



Daily, seasonal, and interannual variability of airborne pollen of *Araucaria angustifolia* growing in the subtropical area of Argentina

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Abstract *Araucaria angustifolia* is an anemophilous conifer native to Southern America threatened with extinction, with a noticeable decrease in its distribution area and seed production. To better understand the reproductive dynamics, the aerobiological curves obtained with Hirst methodology were analyzed during 7 years in San Antonio (Misiones, Argentina), including productivity, seasonality, start, end, duration, and peak, along with the role of meteorological/seasonal climate factors. An alternation between 1 year of high pollen values (1685 pollen grains day⁻³, on average), followed by 2 years of a progressive reduction (456 pollen grains day⁻³, on average) in productivity, was observed. This pattern was negatively related to temperature during the month preceding pollination; August minimum

temperature yielded the best fit (correlation coefficient $r = -0.9$, $p < 0.01$). In only 36 days, including October, 90% of the annual pollen was released. The daily pattern showed a curve with higher concentrations between hour 8 and hour 14. The daily maximum at hour 10 suggests pollen inputs from local sources. The eolic transport is limited due to the big size and weight of the grains and the unfavorable atmospheric conditions that prevail in this subtropical forest (high humidity and low wind speed). The average airborne pollen curve showed a peak during the second fortnight of October. Rain induced a noticeable reduction in pollen concentration modifying the shape of the aerobiological curve. Aerobiological analyses provide reliable information for the design of conservation strategies, such as ex situ planting and selective harvesting of seeds.

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1 Introduction

Araucaria angustifolia (Bert.) O. Kuntze is a dioecious conifer native to southern Brazil and northeastern Argentina. It has become a critically endangered species in its natural forests during the last century due to its indiscriminate exploitation for the high economic value of its timber (Thomas 2013). Its natural

distribution area has decreased, and its forests account for only 3% of its area of origin. This has generated a connectivity reduction between the population remnants, which has led to a decrease in the genetic diversity and thus limited natural regeneration. Reforestation management has been severely restricted as a result of the progressive decrease in the volume of seed harvest during the last years in Misiones, Argentina (Fassola et al. 1999).

Pollination is the phenologic phase necessary for fertilization and seed formation, which occurs 18 months later. The limitation for the reproductive success may be associated with the low number of pollen grains available for fertilization and thus the low cross-pollination ratios. If fertilization is limited or diminished, a smaller number of seeds will be produced. This direct relationship between pollen production and seed production occurs mainly in woody plants (Cour and van Campo 1980). On the other hand, variations in temperature and climate generally affect and modify plant response, especially regarding their reproductive capacity (Newnham 1999). Airborne pollen variations (daily, annual, and pluriannual or cyclic) are bioindicators of the organisms' response to the climate and environmental conditions where they live (Luomajoki 1993; Majeed et al. 2018). In particular, pollen productivity is mainly associated with the seasonal climate conditions preceding the emission phase, temperature being one of the key variables involved (Emberlin et al. 1993; Menzel et al. 2006; Newnham et al. 2013). Global warming seems to be persistent and progressive (IPCC 2001–2007), and, in northeastern Argentina, it follows this same trend (Villalba et al. 2014). This makes *A. angustifolia* especially vulnerable, even more so in the light of the change in land use that has occurred in the last 50 years.

In a preliminary 2-year study conducted, a significant decrease in the number of sporophylls of *A. angustifolia* plants growing in Misiones (Argentina) was identified during the years in which the average temperature during its formation was higher (Fassola 2005). Simón et al. (2018) compared the pollen productivity of plants growing under two different environments: in their natural area with a warm climate and in a temperate region. They noticed significant differences that allowed to conclude that this reproductive phase was favored by the colder winters registered in the temperate area. Based on the

foregoing, a negative effect of high winter temperatures on the number of pollen grains produced in the male *A. angustifolia* catkins, which are then released into the air, was postulated. Seed production after a low-pollen-production year will be scarce due to the limited fecundation ascribed to the reduction of reproductive material that reaches the female cones. The characterization of the reproductive cycle comes from Brazilian populations (Anselmini et al. 2006), where the species grows in relatively high areas with cooler winter temperatures in relation to those in Argentina. To learn about the phenological dynamics of pollen production/release of *A. angustifolia* in Misiones (Argentina), the main characteristics of the aerobiological curve during its reproductive cycle were analyzed, including intensity (amount of pollen produced/released), seasonality, start, end, duration, and peak. To explain the interannual variation of the reproductive phases, pollen values were related to the previous seasonal climate conditions as well as to the prevailing weather during the pollen season in Misiones (Argentina) for 7 years.

Long-term airborne pollen monitoring data provide relevant information on the vulnerability of the species in response to the environmental changes (Fernández-Llamazares et al. 2014). Thus, the aerobiological analysis can be considered as a climate indicator (Schwartz 1999). If the production of reproductive material decreases in a progressive fashion in this species, the possibility of implementing ex situ conservation should be considered (Simón et al. 2018).

2 Materials and methods

The studies on the aerobiology of *Araucaria angustifolia* were carried out in Manuel Belgrano Field (Campo Anexo Manuel Belgrano, CAMB) in San Antonio, Misiones, Argentina (Lat. S 26° 3', Long. W 53° 46', 544 m.a.s.l.). The climate is humid subtropical with precipitations all the year round (Burgos 1970), ranging from 1700 to 2400 mm (mean 1981–2010: 2050 mm). November is the driest month. The mean temperature (1981–2010) is 21 °C; 25 °C in summer (January, February, and March) with maximum temperatures of 39 °C, and 16 °C in winter (June, July, and August) (Servicio Meteorológico Nacional 2010).

Aerobiological monitorings were performed throughout the pollination period (from August to

December) (Latorre et al. 2013) for seven consecutive years (2010–2016). A continuous and volumetric pollen sampling trap (Hirst 1952), located 15 m above the ground in an open area (Hicks et al. 1996), was used. The CAMB represents one of the largest plantation areas of *A. angustifolia* in Misiones Province, and, according to Moscovich et al. (2006), there are about 400 ha where ages over 60 years prevail. Approximately 30 years ago, due to the lack of management strategies, tree mortality occurred and a silviculture plan was implemented. Currently, the average density of mature stands is about 200 stems per ha (Fig. 1), with heights ranging from 20 to 30 m. The whole area surrounding the CAMB, both in Argentina and Brazil, is destined to agricultural production with small patches of primary *A. angustifolia* forest with trees around 200 years old.

The microscopic analysis was performed along vertical lines every even hour: H2, H4, H6, H8, H10, H12, H14, H16, H18, H20, H22, and H24. Daily pollen concentrations, expressed as the number of pollen grains registered per air volume (m^3), were calculated (Rogers and Muilenberg 2001). For longer periods (week, month, year), the pollen integral (PI) was used and obtained by adding up the average daily

concentration over the given period of time, and it was expressed as pollen day m^{-3} (Galán et al. 2017).

In order to learn about the yearly pollen dynamics and establish the aerobiological pattern, concentration variations were analyzed along time. The amplitude and magnitude of the pollen season were determined, along with the characteristics and seasonality of its main phenophases: start, peak, and end. These parameters were considered for both the pollination period (PP) and the principal pollination period (PPP). PP extends from the day on which the first pollen grain is registered to the day on which the last grain of the year is recorded (Latorre and Belmonte 2004). PPP covers between 5 and 95% of the total accumulated pollen (Nilsson and Persson 1981).

Climate statistics were calculated from the meteorological data given by the National Meteorological Service. In situ data were provided by the INTA meteorological station (Fig. 1). The variables used were mean, maximum and minimum temperatures (T_m , T_{mx} , and T_{mn} , respectively), precipitation, relative humidity (RH), and wind speed (VV).

Basic statistics of different variables were calculated (mean, dispersion, median, range, and the coefficient of variation calculated as a percentage of the rationale between the dispersion and the mean).

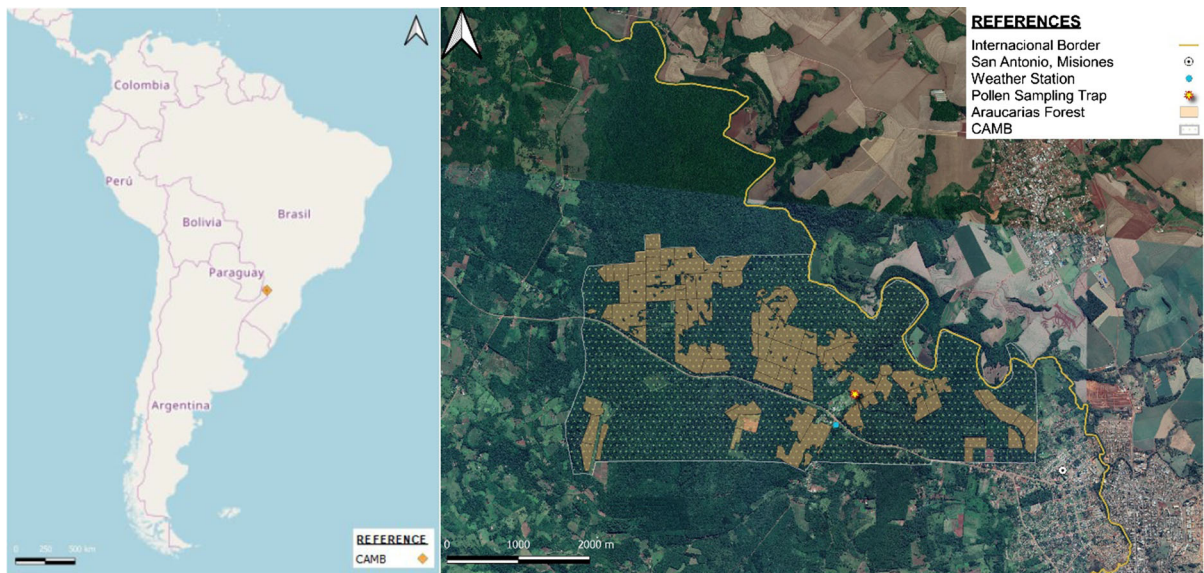


Fig. 1 Location of the study site. The Manuel Belgrano Field (Campo Anexo Manuel Belgrano, CAMB) in San Antonio (Misiones Province, Argentina) belongs to INTA (National Institute of Agricultural Technology). The meteorological

station is located near the pollen trap within the study site (National Geographical Institute <http://www.ign.gob.ar> and Google Earth)

Simple linear analyses were performed between different pollen season features. Pearson coefficients of correlation (r) were calculated between atmospheric pollen and weather conditions previous to PP start and during PPP in order to detect the effect on pollen production/dispersion aerobiological processes. Linear regression analyses were performed between pollen as a dependent variable and different previous seasonal weather as an independent variable, selecting a different variable each time. The purpose of this analysis was to explain the interannual variations observed and establish the main critical condition for pollen production. Daily pollen concentration data (p) did not yield a normal distribution, so data normalization was necessary to apply statistical tools, which presupposes linear associations between variables (Recio et al. 1996). To normalize data, the following transformation was used: $\ln(p + 1)$. The daily scale analysis of pollen data with meteorological variables during the PPP period was performed using the average of Tm, Tmn, and Tmx from the months preceding pollination: August, July, June, and the winter period (from June to August). Cluster analyses using Ward's method and squared Euclidean distance were performed to determine groups with similar features (STATISTICA, StatSoft, Inc. 1996).

3 Results

3.1 Pollen productivity

An alternation pattern between 1 year of high pollen values (2010, 2013, and 2016 with an annual pollen integral API of 2150, 1572, and 1332, respectively), followed by 2 years of progressive reduction in intensity (API between 48 and 964), was determined from the aerobiological *A. angustifolia* data collected in Misiones. The 2 years of low production showed the same trend: the first one recorded more pollen than the second one. In 2011, pollen was reduced by 73%, and, in 2012, by 98%, as compared to API 2010; in 2014, by 39% as compared to API 2013, and in 2015, by 85% (Fig. 2).

Based on the cluster analysis conducted, a scale of pollen productivity was established. In this way, the following was defined: (1) years with high pollen values: when the sum of the daily concentrations during pollination exceeded 1000 pollen grains

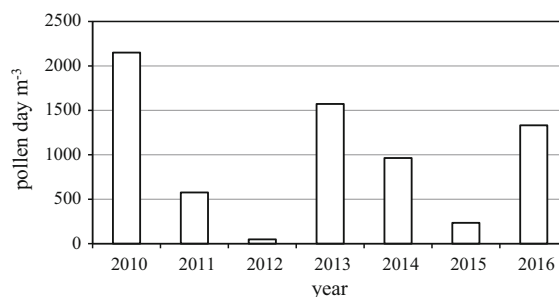


Fig. 2 Annual pollen integral (sum of daily airborne pollen concentrations) in San Antonio (Misiones, Argentina) recorded with a continuous volumetric sampler during the entire pollen period of *A. angustifolia* every year of the studied period

day m⁻³ (group A in Fig. 3), and (2) years with low pollen values: when daily concentrations added up to 1000 grains day m⁻³ or less (group B in Fig. 3). Also, group B was divided into two subgroups based on a pollen production higher than 500 grains day m⁻³ (years 2011 and 2014) or lower than 500 grains day m⁻³ (years 2012 and 2015).

3.2 Pollen season

The PP covered the period September–December and lasted between 2 and 3 months and a half month, depending on the year. Ninety percent of the pollen was released in a short period of time of about 30 days; high productive years were 26 days shorter on average if compared to years of low pollen value. In high productive years, PPP started earlier than in the 2 years after it. The main pollination month was October, during which the maximum pollen concentration occurred, except in 2012 when the maximum concentration was registered at the end of September.

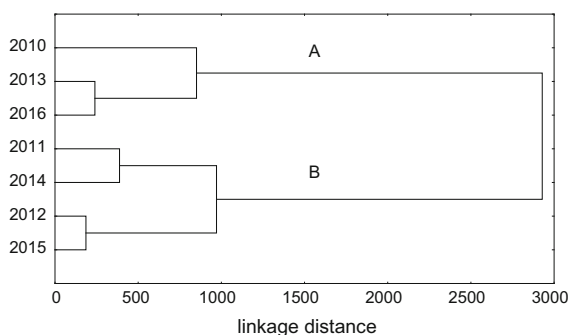


Fig. 3 Cluster analysis performed with the annual pollen integral of *A. angustifolia* data obtained in San Antonio

On average, the maximum daily concentration represented 14% of the API, and until that day, more than half of the API was accumulated, except in 2012 when it only reached 23%. The scarce 48 grains obtained in 2012 were recorded during one of the longest periods, lasting more than 3 months. Days without pollen within the PPP were scarce reaching a low percentage between 0 and 15% within PPP, while in 2012 it was 56% (Table 1).

When the relationships between the different pollen season features were analyzed, it was found that the higher the API, the higher the maximum daily concentration ($r = 0.96$, $p = 0.001$) (Fig. 4a); also an early start of PPP was related to an early maximum ($r = 0.81$, $p = 0.027$) (Fig. 4b). On the other hand, a delayed start of PPP was related to a shorter principal pollination period duration ($r = -0.69$, $p = 0.088$) (Fig. 4c). In turn, a delayed end of PPP was associated with a longer PPP ($r = 0.76$, $p = 0.047$), regardless of PPP start date (Fig. 4d). Since 2016 differed (was outside the confidence limits), these last two non-significant relationships were recalculated without including it. By so doing, those correlations now yield significant values ($r = -0.89$, $p = 0.016$ and $r = 0.84$, $p = 0.035$ for start and end, respectively, in relation to PPP duration).

3.3 Intradiurnal distribution of pollen concentration

When the hourly pattern of *A. angustifolia* airborne pollen was analyzed, a progressive increase from the early morning (H8) to H14 was noticed, after which, it began to decline (Fig. 5a). Between H8 and H14, 48% of the daily total was collected (group A in the cluster analysis, Fig. 5b). The lowest coefficient of variation between years ($CV = 8\%$) was registered at midday (H12), while at night, H22, H24, and H2 accounted for the highest variability ($CV = 45\%$) and were gathered in group B of the cluster analysis (Fig. 5b).

The maximum pollen value was set at H10 with an average of 15% of daily total, except for 2012 (year with the lowest API) when the maximum value was recorded at H12 with a first peak at H8. In 2012, a different pattern of intradiurnal distribution was observed. In the cluster analysis (Fig. 5c), 2012 is shown separately from the other years from in group B. In 2012, high pollen rates were recorded at night: 10% in H24 and 10% in H2, and no significant associations were observed with respect to any other year; the closest relation ($r = 0.61$, $p = 0.035$) was noticed in 2010 in which a peak of 11% was also registered at H2. Group A of Fig. 5c comprises the daily concentration patterns from 2014 and 2015. The highest ranges of variability during the day (values between the maximum and the minimum) were

Table 1 Pollen season features of *A. angustifolia* in San Antonio (Misiones, Argentina)

Year	2010	2011	2012	2013	2014	2015	2016
Annual pollen integral	2150	576	48	1572	964	234	1332
Start of PP (first day with pollen)	9 Sep	15 Sep	7 Sep	10 Oct	12 Sep	24 Sep	13 Sep
End of PP (last day with pollen and 10 consecutive days without pollen)	25 Dec	29 Dec	20 Dec	6 Dec	16 Dec	18 Dec	25 Dec
Number of PP days	108	106	102	58	96	86	104
Maximum day	14 Oct	17 Oct	26 Sep	28 Oct	25 Oct	30 Oct	13 Oct
Maximum concentration (pollen m ⁻³)	293	69	5	251	131	52	119
Accumulated percentage up to maximum	54	54	23	64	71	60	70
Number of days up to maximum	36	33	20	19	44	37	31
Start of PPP (5%)	5 Oct	3 Oct	22 Sep	20 Oct	04 Oct	16 Oct	27 Sep
End of PPP (95%)	04 Nov	12 Nov	19 Nov	7 Nov	24 Nov	12 Nov	24 Oct
Number of PPP days	31	42	55	19	52	28	28
Days without pollen during PPP	1	3	31	0	8	1	0

PP pollination period, PPP principal pollination period

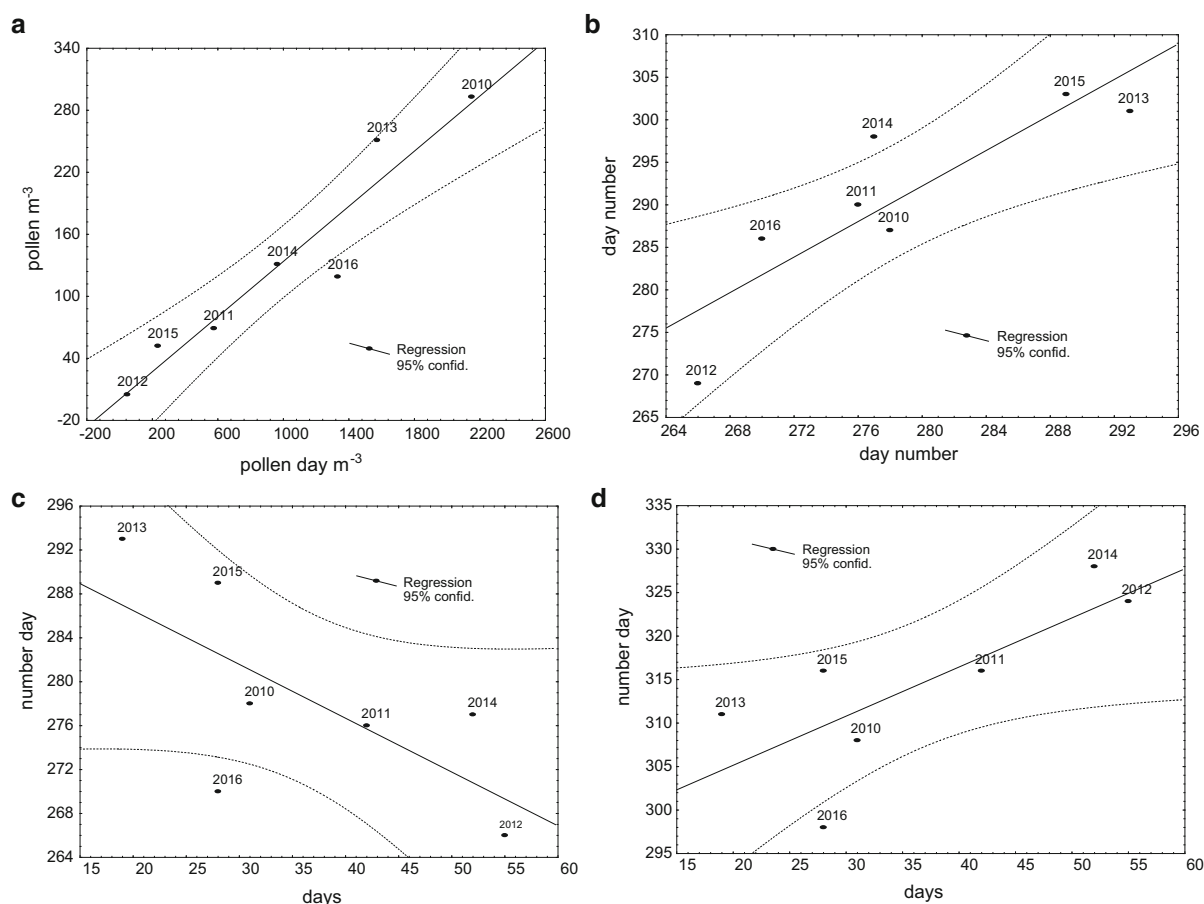


Fig. 4 Relationship between pollen season features: **a** total annual versus maximum concentration, **b** PPP start versus maximum concentration, **c** PPP start versus PPP duration, **d** PP end versus PPP duration

obtained during these years (Fig. 5d), with a secondary peak at H20. The correlation between years for each hour was high and significant ($r = 0.72$, $p = 0.008$).

3.4 Weekly pattern

The maximum pollen counts were registered in the second fortnight of October during which 50% of the average annual pollen was recorded. The average weekly concentration peaked on these 2 weeks: 42 and 43.

Differences in this mean weekly pattern were observed in 2011 and 2012, where two peaks of high pollen sums were registered (bimodal type). The weekly sums of daily concentrations are represented in Fig. 6, along with precipitations. This meteorological variable was considered a priori as the number one

factor that triggered interannual differences. In 2011, the sharp decrease at week 44 was attributed to the 107 mm of rainwater that fell between the peak and the end of PPP (85 mm at weeks 43 and 44); in that same period of 2012, 419 mm was recorded. During week 42 of year 2016, 112 mm of water was recorded, though the slight decrease in airborne pollen had occurred in the previous week. The patterns corresponding to years 2010, 2013, 2014, and 2015 were of the ordinary type.

3.5 Meteorological conditions during the pollination period

Pollen concentrations during PP were not significantly associated with any meteorological variable, though they were during PPP.

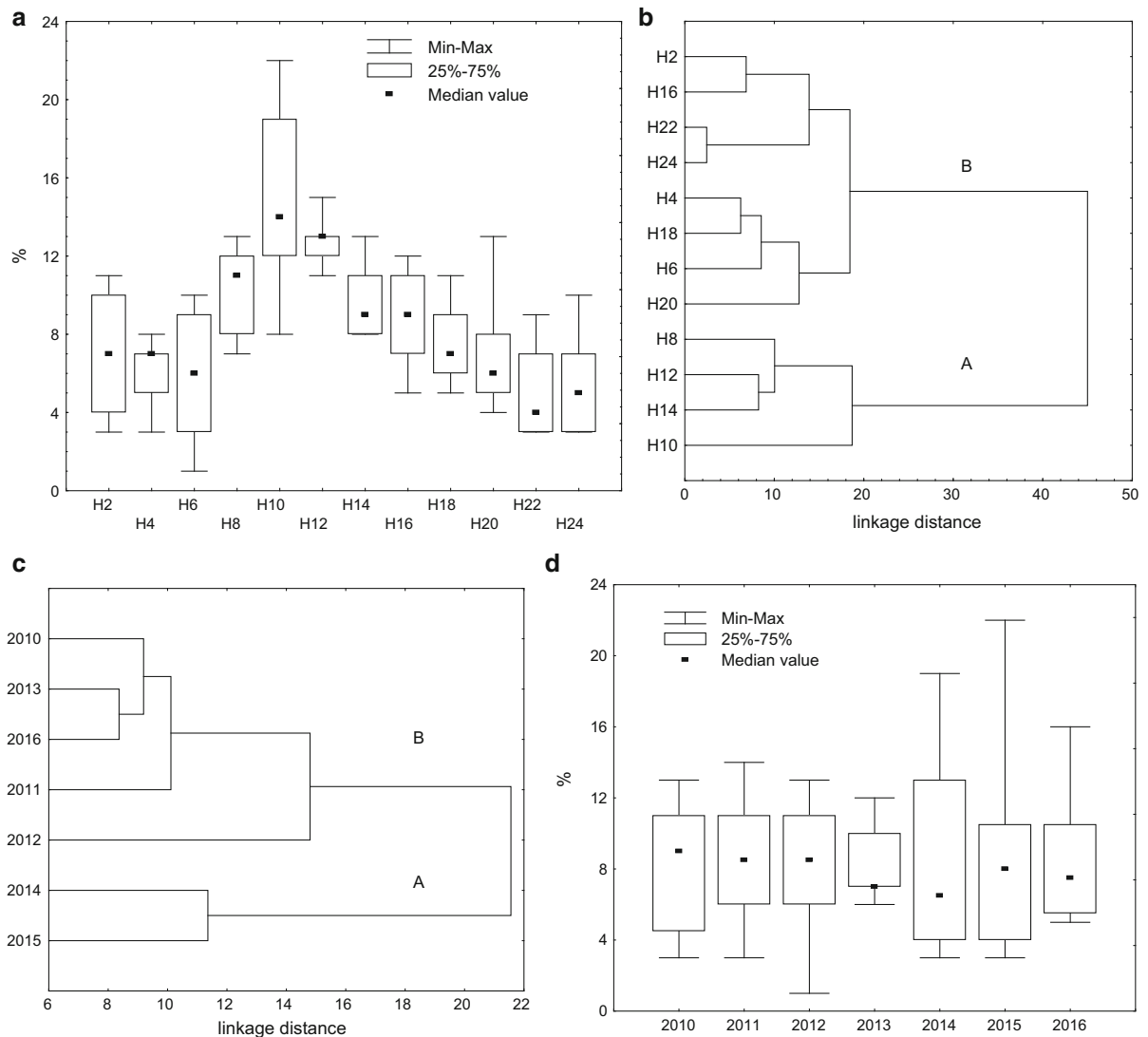


Fig. 5 Distribution of pollen concentration of *A. angustifolia* throughout the day. **a** Bi-hourly interannual variation from 7 years, **b** hour clustering according to years, **c** years grouped

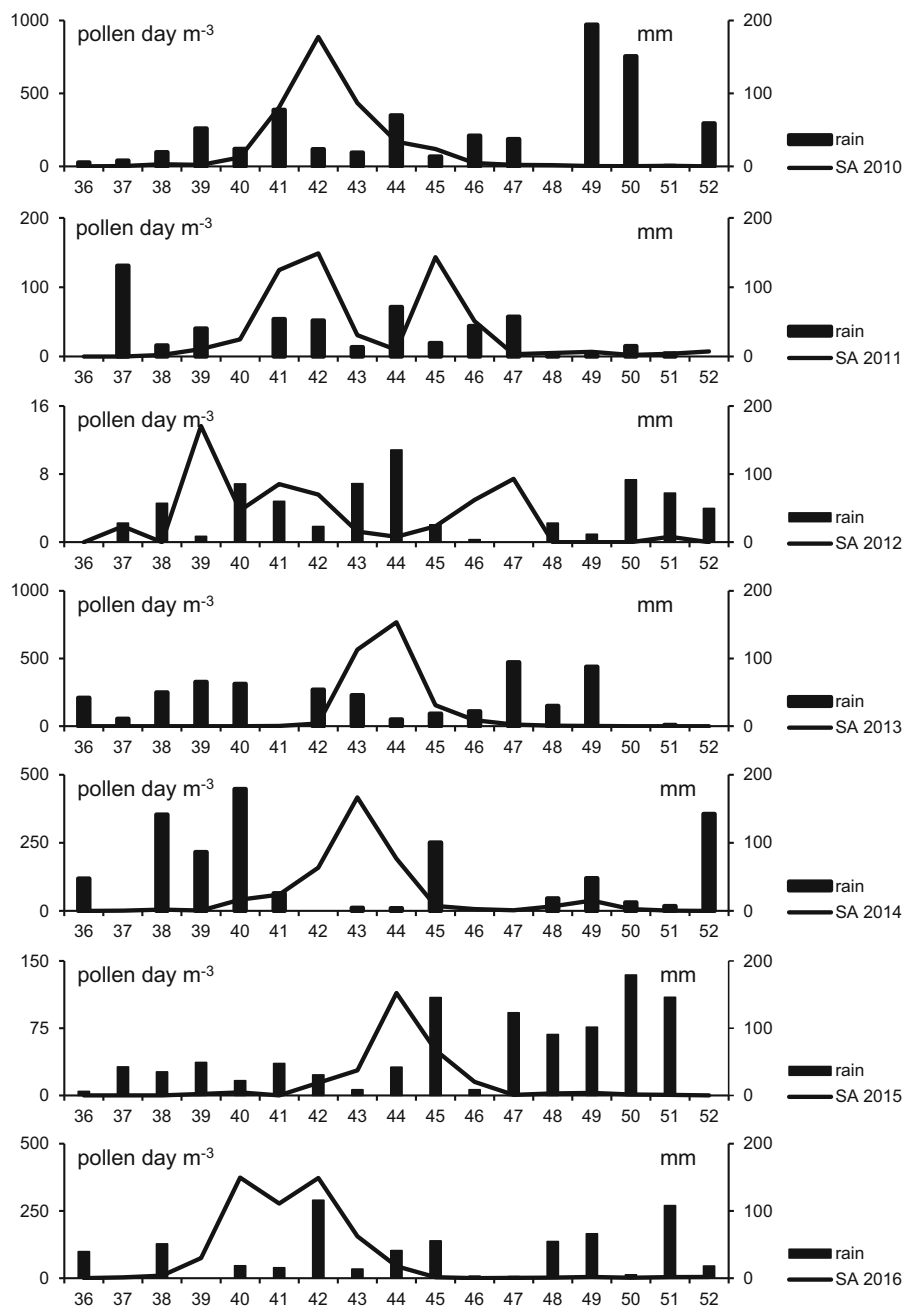
according to diurnal variation, and **d** intradiurnal variation each year. **a**, **d** y-variable: pollen percentage; **b**, **c** grouping variable: hourly percentage of total pollen

Annual pollen sums during PPP correlated negatively with precipitations, though in a nonsignificant manner ($r = -0.65$, $p = 0.11$). On average 31% of the days during this period were rainy (between 17 and 46% depending on the year). During 2012, the year with the lowest API value, 40% of the days during PPP were rainy. Precipitations during the 2012 PPP totaled 428 mm, a value that doubled the water mean during the other years (266 mm more than average). On the other hand, rains were similar in years with opposite API values, like in 2010, with high

pollen counts and 2015 with low pollen counts. Throughout these years, rains accounted for 209 mm and 190 mm, respectively, during the PPP (Fig. 7).

More than half of the days during PPP were non-rainy (69% on average). If only those dry days are considered, the relationship between pollen and HR and that between HR and VV are opposite and significant ($r = -0.17$, $p = 0.024$ and $r = -0.26$, $p = 0.001$, respectively).

Fig. 6 Weekly sums of pollen concentrations and precipitations during the pollination period each year. SA San Antonio



3.6 Temperatures prior to pollination

Among the preceding monthly temperatures tested, August temperatures were shown to be the most correlated with pollen. In years with a pollen value higher than the mean (2010, 2013, and 2016), the maximum temperature of August was lower than the average of the analyzed period (25 °C).

The historical average (1986–2009) of mean temperature corresponding to August was 17 °C, and its variation range fluctuated between 16 and 18 °C. In years with minimum pollen values (2012 and 2015), the average mean temperature of August was higher than the historical values (Fig. 8).

Annual pollen showed a stronger correlation with August minimum temperature ($r = -0.91$, $p < 0.01$)

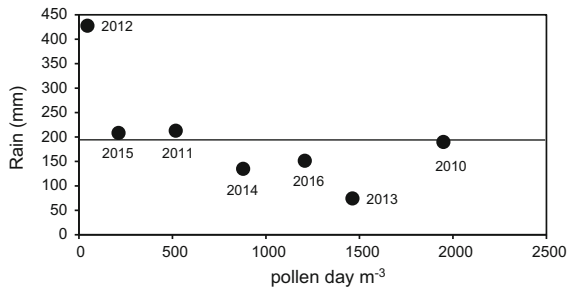


Fig. 7 Sum of pollen concentrations and rains during the principal pollination period (PPP)

in relation to the maximum and mean temperatures of that same month previous to the pollination period. So this meteorological variable was then used to establish a preliminary predictive equation. The adjustment to a predictive equation was successful in 80% of the cases, and the resulting regression formula was: $API = 4795 - 363 T_{mn} \text{ Aug}$ ($p = 0.004$) (Fig. 9).

4 Discussion

The aerobiological analysis of *A. angustifolia* in Misiones (Argentina) during 2010–2016, supported by the cluster analysis conducted, allowed to establish a triannual pattern of pollen productivity with a cycle that alternates between 1 year of high pollen values (when the sum of the daily average concentrations during pollination exceeded 1000 pollen grains days m^{-3}), followed by 2 years with progressive low pollen values (when the average annual daily concentration added up to 1000 pollen grains days m^{-3} or less). This pattern was repeated twice, confirming the beginning of a third cycle. The difference in the total

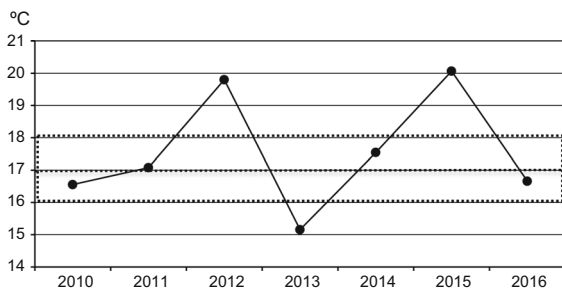


Fig. 8 Interannual variation of the mean temperatures of August prior to pollination. Dotted line: August mean temperature from the last 30 years (17 °C) and the range of one standard deviation

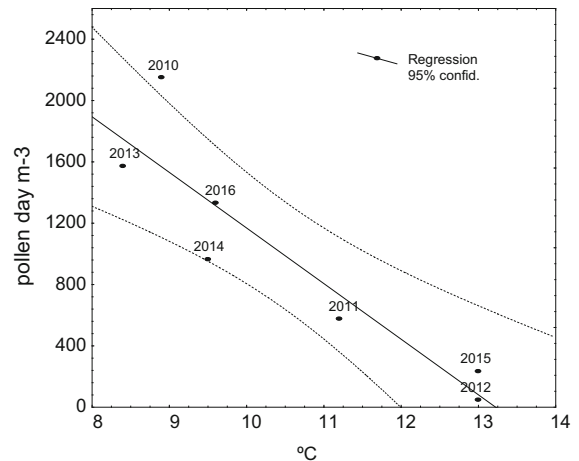


Fig. 9 Annual pollen integral versus minimum average temperature of August

pollen index between one productive year and the other two was 74% on average. This annual pollen intensity pattern of one cycle every 3 years coincides with the alternance in the seed harvest described by Mattos (1994) and by Bertolini (1999), so the effect of the previous climate seasonal conditions as a determining factor deserves greater consideration. Results from other species, such as *Pinus nigra* (Tíscar Oliver 2009), are not conclusive to attribute this pattern to a cyclic event inherent to the physiology of the species and, to a certain extent, independent of the environment. On the contrary, in this work, a weather influence on the reproduction of *A. angustifolia* was established: the temperature of the month prior to pollination was the most relevant factor determining the intensity of this phenological event. The maximum and mean temperatures of August, higher than the historical average, were related to low pollen indexes, lower than the average value. The variable that best explained the interannual variation observed was the minimum temperature of this month just before pollen release: the lower the minimum temperature in August, the higher the pollen value recorded in that year. This preliminary statistical model for estimating pollen productivity based on August minimum temperature will allow to predict well in advance whether a year with high possibilities of fertilization may follow, and so, whether a greater number of seeds will be yielded 20 months later. This model should be adjusted with subsequent years' data. The reproductive cycle of the species is very long; seeds result from

the successful fertilization taking place 2 years before (Anselmini 2005). Previous results support the hypothesis of a negative effect of high winter temperatures on the reproductive phenophase. A comparative study of the annual pollen productivity of *A. angustifolia* from two climatically different regions of Argentina (subtropical vs. temperate) revealed that significant differences between sites were associated with differences in August temperature (Simón et al. 2018).

Pollination seasonality of *A. angustifolia* in Misiones (Argentina) was similar between years and took place in the last 4 months of the year. Ninety percent of annual pollen was released in only 36 days including October. Some pollen season features showed differences between highly productive years and those of low API. For example, the start of PPP was anticipated in years with more pollen amounts because of the favorable meteorological conditions for pollen emission and dispersion, and its duration shortened probably owing to the synchronization between trees due to the favorable conditions during the reproductive development. On the contrary, 2012 yielded the lowest pollen production values and the longest PPP, with many days without airborne pollen grains. A long period of pollen emission with a low API along with several days without pollen grains in the air within the PPP, as it occurred in 2012, could be disadvantageous for the fertilization process, since the pollen receptivity period of female cones lasts few days and does usually exceed a week (Pallardy 2007). An aerobiological study carried out by Latorre et al. (2019) using Hirst methodology showed that the API from this species in a temperate climate was four times greater than the API produced in its subtropical natural area of San Antonio. However, its PPP lasted half of the days and such fertilization period resulted, 20 months later, in six times more seeds. Once pollen is discharged, it does not remain suspended for a long time (see below). Therefore, an intense pollen production would, in principle, be better than a less productive and longer period. Indeed, further studies should be conducted to support this statement. The maximum values in 2012 were registered in September, while the peak of the other yearly curves occurred in October. Direct relationships were observed between API and maximum concentration, and between the start of PPP and the day on which the maximum was registered. The year 2016 was

somewhat different, because its PPP duration was shorter than expected by the starting/ending PPP date, probably due to the intense rain that fell the week after the maximum concentration occurred.

The daily pattern of pollen concentration increased from H8 to H14 when the decline phase started. The curve peak in the first half of the day was in line with the aerobiological records from other conifers, such as Cupressaceae (Latorre and Caccavari 2009). This was interpreted as an indicative feature of several sources that lie at a short distance (Galán et al. 1991). To support this, Latorre et al. (2014) verified the scarce dispersal capacity of *A. angustifolia* pollen and they attributed it to its substantial size and weight (Caccavari 2003). Pollen wind-dispersal studies carried out by Latorre (2018) with portable Hirst spore traps at different distances from the forest boundary and in the direction of the prevailing winds confirmed the short distance travelled by pollen; 60% of the pollen released reached a distance of as much as 100 m, and 90% of the pollen fell before 200 meters. Limitation in wind pollination was also inferred from a parentage analysis conducted by Bittencourt and Sebbenn (2008) in a Brazilian forest. Also, even if the increase in temperature and the decrease in relative humidity at midday favor the release conditions (Recio et al. 1997), and wind dispersal occurs under turbulent atmospheric conditions (Käpylä 1984), in wooded areas like the one studied here, wind dispersal is limited to the particular microenvironment within the forest (Tauber 1965). Relative humidity was high on most days within the principal pollination period (average RH 74%), and wind speed was low. This atmospheric condition affects the maintenance of suspended grains and limits pollination. This type of characteristics prevails in humid subtropical environments like Misiones and would not favor fertilization. Caccavari et al. (2000) supported the idea that this pollen type is not adapted to long-distance pollination, and only flotation in local mass currents within the forest would be favored. It can be inferred that distance between plants is crucial to forest rehabilitation in order to maintain gene flow. On the other hand, the increases of pollen at the end of afternoon (H18 and H20) detected in 2011 and 2013 would not result from contributions of distant sources as in other environments (Latorre et al. 2001) given the limitation of wind transport of *A. angustifolia* pollen explained above and also its large grain size (Latorre et al. 2014).

On the other hand, the intradiurnal pattern of 2010 and 2012 showed a nocturnal increase in concentration (H2). This secondary increase could be attributed to the local pollen release that remains suspended in the forest by atmospheric stability conditions that typify that time of the day. The nocturnal atmospheric stability hinders vertical transport (Giostra et al. 1991), so the presence of pollen during the night hours is interpreted as a pollen fall phase from greater heights from the tree canopies. In order to study this particular phenomenon that depends on the hourly scale, it would be appropriate to count with in situ hourly meteorological data.

The weekly concentration pattern was of the normal type with a peak in the second fortnight of October. This shape corresponds to the progress of pollination (Gauchat et al. 2019). According to Latorre and Fassola (2014), the aerobiological curve was in line with the direct phenological observations on the progress of male cone maturation in terms of intensity and seasonality. The correlation between pollen and flowering has previously been reported in comparison with arboreal species (Latorre 1997; Sánchez and Latorre 2011). The deviations from this pattern were related to the depressing effect of rainfall on pollen concentration (Latorre and Bianchi 1998) which generated bimodal patterns as those from 2011 and 2012. Example of these cases were observed in *Ulmus*, *Salix*, and *Betula* (Latorre 1999), where the rhythm of emission, given the external factors, was represented in the pollen curve with two important increases in concentration. On a daily scale, a quantitative influence of precipitations was also observed. When the rain occurs on the same or the next day, it usually causes a depression effect on the concentration registered, though intensity varies depending on how close the maximum is. Rainfall itself during PPP could justify the difference between 2012 and the other years. However, it would not be enough to explain, for instance, the low API in 2015. The rainfall effect is also qualitative because it significantly reduces airborne pollen and compromises, on a potential basis, pollination if rain recordings double the average value (200 mm) during PPP. This value is close to the historical mean (1988–2010) of the main month (October) with 272 mm.

Aside from the environmental factors affecting the pollen maturation phase and grains transportation by wind as discussed above, the impact of weather

conditions on the early stages of the reproductive cycle should also be considered, e.g., during the reproductive structures formation. According to studies carried out in Brazil by Anselmini et al. (2006), the high temperatures and precipitations in the summer previous to *A. angustifolia* pollination period favor cone development. These weather conditions during the reproductive structures development could affect pollen productivity. An example is 2012, the year with the lowest amount of pollen, since the monthly rains from November 2011 to April 2012 (period of strobilus formation) were 37 mm lower on average than those in 1998–2010 according to statistical data, as well as minimum summer temperatures (2 °C lower, on average). Moreover, the minimum temperature sums in San Antonio during January 2010 were 7 °C higher than in the rest of the years analyzed. Simón et al. (2018) compared two different areas of Argentina where this species lives and found that high maximum summer temperatures were favorable for the induction of reproductive structures. They also established that differences between years for pollen and seed production were smaller than the difference between environments. Pollen productivity and seed values resulted very much higher in temperate areas. This kind of comparative surveys is still being conducted in order to deepen our understanding of the climate effect on reproduction. The thorough study of *A. angustifolia* reproduction from an aerobiological perspective highlights the role of this kind of data as climate bioindicators applied to the conservation of biodiversity (Fernández-Llamazares et al. 2014). The generated knowledge supports the use of specific management tools such as ex situ conservation and the selective collection of seeds on predictably better years.

The relevance of establishing the years of increased production lies in the possibility of scheduling understory cleaning after a productive pollen year in order to favor the development of seedlings once seeds mature, and thus contribute to the natural regeneration of the species.

5 Conclusions

The aerobiological study carried out during seven reproductive periods of *A. angustifolia* growing in the

northern end of its natural distribution area allowed to draw the following conclusions:

- *A. angustifolia* showed a cyclical annual pollen intensity pattern that is repeated every 3 years.
- The PP begins in mid-September and ends in mid-November.
- The PPP comprises 1 month, and the peak occurs on the second fortnight of October.
- The highest pollen integral is recorded in years where pollination periods are shorter and begin earlier.
- The intradiurnal concentration pattern shows a maximum at midday supporting pollen income from local sources.
- Precipitations during PPP affect the aerial displacement of pollen and reduce the airborne grains.
- August minimum temperature prior to pollination is a good predictor of pollen production.

We continue with the registration of aerobiological data to confirm the trends found herein and validate the predictive model obtained. Through this model, periods of high concentration of atmospheric pollen could anticipate an increase in the chances of fertilization and seed formation 20 months afterward. This would allow to plan the supply of reproductive material available to producers and generate actions in the forest which would favor the development of seedlings from these seeds.

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