ab	34.41 ± 6.93 b	22.48 ± 3.15 a	**30.39 ± 7.30**	59.26	0.00	**27**
Phenyl-alanine	49.44 ± 9.94 b	39.10 ± 2.46 ab	37.77 ± 10.29 ab	48.54 ± 9.21 b	32.02 ± 5.06 a	**41.37 ± 7.39**	96.15	37.10	**52**
Threonine	83.16 ± 16.39	80.06 ± 29.61	80.94 ± 20.32	89.42 ± 13.19	78.39 ± 16.39	**82.39 ± 19.18**	90.32	44.58	**31**
Valine	89.00 ± 13.30 ab	85.33 ± 16.53 ab	85.91 ± 20.49 ab	84.63 ± 9.72 ab	98.00 ± 22.6 b	**88.57 ± 16.53**	94.19	40.33	**43**

Values are represented as percentages of the FAO (2013) recommended ideal protein amino acid intake for children (6 months to 3 years). Where one-way ANOVA was significant ($P < 0.001$), a Tukey test was carried out. Means with different letters are significantly different ($P < 0.05$). Where there are no letters, no significant differences were noted for the one-way ANOVA. [z]Bold values represent the average amino acid score (AAS) of *Neltuma* flours. For comparison, previous AAS scores for wheat ([9]Abdel-Aal and Hucl, 2002) and soybean flours are included ([10]Kudełka et al., 2021;[11]Friedman and Brandon, 2001). Represent the required mg/kg/d of essential amino acids.

the potential of these food staples to improve nutrition in the drylands where these trees grow.

The two non-essential amino acids found in higher concentrations in *Neltuma* flours from species studied are proline (69.8–145.4 g/kg DW) and glutamate (69.3–121.3 g/kg DW). Proline is key for protein structure and maintenance of cellular redox homeostasis (Vettore et al., 2021), while glutamate is considered the master neurotransmitter and important for memory, cognition and mood regulation (Pal, 2021).

Information about amino acid composition of *Neltuma* flours is scarce, however, when available, this amino acid composition is variable or similar to our findings. For example, for *N. juliflora,* Marangoni and Alli (1988), report values of histidine of 10.8 g/kg DW, isoleucine of 26.5 g/kg DW and leucine of 42.5 g/kg DW. This is in contrast to the *N. juliflora* pod flour from Kenya collected for this study, for which the values identified were histidine 16.48 g/kg DW, isoleucine 16.57 g/kg DW and leucine 39.65 g/kg DW. These differences maybe due to the geographical location, environmental conditions and processing conditions of the samples used in both studies.

Flours of *Neltuma laevigata* and *N. juliflora* show the highest values for the non-essential amino acids alanine, arginine and aspartate. *Neltuma velutina* also shows higher levels of aspartate compared to the hybrid *N. laevigata* × *N. odorata* and *N. pallida.* No statistically significant differences are detected in cysteic acid levels. Glutamate levels are higher in *N. laevigata, N. juliflora, N. laevigata* × *N. odorata* and *N. juliflora,* compared to those in *N. pallida*. Glycine and tyrosine levels are higher in the hybrid *N. laevigata* × *N. odorata* compared to other *Neltuma* flours. *Neltuma pallida* shows the highest levels of proline compared to other *Neltuma* flours. Serine levels are highest in *N. laevigata* × *N. odorata* and *N. juliflora.*

Compared to wheat, levels of alanine are comparable except for *Neltuma pallida* that has about 0.3-fold less than wheat. Arginine levels are higher in *N. laevigata, N. laevigata* × *N. odorata* and *N. juliflora* by about 1.4- to 1.5-fold, with comparable levels in *N. velutina* and lower levels in *N. pallida.* Interestingly, aspartate levels are higher in *Neltuma flours* by about 2.25- to 2.7-fold compared to wheat, except for *N. pallida* with slightly higher levels. Cysteic acid levels are lower in *Neltuma* by about 2.3- to 3-fold compared to wheat, while glutamate levels are lower by about to 2.8- to 4.9-fold. Glycine levels are comparable to wheat except for those of *N. pallida* that are about 1.6- to 2-fold lower. Proline levels are similar compared to wheat, except for those of *N. pallida* that are about 1.6- to 1.7-fold higher. Serine and tyrosine levels are lower in *Neltuma* flours compared to wheat by about 1.3- to 2-fold and 1.3- to 1.7-fold respectively (Table 4). Compared to soybean, *Neltuma* flours show comparable or higher amounts of non-essential amino acids (Table 4).

Amino acids are required to meet the essential metabolic needs of humans. Amino acid requirement in humans is different and varies with age. For example, the requirements in children and pregnant women are different to those of a fully-grown adult male. Amino acids are evaluated by a scoring system developed by FAO (2013). The Amino Acid Score (AAS) can be used as an indicator of the completeness of a protein. With a score of 100% or more a protein can be considered as complete, however a protein lower than 100% is considered as incomplete (Siddiqi et al., 2020). Here we calculated the AAS from amino acids identified in *Neltuma* flours and compared them with those from wheat and soybean.

Protein completeness of *Neltuma* flour varies within the species analysed. *N. pallida* scored the lowest AAS values for all essential amino acids except for valine with a score of 98%. The highest score for AAS values of histidine was found in *N. laevigata* × *N. odorata* with 94%. *Neltuma* AAS for histidine ranged from 58 to 94% (with an average of 78% for the *Neltuma* species studied), which is lower than wheat (113%) and higher than soybean (58%). Isoleucine AAS for the *Neltuma* species studied ranged between 38 to 55% (the highest AAS was observed in *N. laevigata)*. The isoleucine AAS average for the *Neltuma* species studied was 47%, which is lower than wheat (84%) and soybean (53%).

Neltuma AAS for leucine ranged between 49 and 72%. The highest AAS was observed in *N. laevigata* and the average for the studied species was 58%, which is lower than wheat (104%) but higher than soybean (43%). Interestingly, *Neltuma* AAS for lysine ranged between 36 and 61%. The highest AAS was observed in *N. laevigata* × *N. odorata.* The average of all species studied was 52%, which is higher than wheat (38%) and soybean (42%).

The highest score for AAS values of methionine sulfone was found in *N. laevigata* × *N. odorata* with 33%. *Neltuma* AAS for methionine sulfone ranged from 23 to 33%; with an average of 30% for the *Neltuma* species studied, which is lower than wheat (59%) but higher than soybean (0%). Phenylalanine AAS for the *Neltuma* species studied ranged between 32 to 50%; the highest AAS was observed in *N. laevigata*. The phenylalanine AAS average for the *Neltuma* species studied was 41%, which is lower than wheat (96%) but higher than soybean (37%).

Neltuma's AAS for threonine ranged between 78 and 89%. The highest AAS was observed in *N. juliflora* and the average for the studied species was 82%, which is lower than wheat (90%) but higher than soybean (45%). *Neltuma's* AAS for valine ranged between 85 and 98%. The average of all species studied was 89%, which is lower than wheat (94%) but higher than soybean (40%). Reported wheat flour AAS levels for histidine and leucine are higher than 100, therefore according to Siddiqi et al. (2020), this would be considered a complete protein. These results suggest *Neltuma* proteins are more complete than those of soybean and similar to wheat except for isoleucine, methionine sulfone and phenylalanine. The limiting amino acid for *Neltuma* proteins is methionine sulfone.

Cittadini et al. (2024) report completeness of *Neltuma* flours (according to the FAO reference pattern and the requirements for human adults) for histidine, threonine, and lysine, with AAS of 1.95, 2.87 and 1.57 respectively. They report deficiencies for valine, methionine and leucine with AAS of 0.64, 0.95 and 0.92 respectively. Isoleucine was not detected. The difference in the values reported by Cittadini et al. (2024) with our results can be explained because in their study *Neltuma* flours were extracted from seeds only. Seeds concentrate about 82% of the protein content (Harden and Zolfaghari, 1988), suggesting that if a richer source of proteins is desirable, *Neltuma* seeds could be used to prepare flour, however, the seed flour would not contain fibre and other nutritious properties conferred by the pericarp. Moreover, these authors studied *N. flexuosa, N. nigra, N. chilensis* and *N. alba* growing in Argentina, in contrast, the species used in this study include *N. laevigata, N, velutina, N. juliflora, N. pallida, N. pallida* and the hybrid *N. laevigata* × *N. odorata* from Mexico, Kenya and Tanzania. In addition, they calculated the AAS considering the nutritional requirements of an adult. In contrast, we considered the nutritional requirements for young children, which is higher than for adults explaining also why the AAS presented in this study are lower for *Neltuma* flours. In our study we were able to detect isoleucine with an average AAS of 47.41. Isoleucine is important to improve mitochondrial function and to reduce oxidative stress (Sharma et al., 2024). Interestingly, Balcázar-Zumaeta et al. (2024) have demonstrated that spontaneous or enriched (*Saccharomyces cerevisiae*) fermentation of cocoa beans increases the concentration of essential amino acids. If fermentation is applied to mesquite flours, it is likely possible to improve their nutritional qualities and their AAS, making them a more complete food staple.

To understand the percentage of the daily requirement of essential amino acids that *Neltuma* flour provides it is necessary to perform digestibility analyses, which are beyond the scope of this paper. The amino acid scores calculated for the different *Neltuma* flours studied suggest *Neltuma* flours as potential candidates to improve nutrition. Moreover, there is evidence that protein malnutrition increases susceptibility to infectious diseases and can impair the immune system (Li and Wu, 2022; Li et al., 2007). Marginalised dryland communities suffer from both. Using, combining, or supplementing the *Neltuma* flour could potentially provide the required nutritional needs for children and adults and reduce morbidity and mortality.

3.4. Fatty acid content

Fatty acids (FAs) are energy sources and components of cellular membranes and play fundamental roles in metabolism and in gene transcription. Humans and other animals cannot metabolise linoleic and α-linolenic acids. Therefore, their bodies need to assimilate them from plant sources (Glick and Fischer, 2013). Here we analysed and estimated the relative amounts of fatty acids present in pod flours from *Neltuma* species identified in this study. From the thirty-one fatty acids identified, linoleic (30.0 to 35.7%), oleic (19.3 to 24.2%) and palmitic (17.2 to 19.5%) acids were found as major FAs.

This is consistent with previous data reported for other legumes (Bhat and Karim, 2009; Grygier et al., 2023; Padhi et al., 2017). *N. juliflora* has the highest amount of linoleic acid, in contrast *N. laevigata* × *N. odorata* has the highest level of oleic acid, while *N. laevigata* has the highest concentration of palmitic acid. Cittadini et al. (2024), reported that linoleic, oleic and palmitic acids are also higher in seed fours from *N. alba, N. Chilensis, N. nigra* and *N. flexuosa*. The values for linoleic (32.0 to 51.5%) and oleic acids (27.2 to 43.7%) are higher than those observed by us. Surprisingly, palmitic acid levels reported by these authors are lower (10.9 to 15.3%) than those identified in pod flour of *N. laevigata, N. laevigata x N. odorata, N. velutina, N. juliflora,* and *N. pallida* used in this study. Our results for the FAs content in *N. laevigata* are similar to those reported by Cruz-Gracida et al. (2019). The differences observed can be explained by the genetic variability of the *Neltuma* species analysed in each study.

We observed significant differences ($p<0.001$) in the content of pentadecanoic (C15:0), palmitoleic (C16:1), arachidic (C20:0), behenic (C22:0) and eicosatetraenoic acid ETE (C20:3n3) acids. The highest amount of pentadecanoic acid was found in *N. juliflora* and *N. laevigata* while the lowest was present in *N. velutina. N. laevigata* showed the highest amount of palmitoleic acid, while *N. pallida* showed the lowest amount. However, *N. pallida* and the hybrid *N. laevigata* × *N. odorata* showed the highest amount of arachidic acid. Behenic and ethanolamine (ETN) acids were also highest in *N. pallida* while *N. juliflora* showed the lowest amount (Table 6, Supp. Table 1).

The content of linolenic and stearic acids found in pod flours of the

Table 6
Fatty acid composition of whole *Neltuma* pods from Mexico, Kenya and Tanzania.

Fatty acid	*N. laevigata Durango*	*N. laevigata× N. odorata Durango*	*N. velutina Sonora*	*N. juliflora Kenya*	*N. pallida Tanzania*	^{y}ANOVA P value.
Palmitic (C16:0)	19.510 ± 2.817	17.206 ± 1.012	17.975 ± 1.519	18.778 ± 2.358	17.501 ± 1.904	0.236
Stearic (C18:0)	7.600 ± 1.007	8.542 ± 0.674	7.701 ± 1.381	7.566 ± 0.649	8.824 ± 1.450	0.066
Arachidic (C20:0)	2.584 ± 0.288 a	3.117 ± 0.121ab	2.807 ± 0.695 a	2.670 ± 0.533 a	3.559 ± 0.666b	0.003
Behenic (C22:0)	3.091 ± 0.793ab	3.661 ± 0.628 ab	3.908 ± 1.216 ab	2.913 ± 0.641a	4.142 ± 0.944b	0.018
Lignoceric (C24:0)	2.134 ± 0.95	2.838 ± 0.941	4.196 ± 2.912	2.509 ± 1.287	4.086 ± .030	0.096
Oleic (C18:1n9c)	21.236 ± 2.289	24.166 ± 1.857	19.932 ± 4.670	19.292 ± 2.046	22.118 ± 2.619	0.075
cis-11-Eicosenoic (C20:1)	1.129 ± 0.205	0.955 ± 0.256	1.011 ± 0.262	0.954 ± 0.278	0.931 ± 0.242	0.542
Linoleic (C18:2n6c)	32.503 ± 4.627	30.003 ± 2.429	33.005 ± 5.512	35.723 ± 4.212	30.190 ± 5.175	0.097
α Linolenic (C18:3n3)	7.204 ± 1.33	7.039 ± 0.499	6.674 ± 1.746	6.913 ± 1.241	5.799 ± 1.666	0.275

Individual fatty acids are expressed as mean % of the total of all fatty acids detected by GCMS ± standard error of the mean (SEM). Fatty acids with <1.0% abundance, are shown in supplementary Table 1. ^{y}ANOVA one-way P value. When $P < 0.05$, a Tukey test was carried out. Means with different letters are significantly different ($P < 0.05$). Where there are no letters, no significant differences were noted for the one-way ANOVA. *N. velutina* n=12, *N. laevigata* n=7, *N. laevigata* × *N. odorata* n=3, *N. juliflora* n=12, *N. pallida* n=12.

Neltuma species studied here is about 6-fold and 1.5-fold higher respectively than those reported by Cittadini et al.(2024), for seed flours of *N. alba, N. Chilensis, N. nigra* and *N. flexuosa*.

Nikolić et al. (2011), reported the following values for wheat flour: palmitic:19.45 ± 0.45%, stearic: 1.36± 0.14%, oleic: 20.23 ± 0.21%, linoleic: 57.91± 0.72% and behenic: 0.26± 0.06%. Vivar-Quintana et al. (2023), reported the following values for two commercial soybean flours: palmitic: 11.11 to 21.69%, stearic: 4.61 to 9.62%, oleic: 24.81 to 33.65%, linoleic: 28.12 to 48.09%, and arachidic: 0.46 to 0.88 %; myristic: 0.16 to 0.7%; behenic: 0.62 to 0.89%, pentadecanoic: 0.045 to 0.2%, palmitoleic: 0.08 to 0.11%, and 3n3 linolenic: 1.5 to 8.36%; heneicosanoic 0.05 to 0.8%, cis-11,14-Eicosadienoic: 0.04 to 0.06%. EPA: 0.2 to 0.36%, capric, cis-10-pentadecanoic, tricosanoic, and cis-11-eicosenoic acids are not reported. ETE and lignoceric are reported as not detected.

When compared with available fatty acid information from wheat and soybean flours, we found that the palmitic acid content in *Neltuma* pod flours is comparable to that of wheat and soybean. The levels of stearic acid in *Neltuma* pod flours are higher than wheat by about 3-fold and similar to those reported for soybean. Oleic acid content is similar in *Neltuma*, wheat and soybean flours. Linoleic acid amounts in *Neltuma* flours are about half of those found in wheat and similar to those of soybean flours. Arachidic acid is not reported as present in wheat flour. Arachidic and behenic acid in *Neltuma* pod flours are 3-6 times and 4-6 times higher than in soybean respectively. Levels of myristic, pentadecanoic, palmitoleic and 3n3 linolenic acids in *Neltuma* flour are similar to those of soybean, while EPA levels are lower. Heneicosanoic acid levels in *Neltuma* flours are lower in one of the commercial soybean flours but higher than the other. Cis-11,14-Eicosadienoic acid level is higher in *Neltuma* flours than those reported for soybean commercial flours (Table 6, Supp. Table 1). *Neltuma* flours contain detectable and significantly different levels between species of ETE not reported for wheat and soybean. Other detectable fatty acids in *Neltuma* flours studied include cis-10-pentadecanoic and tricosanoic acids.

These results show that the content of fatty acids of *Neltuma* flours are comparable to those of wheat and soybean, supporting the argument that *Neltuma* flours are potential food staples that could alleviate malnutrition where these trees grow. The nutritional properties of flours prepared from whole pods from different *Neltuma* species and growing in different geographical locations is different, suggesting that the genetic information and environmental conditions are important to determine the nutritional qualities in any given year. To our knowledge this is the first study comparing the nutritional and antinutritional composition of *Neltuma* pod flours obtained from different species and a hybrid, growing in two continents.

The results presented in this paper provide evidence for governments to stimulate consumption and reforestation of mesquite where it is native and management by utilisation where it has become invasive. It is crucial however, that the story of soybean is not repeated. Although immediate economic gains have been observed cultivating soybean (Dreoni et al., 2022), these are obtained at great expense to local communities, and in the long run, negative economic, environmental and social impacts are greater. For example, the livelihoods of vulnerable communities in the Amazonia have been affected and they have been displaced and stripped of their lands, increasing social conflicts. The environmental consequences of soybean expansion include deforestation, loss of biodiversity and water pollution, which could trigger an irreversible environmental situation that could result in a collapse of the forest-climate system (Nóbrega et al., 2023). In *Neltuma's* case, the collapse would be at the dryland-climate system level. Showing communities how to sustainably use *Neltuma* pods can empower them to improve their social and economic wellbeing. In Africa, managing *Neltuma* by utilization can contribute to the reduction of its spread and the rebalancing of natural habitats.

4. Conclusions

There are significant differences in nutritional content between *Neltuma* pod flours from species growing naturally in the drylands of Mexico, Kenya and Tanzania. Flours of *N. laevigata* and *N. juliflora* are more complete than those of *N. velutina* and *N. pallida. Neltuma* flours have nutritional and antinutritional contents comparable to those reported for wheat and soybean flours, except for phenolic content and trypsin inhibitors that are higher and lower in *Neltuma* flours respectively. *Neltuma* flours contain all essential amino acids and have comparable or better levels of non-essential amino acids than wheat and soybean. *Neltuma* flours contain thirty-one fatty acids, the most abundant are linoleic, oleic and palmitic acids, and have higher concentrations of arachidic, behenic and cis-11,14-eicosadienoic compared to wheat and soybean flours. Additionally, eicosatrienoic acid, is present in *Neltuma* flours but not in wheat or soybean flours. Grinding *Neltuma* pods where the trees have become invasive, can help reduce seed spread and lower negative impacts on native ecosystems. It is important that *Neltuma* trees are used to support communities in the drylands and that their pods do not become the new soybean and displace or affect the already poorest and most marginalised rural and indigenous groups and their ecosystems. It is crucial to co-produce with local communities, and other stakeholders, ethical, sustainable solutions that prioritize their needs, perspectives and traditional knowledge to preserve their lands and resources, and to stimulate local economies.

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Ethics approval

Internationally Recognised Certificate of Compliance ABSCH (Nagoya Protocol) SGPA/DGGFS/712/0668/20.

CRediT authorship contribution statement

Zinnia H. González-Carranza: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Visualization, Writing – original draft. **Gabrielle Bone:** Investigation. **Arturo Castro-Castro:** Investigation, Resources, Supervision. **M. Socorro González-Elizondo:** Resources, Supervision. **Xochitl Soto-Luzania:** Methodology, Supervision. **Yolanda L. López-Franco:** Supervision. **Oscar Koech:** Supervision. **Tim Parr:** Data curation, Formal analysis, Methodology, Funding acquisition, Resources, Supervision. **Charles J. Kilawe:** Supervision, Resources. **Sahian E. Velázquez-Quiñones:** Investigation. **Rubén F. González -Laredo:** Supervision. **Julio C. Ríos-Saucedo:** Resources, Methodology.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

Data availability

All data created during this research are openly available from the University of Nottingham data repository at: DOI: https://doi.org/10.17639/nott.7393.

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Supplementary material

Supplementary Table 1. Fatty acid composition of whole *Neltuma* pods from Mexico, Kenya and Tanzania with values lower than 1%. For the purpose of open access, the author(s) has applied a Creative Commons attribution 4.0 (CC BY) licence. Supplementary material associated with this article can be found, in the online version, at 10.1016/j.fufo.2024.100434

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