Reproductive patterns in *Araucaria araucana* forests in the Andean range, Chile

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Abstract

Background *Araucaria araucana* is a mast species that presents a high variability in annual cone production. Researchers have recorded synchronization events in cone production in different populations, which allows the seed production to be concentrated, reducing the percentage of seeds consumed by different animal species.

Methods We sampled three populations located in the Andes Mountains, Araucanía Region, Chile. In 2004 we began the collection of data on cone production, for which we installed permanent plots (1200 m^2 each) at each location. We identified and labeled each female tree in each plot to monitor its cone production. In 2012 we selected a total of 30 trees near the plots to evaluate the number of seeds per cone. In each February from 2012 to 2014 we selected two mature cones and covered them with a porous mesh for subsequent collection and storage in March. At the beginning of June, we counted and weighed the seeds, determining the average weight, the number of seeds per cone, the germination capacity (GC), and the germination speed (GS).

Results Cone production was synchronous across the three locations. We observed significant differences among the locations and years evaluated. The cones had fewer seeds in 2013 (high production) compared to those in 2012 (low production), but their weights were similar. In 2014 the cones produced smaller seeds in fewer quantities. The difference between the years 2013 and 2014 resulted from the high-energy expenditure in 2013. Regarding GC and GS, there were significant differences among the three locations (GC: $F = 45.41$, $p < 0.01$; GS: $F = 96.08$, $p < 0.01$), where the highest values were observed in 2013.

Conclusions Both GC and GS are related to seed weight but not to the number of cones produced in a given year. These annual fluctuations in seed production are determining factors in the population dynamics of forest species. Our results allow a better understanding of the reproductive phenology of *A. araucana* and could help define sustainable use and conservation actions for this species.

Keywords Seed weight, Germination potential, Masting species, Sustainable use, Dioecious species

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Introduction

Studies on seed production have made it possible to understand the complex ecological processes of plant reproduction and regeneration (Obeso 2002). Seeds are not only the main mode of plant propagation but also an important food source for people and many animal species; therefore, knowledge of seed production is necessary to designing management procedures for its collection and use (Yu et al. 2020). However, it is also necessary to compare data from several years to understand production cycles, especially in those species with slow growth and irregular seed production (Obeso 2002). The concept of masting refers to the variability and synchronization of seed production with a concentration of reproductive effort, which means there are few but intense seed production events; its effect on the ecosystem will depend on the extent and spatial synchronization of this process (Hacket-Pain 2021; Journé et al. 2023). *Araucaria* genus produces large cones that carry edible seeds, which take almost 2 years to mature and then release seeds that are highly nutritious and consumed by various species and humans (Hadad et al. 2021). This variability in cone production directly affects wild animals and people because it is the main food the forest offers and has a notable effect on the ecosystem (Sanguinetti and Kitzberger 2009; Chechina and Hamann 2019).

Araucaria araucana (Mol.) K. Koch (Araucariaceae) is an endemic species from the subantarctic forests in Argentina and Chile. It is one of the longest-lived plant species, living more than 1000 years (Aguilera-Betti et al. 2017). It is a dioecious tree species requiring two vegetative periods to complete fruit maturation. Hence, mature and immature cones can be found in the same plant (Hadad et al. 2021). The appearance of female flower buds during the winter (August and September) marks the beginning of a reproductive cycle. By January and February (summer), the wind carries pollen to the female strobili for fertilization. The cone develops during the second year of the cycle. Finally, from February to May, when the cones reach maturity, they disperse seeds (González et al. 2013).

Seed production in *A. araucana* is irregular, fluctuating from year to year, and it has not been possible to establish a cycle or pattern for this behavior (Sanguinetti and Kitzberger 2008, 2009; Donoso et al. 2010; Sanguinetti 2014). Furthermore, there appears to be a high level of synchrony in seed production among trees within the population, even on a regional scale between the *A. araucana* populations in Argentina and Chile (Sanguinetti and Kitzberger 2008; Sanguinetti 2014).

The reproductive characteristics and the slow growth of the species have implications in the structure, forming mixed multistage forests of *A. araucana* with southern beech trees (Navarro-Cerrillo et al. 2014). The human communities living around these forests, developing activities such as cattle ranching and the collection of *A. araucana* seeds to obtain direct benefits from these forests. The number of seeds remaining in the forest is significantly reduced in locations with a greater number of families and greater cattle pressure per hectare (Donoso et al. 2010). Consequently, the natural regeneration of *A. araucana* is significantly lower in these locations (Donoso et al. 2010). Therefore, a deeper knowledge of the ecological processes involved is important to predicting annual seed production and defining appropriate management guidelines for seed collection and cattle pressure because both situations directly affect the regeneration of *A. araucaria*. Adequate management would allow the sustainable use of these forests (Aagesen 1998). Having comprehensive knowledge about a species' reproductive behavior is crucial for effective management decisions. Therefore, it is important to consider not only the number of seeds but also the germination capacity (GC) and germination speed (SG), which determine seed viability (Ramírez-Santiago et al. 2020).

Some studies was analyzed the variability in cone production of *A. araucana*, but most of them are short-term, and only a few relate the influence of different levels of cone production to the number of seeds per cone, their weight, GC and GS (Donoso et al. 2010; Sanguinetti 2014). In the present study, we analyze cone production and its relationship to seed number per cone, GC and GS of seeds for 3 years of seed production. This study aims to answers the following questions: Is there a difference in the number of seeds per cone between years? Does a higher cone production correspond to a higher number of seeds per cone? Is there a relationship between cone production and GC and GS values?

Methods

Study area

The study and seed collection were performed in three locations (also called populations) in Lonquimay municipality (38° to 39° S, and 71° to 72° W), including Mallín del Treile, Cruzaco, and Quinquén in Araucanía Region, Chile (Fig. 1). We chose these locations in 2003 for a research project (Lizana 2009; Donoso et al. 2010) and had hundreds of hectares of *A. araucana* forests, where permanent plots were distributed to monitor cone production and regeneration.

The climate in the area shows a minimum average temperature of −4.4 °C and a maximum of 19.5 °C. Mean precipitation is 3.829 mm per year, mainly as snow. Annual rainfall records in Lonquimay showed little variation between 2010 and 2014. The mean temperature increased from 16 °C in 2010 to 18 °C in 2013 but went back to 16 °C in 2014. The minimum temperature decreased slightly from 2011 to 2013. Soils originated
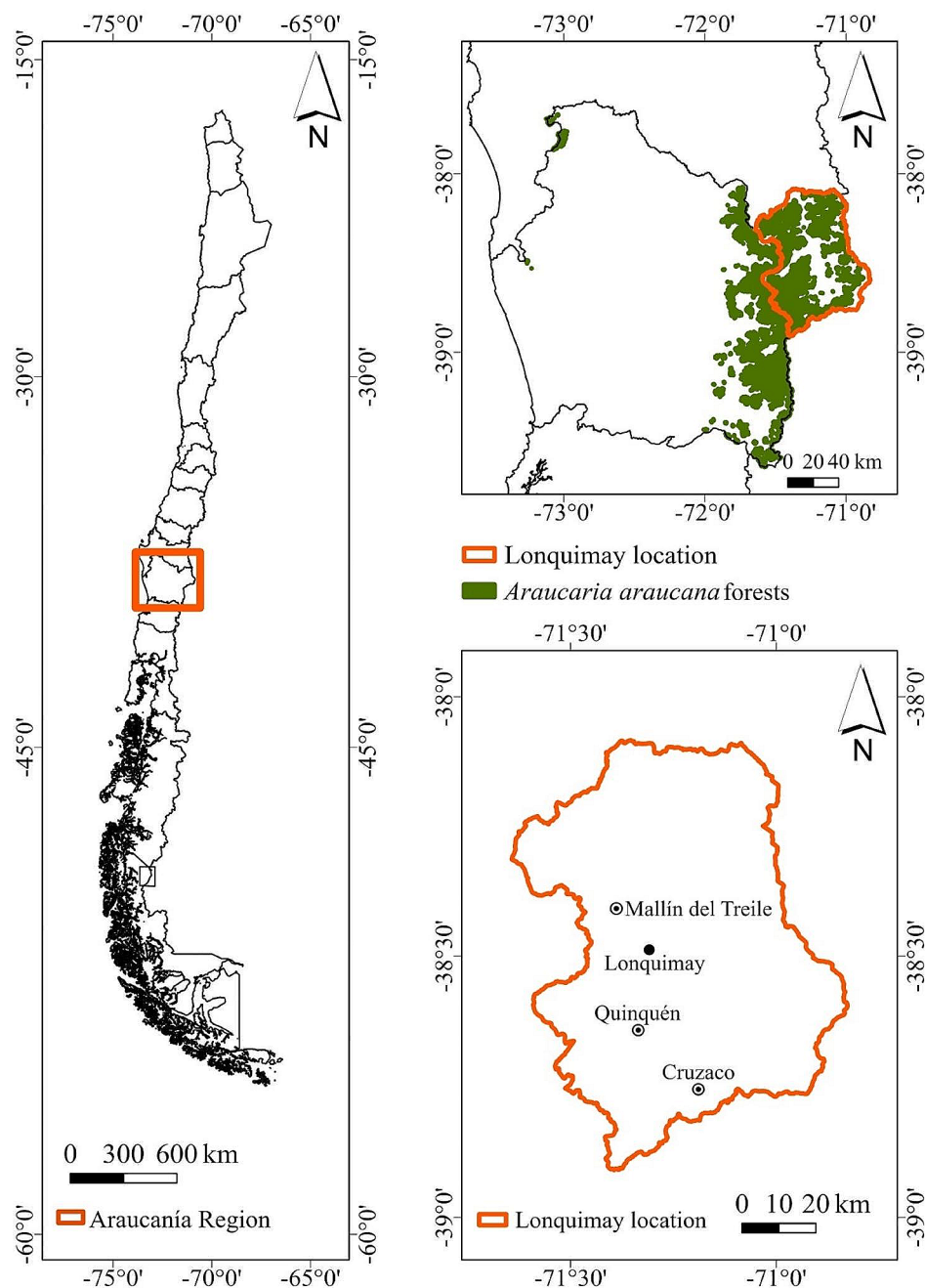
Fig. 1 Location of the study areas in the Araucanía Region, Chile

mainly from volcanic deposits of different natures and granulometries (Rozas et al. 2019).

Cone production

To monitor cone production, we installed permanent plots (1200 m² each) at each location at altitudes between 1200 and 1600 m (Lizana 2009; Donoso et al. 2010). We defined the number of plots according to the characteristics and variability of the forests (e.g. accessibility, slope, tree cover). The total number of plots evaluated was 13,

including 3 in Cruzaco, 4 in Quinquén, and 6 in Mallín del Treile. The average distance between plots per location was 2.3 km for Cruzaco, 0.6 km for Quinquén, and 4.5 km for Mallín del Treile. At each plot, we identified and labeled all the female trees (10–14 trees per plot), and the monitoring and counting of the cones were performed visually using binoculars, according to the method used by Gallo et al. (2004) and Lizana (2009). Because the reproductive cycle of *A. araucana* lasts almost 2 years from the formation of the female cones to

the dissemination of the seeds in the crown, both mature cones (larger and brown in color) and immature cones (smaller and green in color) can be distinguished (Sanguinetti et al. 2023). For this reason, we determined by direct observation the number of cones produced in each location per year (2004–2014). This allowed us to define each year (2012, 2013, and 2014) as high, intermediate, or low in terms of cone production.

To classify a year as masting, we used one of the quantitative methods described by LaMontagne and Boutin (2009). For this, the following equation was considered:

$$Annual\ deviate\ from\ the\ long-term\ mean\ i =$$
$$\frac{mean\ seed\ production\ in\ year\ t - long-term\ mean\ seed\ production\ i}{standard\ deviation\ calculated\ over\ all\ year\ i}$$

For each location i the number of standard deviations from the long-term mean seed production in year t was calculated (deviation from long-term mean). With the above equation, negative values (seed production lower than average) or positive values (seed production higher than average) are obtained. With this information it was determined whether or not a year was a masting year. If the standard deviation was greater than the absolute value of the lowest standard deviation per location, it meant that a masting event occurred in that year.

Number of seeds per cone

To determine the number of seeds per cone, in 2012 we selected a total of 30 trees close to the plots to avoid disturbing the permanent plots and based on cone accessibility for collection. The selection was distributed as follows: 15 in Mallín del Treile, 8 in Quinquén, and 7 in Cruzaco. We numbered, georeferenced, and measured each tree (DBH, diameter at 1.3 m height). Every year (2011–2013) in February we selected 2 mature cones from each tree and wrapped each of them with a porous mesh to prevent predation or seed loss. In March we collected the cones previously selected in February. We carefully labeled each cone with information on the location and tree from which it was collected. Subsequently, we kept the cones in bags, storing them in a cool place to avoid moisture loss until evaluation. In early June we counted and weighed the seeds to determine mean weight and number of seeds per cone. Some authors indicated that one cone has on average between 90 and 200 seeds (Lizana 2009).

Seed germination test

The seeds of *A. araucana* are short-lived or recalcitrant and present physiological dormancy; a recommended prior treatment is therefore cold stratification with humid substrate (González et al. 2013). In June of each year we randomly selected 20 seeds per cone, leaving out (if present) the empty seeds. It is worth mentioning that the seeds that do not fall to the ground do not suffer predation by insects, and only a low percentage is preyed on by the bird *Enicognathus ferrugineus* (cachaña), which in turn helps in the dispersal of the seeds when trying to obtain food.

Before sowing, we evaluated GC, for which we hydrated the seeds for 24 h. Once the hydration period was over, we applied a cold stratification treatment for 30 days, placing the seeds inside previously labeled plastic bags with sterilized and moist sand, refrigerating them at −5 °C. Once stratification was completed, we sowed the seeds in plastic containers labeled according to their origin, tree number, and cone. The germination substrate was sand sterilized at 105 °C for 1 h and then moistened with a solution of distilled water and a contact fungicide with preventive action (Pomarzol® Forte 80% WG, Tetramethyl-thiuram-disulfide). We subsequently placed them inside labeled plastic containers to finally enter a germination chamber at 25 °C.

We monitored germination every other day. After 60 days, we evaluated the following: (a) GC, the percentage of seeds germinated at the end of the experiment; and (b) GS, through the determination of maximum Czabator value (maximum average daily germination) (Czabator 1962). We considered a seed germinated when its radicle was 2 mm long. We could then compare the germination potential of seeds based on GC and GS.

Data analyses

In all female trees, their cones were counted within the plot, and the value obtained was expanded to hectare levels, the information was analyzed at location level. With the cone production dataset from the three locations, we calculated cone production for each year and compared them across years (2012, 2013, 2014) using an ANOVA ($\alpha = 0.05$) and Tukey test. We compared the results with the cone production dataset (2004–2014) and established 3 levels of production (high, medium, low). Using the mean as an intermediate level, we classified any value above the sum of the mean plus 0.5 standard deviations as high-level and any value below the subtraction of the mean minus 0.5 standard deviations as low-level. The number of seeds per cone and seed weight was aggregated for year level, because a year 2011 and 2013, we recollect a reduced number of cones at some location, allowing analysis only to the year level. After applying a logarithmic transformation of the data, we also analyzed the number of seeds per cone and seed weight using ANOVA and the Tukey test to compare among years. Finally, we compared seed production years using the parameters from the germination test. Here also we transformed the data and used ANOVA followed by the Tukey test. These comparisons allowed us to determine

the effect of the level of cone production on the germination and viability of seeds.

Results

Cone production

Analyses of cone production showed significant differences among years. The year 2012 was in the lower level of cone production per hectare (68±22), 2013 was a high-level year (1548±430), and 2014 was intermediate (211±112). Although there was a decrease in cone production in 2014 compared to the previous year (2013), it was still higher than in 2012 (Fig. 2A). The annual average production of cone per hectare in 2012 was similar to other years of low cone production (2004, 2005 and 2011), in 2007 there was an increase in the production of cones, this peak does not compare to that recorded in 2013, the amount of which greatly exceeds that of previous years. Throughout the years evaluated, it is observed
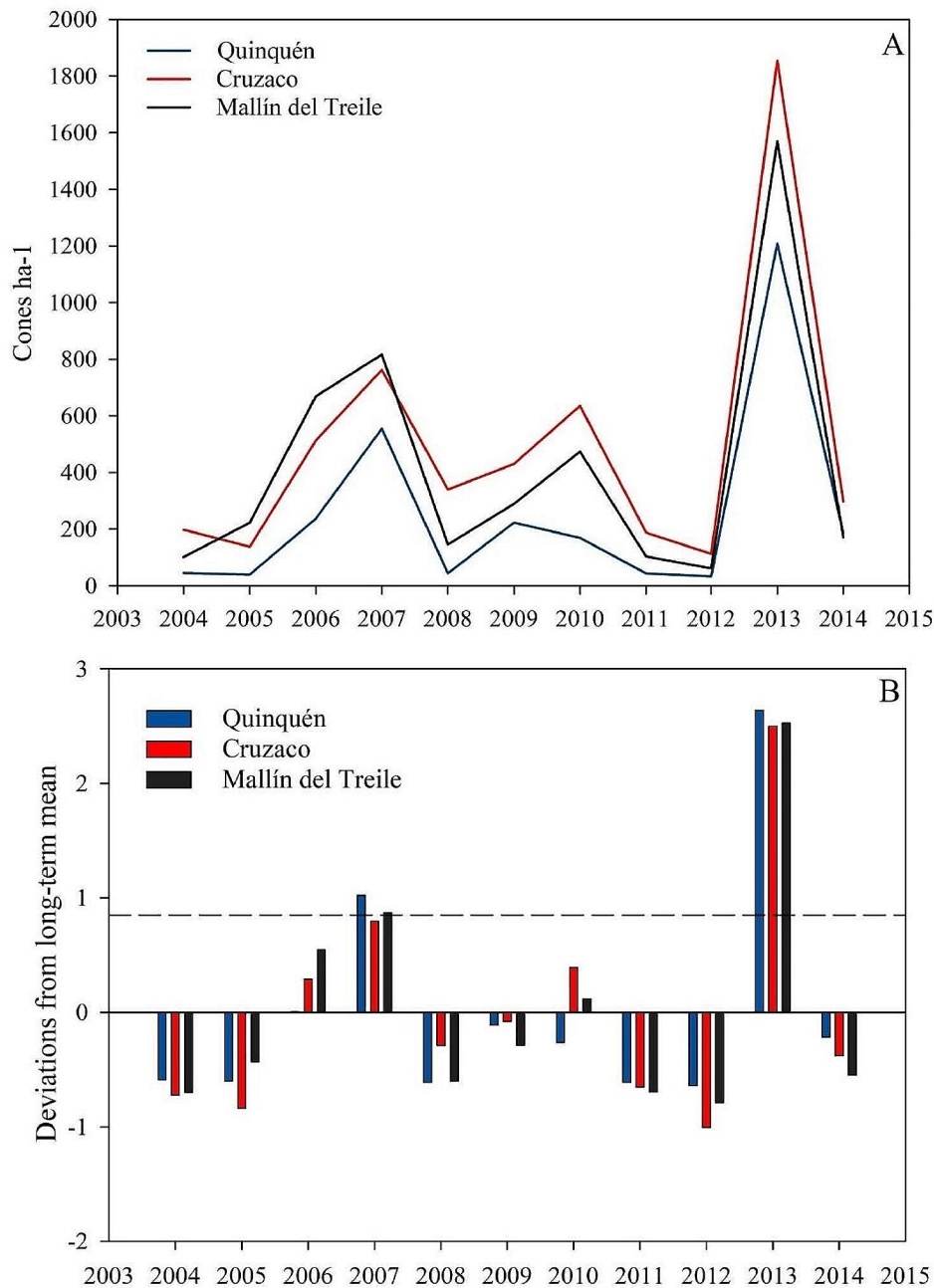
Fig. 2 (**A**) Mean annual cone production per hectare in the locations of Cruzaco, Mallín del Treile and Quinquén. (**B**) Deviations from the long-term mean annual cone production per hectare. The segmented line represents the absolute value of the smallest standard deviation which was used as a cut-off value for the identification of masting years

Table 1 Average annual cone production per hectare in the study sites

Year	Cruzaco	Mallín del Treile	Quinquén
2012	113 Aa	61 Aa	33 Aa
2013	1854 Ca	1569 BCa	1208 ABCa
2014	298 ABa	171 Aa	185 Aa

Different uppercase letters indicate significant differences among years, and different lowercase letters indicate significant differences among locations by Tukey test ($F=26.02$, $p<0.01$).

Table 3 Germination capacity (GC) and germination speed (GS) for the 3 years of the study

Production level of cones (year)	GC (%)	GS(% day^{-1})
Low (2012)	78.7 ± 3.47 B	2.2 ± 0.16 B
High (2013)	91.7 ± 1.53 A	3.0 ± 0.13 A
Intermediate (2014)	18.5 ± 7.89 C	0.43 ± 0.16 C

Different letters indicate significant differences among years by the Tukey test ($p \le 0.05$). GC: $F=96.08$, $p<0.01$; GS: $F=45.41$, $p<0.01$.

that the synchrony among the locations is maintained (Fig. 2A). Cruzaco showed the highest production for most years with a mean value of 755 cones per hectare, Mallín del Treile was at the intermediate level with a mean value of 600 cones per hectare, and Quinquén was at the lowest level in most years, with a mean value of 476 cones per hectare ($F=26.02$, $p<0.01$; Table 1).

Seeds per cone and seed weight
During the three years of the study, there has been no evidence of seed depredation or damaged by insects or birds. Mean seed number per cone differed significantly across years in 2012–2014 ($F=10.66$, $p<0.01$), but the level of cone production for each year did not correspond with seed production per cone. At the low level of cone production, more seeds per cone (150) were produced in 2012 than in 2013, with only 117 seeds per cone. In the intermediate level of cone production, 2014 saw the least seeds per cone (8) (Table 2). Seed weight did not differ significantly between 2012 and 2013, with only a 3.3 g difference in mean weight. The year 2014 differed significantly from the other 2, with 2.5 g of mean weight ($F=9.71$, $p<0.01$; Table 2).

Germination test
After carrying out the cutting tests, we observed that only 1% of the seeds did not have an embryo. Therefore, the seeds we selected for the different analyses (weight and germination) were in good condition (without physical damage) with 99% viability. The 3 years differed significantly in both germination variables evaluated (GC: $F=96.08$, $p<0.01$; GS: $F=45.41$, $p<0.01$; Table 3). Both GC and GS values had the best results in the year with a high cone production level (2013).

Discussion
The 3 locations studied showed a trend toward synchrony in the production of cones, that is, when production increased, we observed the increase in all 3 locations independent of the number of cones. When production decreased, we recorded a reduction in cone production in all locations. Other authors confirmed this pattern, concluding that *A. araucana* has a high variability in annual cone production (Sanguinetti and Kitzberger 2008, 2009; Sanguinetti 2014). We explained this pattern with the hypothesis of the economy of scale, where by concentrating reproductive efforts in a few events is more efficient (Silvertown 1980; Bogdziewicz et al. 2020; Ascoli et al. 2021; Zhang et al. 2022). We know that the costs of reproduction are defined in terms of losses in potential future reproductive success that current investments in reproduction causes (Seget et al. 2022). If resources are limited, the organisms can only acquire a limited number of resources and energy for which processes compete directly, and an increase in energy allocated to one must then result in a decrease in energy allocated to the others. This is the principle of allocation (Levins 2020), by which plants have to distribute energy in direct costs (somatic costs of reproduction during the current reproductive season) and indirect costs (demographic consequences of resource investment in the reproductive process such as mortality rate and frequency of future reproduction). Other authors have found differences in the variability in costs of reproduction due to habitat (Biere 1995; Hemborg and Karlsson 1998). Therefore, the costs of reproduction would be most apparent in habitats with low resource availability or other stress conditions (Wion et al. 2020). These data are particularly interesting because they reveal the role of environmental factors in costs of reproduction expression in some patterns (Biere 1995; Wion et al. 2020).

Table 2 Number of seeds per cone and per kilogram in the 3 years of the study

Production level of cones (year)	Number of seeds per cone			Number of seeds per kilogram		
	Mean	Maximum	Minimum	Mean	Maximum	Minimum
Low (2012)	150 A	206	103	297 A	473	193
High (2013)	117 B	208	53	305 A	475	190
Intermediate (2014)	83 C	141	36	420 B	538	261

Different letters indicate significant differences between years by the Tukey test ($p \le 0.05$).

Depending on several factors, after years of low and intermediate production of cones, *A. araucana* had an intense reproductive year in 2013, significantly higher than in 2012 and 2014. The quantitative method of standard deviation was applied to all datasets. As indicated by LaMontagne and Boutin (2009), 2013 was classified as a masting year because the calculated long-term value per location was much higher than the absolute value of the lowest long-termper location (Fig. 2B). According to the previous method, 2007 was classified as a masting year for the locations of Quinquén and Mallín del Treile, but not for Cruzaco.

Mast seeding (masting) is a common reproductive strategy exhibited by some species of perennials (Yang et al. 2020), defined as the synchronous production of seeds at irregular intervals by a plant population (Silvertown 1980; Herrera et al. 1998; Koenig and Knops 2005). Among tree species, synchronous alternate seed production is well described (Herrera et al. 1998; Koenig and Knops 2005; Hacket-Pain et al. 2018), although the intervals between masting years can also be highly irregular (Silvertown 1980). Hadad et al. (2021) reported synchrony in the *A. araucana* forests, where we observed great cone production in 2013. Other studies showed a similar reproductive pattern in *A. araucana* from other areas. In the National Park Lanín (Argentina), in 2000, 135 ± 8 seeds cone^{-1} were produced (high production), followed by 90 ± 12 seeds cone^{-1} in 2001 (intermediate production) (Sanguinetti 2014). In addition, 2007 was a high cone production year, followed by a significant drop in 2008 (Sanguinetti and Kitzberger 2008), a similar trend was observed in this research.

Differences in cone production between locations may be because of factors such as topography, forest structure, tree size/age and the composition of forest species (Obeso 2002; Lizana 2009; Sanguinetti 2014), but mast seeding events could display patterns like high temporal variability and high synchrony in seed production among individuals of a population (LaMontagne and Boutin 2009; Liebhold et al. 2004a; Ostfeld and Keesing 2000). For instance, if more daylight reaches its crowns, *A. araucana* trees produce more cones (Lizana 2009; Sanguinetti 2014). The higher cone production we found in Cruzaco and Mallín del Treile could be the result of more open canopy than in Quinquén. Liebhold et al. (2004b) suggested that the spatial variation in mast years between plots and variability in individual synchrony could reflect varied habitat conditions.

A classic example of large variability in reproductive output is the masting of tree species and the responses to seed-eating species that present eruptive behavior when exploited as a food source (Speziale et al. 2018). Among tree species, synchronous alternate seed production is well described (Herrera et al. 1998; Koenig and Knops

2005), but intervals between masting years can also be highly irregular (Silvertown 1980). The reproductive cycle of *A. araucana* takes almost 2 years. In the same year, a tree can display mature cones and produce new cones that will reach maturity the following year (Lizana 2009). *A. araucana* cones have 55% of their weight in woody tissue (Sanguinetti and Kitzberger 2008). Seeds are composed of approximately 96% carbohydrates, while the remaining 4% is made up of other elements such as lipids and proteins (Henríquez et al. 2008). Therefore, the formation of reproductive structures implies high energy expenditure in the tree. This would explain why after an extremely high production of cones, as was the case in 2013, the following year's cones were smaller and produced fewer seeds, despite producing more cones than in 2012.

The limited resources hypothesis proposes that fruit and seed production is limited by available resources (Obeso 2002; Journé et al. 2023). In the case of anemophilous species such as *A. araucana*, reducing the number of seeds per cone and their cost (seed weight) allows them to achieve maximum reproductive efficiency (Journé et al. 2023). This would explain the low number of seeds per cone and the number of seeds per kilogram observed in 2014. Hadad et al. (2021) found in *A. araucana* a negative trade-off between tree ring width and cone production in mast years, as observed in this research with high seed production (2013). In this particular year (2013), the formation of immature cones had fewer resources for seed formation, and this is reflected in the lower number of seeds and smaller seeds as well as lower GC and GS values observed in 2014. Seed size (and weight) seems essential to the survival of seedlings in early stages in sites under environmental stress (Lusk et al. 2006; Sanguinetti and Kitzberger 2009); high energy expenditure in 2013 should thus have consequences for population recruitment.

Parameters such as GC and GS are good indicators of seed quality and germination throughout the years with different cone production. In our study, in the year of high production (2013), both GC and GS had higher values than in the other 2 years (Table 3). Similar results were found in *Abies alba* Mill. in a mast year with better seed quality and higher germination potential compared to lower fruiting years (Milesi et al. 2017). In 2014 we found the lowest GC and GS values. This could be related to previous high reproductive efforts (2013) that influenced the development of seeds, decreasing their GC and GS. According to Gutiérrez-Soto (2023) report, seed weight is closely linked to the viability, germination, and vigor of seedlings in certain oak species. Duplancic et al. (2015) concluded that smaller seeds of *A. araucana* are less adapted to stressful conditions, and therefore, its GC in the field would be lower. All these results point out

that a high reproductive effort in mast years considerably decreases resources available for subsequent reproductive events. This implies smaller seeds with less germination potential, as we observed in 2014 in the *A. araucana* forests. However, and as mentioned by Bogdziewicz et al. (2020) masting events are beneficial for this and other species that reproduce especially by anemophily, since increasing the density of cones produces an increase in pollination, and therefore, a lower number of cones with empty seeds. Understanding the relationship between the quantity and quality of the seeds and the plant energy expenditure is a key element in estimating production of cones and consequently the potential for human extraction of pine nuts under sustainable use of these forests (Donoso et al. 2010; Sanguinetti 2014). Pine nuts are an important component of the human diet of those living around the forest. Additionally, wild fauna and domestic cattle consume the nuts (Aagesen 1998; Lizana 2009). A gathering family of 3 adults can harvest a sack of 65 to 85 kg of pine nuts per day. In a highly productive year, families can harvest near 2500 kg of pine nuts (Cortés et al. 2019). This consumption negatively influences the natural population recruitment of *A. araucana* (Donoso et al. 2010).

Synchronous cone production is well described for *A. araucana*, however the time interval between the different masting events is not yet known. It is certainly true that the long-term stability of forests depends on the reproduction of trees, which generates the next generation of plants and determines the composition of future communities. The information obtained allows us to understand that years with intermediate cone production have the lowest CG and CS; therefore, it can be inferred that maximum production events (masting) could be the main source of sexual reproduction. It is even more important in the context of global climate change to understand whether reproduction can balance increased mortality (Senf et al. 2021). Our results undoubtedly allow a better understanding of the regeneration process of *A. araucana* forests and could improve the sustainable use of seeds and actions for the conservation of this species.

Conclusions

Production of cones per hectare was synchronous in all 3 studied locations. *A. araucana* is a mast species with years of great reproductive output with high energy expenditure, followed by years of decreased production of fruits and seeds. Compared to a year with lower fruit production, the cones in the higher reproductive year bear fewer seeds but with similar weight. In a year of high production, the cones have fewer seeds per cone than in a year of low production, but the seeds have a similar weight. In our study, in the year 2014 (intermediate production), the cones carried fewer and smaller seeds. This is possibly the consequence of the high energy expenditure of the previous mast year (2013), which left fewer resources available for reproductive investment. GC and GS are related to seed weight but not to the number of cones produced in a given year. In other words, seeds of lower weight are less likely to germinate, thereby affecting population regeneration. These annual fluctuations in seed production determine the population dynamics of forest species, and understanding these processes is important to managing the sustainable human use of these resources.

Abbreviations
ANOVA   Analysis of variance
GC   Germination capacity
GS   Germination speed

Supplementary Information
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> Supplementary Material 1

Author contributions
SD and KPR contributed to the research, conceptualization, and methodology. CE and CB analyzed and interpreted the data. RSM and ACA contributed to writing the original draft. All authors read and approved the final manuscript.

Data availability
The datasets used and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

Authors' information (optional)
No additional information.

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