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Pollen indices of *Cedrus atlantica* Manetti populations vary with geographical localities in the Moroccan Atlas Mountains

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Photo 1.
Mature tree *Cedrus atlantica* Manetti on the edge of a forest track in the High Atlas Mountains of central-eastern Morocco.
Photo M. Bendriss Amraoui.

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RÉSUMÉ

Les indices polliniques des populations de *Cedrus atlantica* Manetti varient en fonction des localités géographiques dans les zones montagneuses de l'Atlas au Maroc

Les forêts de *Cedrus atlantica* Manetti d'Afrique du Nord sont en forte régression, ayant décliné de plus de 58 % au cours des 130 dernières années, et de nombreux peuplements risquent de disparaître complètement dans les décennies à venir. Cette étude sur les interactions entre les caractéristiques du pollen de *C. atlantica* (production, germination et longueur du tube pollinique) et les paramètres de différentes localités au Maroc, menée sur soixante-dix individus issus de sept populations géographiquement éloignées, montre que les indices polliniques varient en fonction de la station. La production de pollen est élevée dans les populations des stations de Moudemam-1 et Seheb, intermédiaire dans les stations d'Ait Oufella et d'Ait Ayach et faible dans les stations de Zerrouka, Ras elma et Moudemam-2. La germination du pollen est très faible pour les populations des stations de Seheb et Moudemam-1, mais élevée dans les autres stations. D'autre part, les tubes polliniques les plus longs ont été enregistrés dans la population de Moudemam-1, alors que ceux des autres stations sont plus courts. Ces résultats montrent une variation inverse entre les indices polliniques caractérisant les populations des stations étudiées. Les classes de longueur des tubes polliniques les plus courts [0-100] à [300-400] représentent 85,98 % de l'ensemble des classes et ont pu être évaluées pour les stations de Zerrouka, Ait Oufella et Ait Ayach. Dans la population de Moudemam-1, les autres classes sont soit mieux représentées, soit présentes uniquement dans cette station. Ces résultats pourraient avoir des implications non seulement pour évaluer les variations polliniques en fonction des localités géographiques, mais aussi pour optimiser la fertilisation des forêts de cèdres en sélectionnant les meilleurs clones pour cette essence.

Mots-clés : *Cedrus atlantica*, cèdre, population, production, germination, pollen, longueur du tube pollinique, localité, Maroc, montagnes de l'Atlas.

ABSTRACT

Pollen indices of *Cedrus atlantica* Manetti populations vary with geographical localities in the Moroccan Atlas Mountains

North Africa's forests of *Cedrus atlantica* Manetti have declined drastically, by more than 58% in the last 130 years, and many stands are likely to disappear entirely in the coming decades. This study on the interactions between *C. atlantica* pollen characters (production, germination, and pollen tube length) and locality characters in Morocco, using seventy individuals from seven geographically distant populations, showed that pollen indices varied according to station. Pollen production was high in the populations of the Moudemam-1 and Seheb stations, intermediate in the Ait Oufella and Ait Ayach stations, and low in the Zerrouka, Ras elma and Moudemam-2 stations. Pollen germination was very low for the populations in the Seheb and Moudemam-1 stations but high in the other stations. On the other hand, the longest pollen tubes were recorded in the Moudemam-1 population, while those in the other stations were shorter. These results show an inverse variation between the pollen indices characterizing the populations of the stations studied. The shortest pollen tube length classes [0-100] to [300-400] accounted for 85.98% of all classes and were assessed for the Zerrouka, Ait Oufella and Ait Ayach stations. The other classes were more represented or exclusive to the population of the Moudemam-1 station. These results could have implications not only for assessing pollen variations according to geographical localities but also for optimizing fertilization in cedar forests by selecting the best clones for this species.

Keywords: *Cedrus atlantica*, cedar, population, production, germination, pollen, pollen tube length, locality, Morocco, Atlas Mountains.

RESUMEN

Los índices de polen de poblaciones de *Cedrus atlantica* Manetti varían con las localidades geográficas de las montañas del Atlas en Marruecos

Los bosques del Norte de África de *Cedrus atlantica* Manetti han disminuido drásticamente, más del 58 % en los últimos 130 años, y muchos rodales podrían desaparecer completamente en las próximas décadas. Utilizando 70 individuos de siete poblaciones distantes geográficamente, este estudio sobre las interacciones entre las características del polen de *C. atlantica* (producción, germinación y longitud del tubo polínico) y las características de la localidad de Marruecos, mostró que los índices de polen variaban según la localidad. La producción de polen era elevada en las poblaciones de las localidades de Moudemam-1 y Seheb; intermedia en Ait Oufella y Ait Ayach, y baja en Zerrouka, Ras elma y Moudemam-2. La germinación del polen era muy baja en las poblaciones de las localidades de Seheb y Moudemam-1, pero elevada en las demás localidades. Por otro lado, los tubos polínicos más largos se registraron en las poblaciones de Moudemam-1, mientras que los de las demás localidades eran más cortos. Estos resultados muestran una variación inversa entre los índices de polen que caracterizan a las poblaciones de las localidades estudiadas. Las clases de tubos polínicos más cortas, de [0-100] a [300-400], representan el 85,98 % del total de clases, y se evaluaron en las localidades de Zerrouka, Ait Oufella y Ait Ayach. Las demás clases fueron más representadas o exclusivas para la población de la localidad de Moudemam-1. Estos resultados podrían tener implicaciones no solamente para evaluar las variaciones de polen según las localidades geográficas, sino también para optimizar la fertilización en los bosques de cedro seleccionando los mejores clones para estas especies.

Palabras clave: *Cedrus atlantica*, cedro, población, producción, germinación, polen, longitud del tubo polínico, localidad, Marruecos, montañas del Atlas.

Introduction

Gymnosperms are one of the most threatened groups of living organisms, with 40% of the species at high risk of extinction, about twice as many as the most recent estimates for all plants (i.e., 21.4%) (Forest et al. 2018). The Atlas cedar (*Cedrus atlantica* Manetti) is an endangered species endemic to the mountains of North Africa (Thomas, 2013). Due to its wide ecological range, it is attracting increasing international interest for its use in the reforestation of degraded lands (Lanier 1994; Ripert and Boisseau 1994; Labhar 1998; Schaad et al. 2018). Despite this, its range has undergone a considerable reduction in recent decades (Rhanem 2011; Thomas 2013; Schaad et al. 2018). Many threats greatly influence their survival, such as dieback, climate change, fires, and long-term browsing by domestic animals (Quezel and Medail 2003; Chaponniere and Smakhtin 2006; Belhassan et al. 2010; Rhanem 2011; El Jihad 2016; Bouahmed et al. 2019).

The cedar naturally forms seven geographical blocks in North Africa, including four in Morocco, occupying a surface area of 132,000 ha and representing 2.3% of the national forest. In Morocco, the cedar presents very heterogeneous ecological requirements (Maire, 1924; Emberger 1939; Pujos 1966; Lecompte 1969; Donadieu 1977; Achhal et al. 1980). According to edaphic, altitudinal, and climatic criteria, we distinguish, respectively among limestone dolomites and basalts, cedar forests at low (1,600-1,900 m), medium (1,900-2,100 m), and high (2,100-2,500 m) altitudes (Achhal et al. 1980). In the central Middle Atlas, two groups of the geological formations are distinguished by their morphological and phytoecological structure: the group of the tabular Middle Atlas Causse in the North living in subhumid or humid wheather; and the group of the Middle Atlas pleated to the South with semi-arid climate (El Bakkali and Bendriss Amraoui 2022). In the High Atlas, cedar may develop in a semi-arid climate at a high altitude of 1,800-2,400 m between latitudes 32°16’ and 32°53’ (Rhanem 2011).

Several studies have reported that pollen traits condition reproductive success in competition, pollination, seed selection, and offspring quality (Van Breukelen 1982; Lord and Eckard 1984; Cruzan 1990; Gore et al. 1990; Manicacci and Barrett 1995; Delph et al. 1998). Similarly, pollen size and its protein resources have been found to be positively related to stigma depth (Roulston et al. 2000; Cruden 2009) and seed size in a wide range of species (Kirk 1993). Pollen tube size, which varies widely among species, is considered an excellent indicator of pollen viability and ability to fertilize the ovule (Zonia and Munnik 2008; Fayant 2010; Dardelle 2011).

The study of reproduction in *C. deodara* species has revealed a large variability in pollen and ovule characters (Johri and Vasil 1961; Chowdhury 1961; Konar and Oberoi 1969; Takaso and Owens 1995a, 1995b; Khanduri and Sharma 2002, 2009), as well as in the sexual expression of the tree depending on year, site, and tree size (Khanduri and Sharma, 2010; Sharma and Bhondge 2016; Khanduri et al. 2021). Some limited studies have reported significant variability in pollen size of *C. atlantica* depending on several parameters, including site conditions, genome size, adaptations required for wind pollination, and irregular pollen development (Smith 1923; Derridj et al. 1991; Bell et al. 2017; Bell et al. 2018a, 2018b). Likewise, the pollen traits of the Atlas cedar have not been the subject of any other research despite the fact that its variability with the environment has been established by studies; hence, their capital importance for the regeneration, management, and conservation of the cedar forests in these regions (Bell et al. 2018a; Rhanem 2010, 2011). Similarly, among the few studies carried out in Algeria, especially on the physiological aspects of the Atlas cedar pollen, none have provided details on the pollen tube of this species, despite its significance as an excellent indicator of viability and ability to fertilize the ovule (Khanfouci 2005; Krouchi 2010).

The large variability in *C. atlantica* pollen grain size observed by Bell et al. (2017) within individual samples, in some cases by as much as 20 µm, suggests that grain pollen is influenced by a number of complex factors. Furthermore, providing insights into environmental conditions through the size and morphology of *C. atlantica* pollen at the time of development remains controversial until now due to (i) the variability of production, size, and morphology; (ii) the compromise size number; and (iii) the lack of evidence for climatic influence (Bell et al. 2017), underscoring the need for further investigation on cedar pollen grain.

The objective of this paper is to study the interaction of geographical position with pollen characteristics of seven natural populations of *C. atlantica* from Moroccan mountains.

Material and Methods

Study areas

In the High Atlas Mountains of central-eastern Morocco, the geographical limits of cedar are between the northern latitudes of 32°30’ and 32°15’ and the eastern longitudes of 4°24’ to 5°33’ (figure 1), at an altitude of between 1,900 and 3,250 m (Rhanem 2010). These cedar forests live in a continental semi-arid bioclimate and occupy an area of 10,000 ha (Rhanem 2010). In the Middle Atlas, the cedar occupies latitudes between 32°08’ and 33°44’ (Bariteau et al. 1999), altitudes between 1,600 and 2,500 m (Pujos 1966), and covers an area of 70,000 ha (Rhanem 2010) in a bioclimate variable from cold subhumid to very cold through the fresh humid to continental semi-arid.

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Volume 359 – 1st quarter – February 2024 – p. 69-83

Sampling Sites

Male catkins were collected at the time of pollination from 2015 to 2019 in seven geographical populations of *C. atlantica*: Zerrouka, Ras elma, Moudemam-1, Moudemam-2, Seheb, Ait Oufella located in the central Middle Atlas, and Ait Ayach in the High Atlas (figure 1, tables I and II). The pure and dense populations of Moudemam-1, Seheb, and Moudemam-2 are formed on a basalt-calcareous substratum of post-Villafranchian Plio-Quaternary age (basalt and ancaratrite lavas) and characterised by a fresh and stable wet bioclimate. In the forests of Zerrouka and Ras elma, the populations are characterised by the presence of *C. atlantica* and *Quercus rotundifolia* Lam. on substratum rich in carbonate of Ca^{2+} and Mg^{2+} of Liasic age, wealthy in fossils with the cold subhumid climate.

The Ait Oufella forest covers an area of 5,650 ha located on the southern edge of the Middle Atlas, about 40 km northwest of Midelt, on a calcareo-dolomitic Lias associated with the marl-limestone Cretaceous and a few pockets of red clay and Triassic basalts (Rhanem 2011). The general climate of this station is semi-arid, characterised by low rainfall and a marked drought for a long part of the year (Rhanem 2009). The population of Ait Ayach is less than 7 km from the Cirque of Jaaffar and is characterised by the presence of *C. atlantica* and *Q. rotundifolia* Lam. on a calcareous substratum of Villafranchian and Quaternary alluviocolluvial with a semi-arid continental climate.

Extraction, germination and dosage

Our pollen extraction technique consisted in a preliminary mixing of the catkins, then we kneaded them and passed them through a series of sieves arranged in descending order (0.2 mm; 0.125 mm; 0.1 mm; 0.04 mm). The extracted pollen was stored at 4 °C in airtight jars. For the in vitro germination experiments, 10 mg of *C. atlantica* pollen were sprinkled uniformly on a slide (2.5 × 7.5 cm) containing 2 ml of culture medium and then incubated in the dark at 29.5 °C for 3 days in a humid chamber to avoid drying out the slides. The medium contains 0.29 M sucrose, 2.5 10^{-5} M boric acid (Ching and Ching 1976), 6 mg/L penconazol, 0.1 g/L chlorampenicol, 0.1 g/L streptomycin, and 0.5% agar. From the male catkins of the 10 trees at each station, 3 slides per individual were prepared. Starch was determined on 2 g of pollen from the mixture of 500 catkins (Braconnot 1829). Amylase activity was determined on 10 g of pollen after 72 hours of germination (Roychan and Chaudhari 2001).

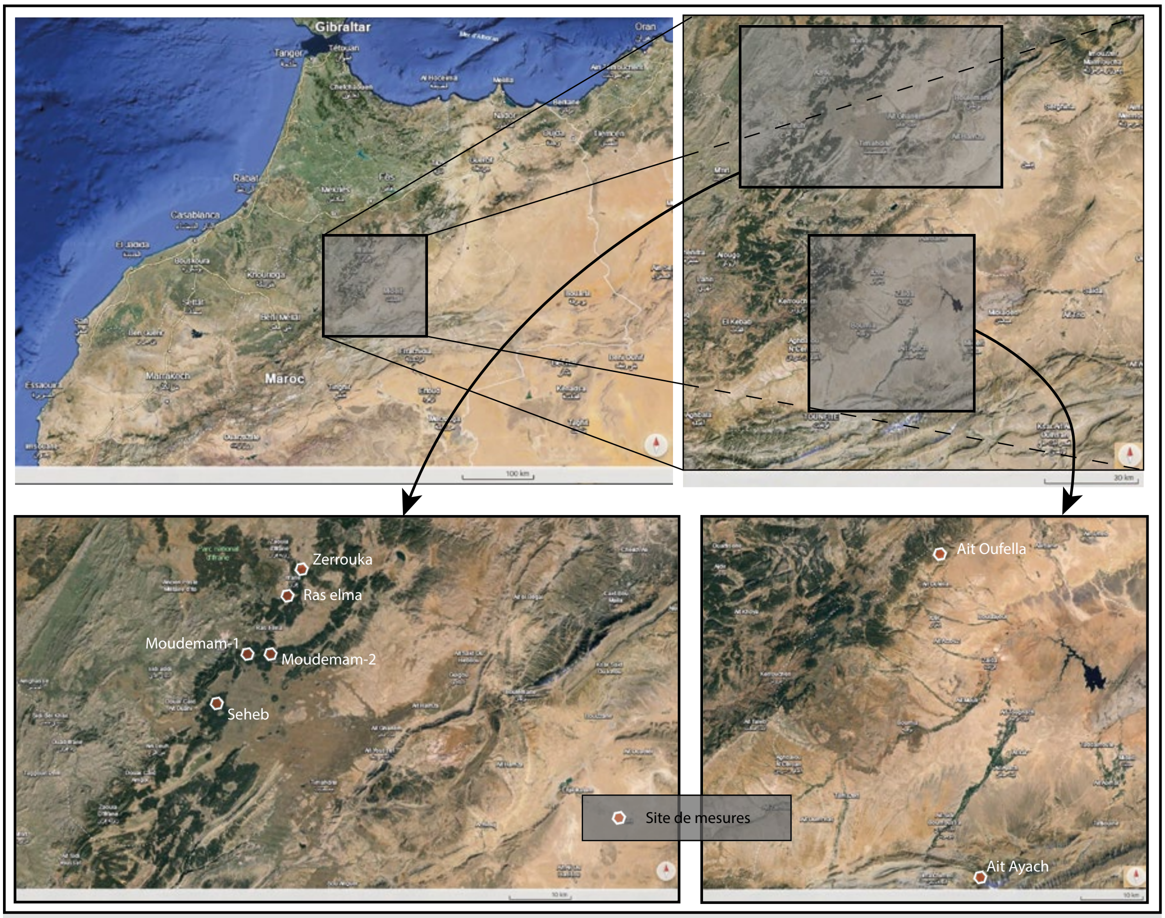

Figure 1.
Locations of the natural areas of the sampled populations of *Cedrus atlantica* Manetti.
Photography is based on topographic data from Google earth version 7.3.6 (Data: SIO, NOAA, U.S. Navy, GNA, GEBCO; Image: Landsat/ Copernicus, IBCAO, U.S. Geological Survey).

Table I.
Sampled populations of *Cedrus atlantica* Manetti according to the location and site parameters.

Mountains	localities	Geographical coordinates	Elevation (m, amsl)	Bioclimate (Koppen-Geiger scale)	Parent rock
Middle Atlas	**Zerrouka**	33°32'N-5°06' W	1637	Csb: Cold subhumid to very cold	Calcareous/ dolomite/ sander
	Ras elma	33°30'N-5°07'W	1659		
	Moudemam-1	33°25'N-5°11'W	1786	Csa: Fresh humid	Basalt-Calcareous
	Moudemam-2	33°25'N-5°09'W	1780		
	Seheb	33°21'N-5°14' W	1800		
	Ait Oufella	32°58'N-5°03'W	1982	Bsk: Semi-arid continental	Calcareous
High Atlas	**Ait Ayach**	32°31'N-4°59'W	1972		

Table II.
Temperatures (°C), precipitations (mm) and humidity (%) during the period of pollen production of the sampled populations of *Cedrus atlantica* Manetti (Regional Directorate of Meteorology North-East Region).

	Localities	May	June	July	August	September
Middle Atlas	**Zerrouka, Ras elma**	13.6 (77) (60)	18.3 (39) (52)	22.2 (25) (44)	22 (33) (43)	17.5 (50) (54)
	Moudemam-1, Moudemam-2, Seheb	13.7 (64) (59)	18.5 (30) (51)	22.4 (20) (43)	22.2 (24) (42)	17.7 (39) (53)
	Ait Oufella	16.5 (39) (42)	21.5 (20) (34)	25.5 (10) (27)	24.5 (15) (30)	19.4 (33) (43)
High Atlas	**Ait Ayach**	16.5 (39) (42)	21.5 (20) (34)	25.5 (10) (27)	24.5 (15) (30)	19.4 (33) (43)

Observations and calculation

On each slide, pollen grains of 20 microscopic fields of 2 mm diameter at × 100 magnification were photographed with an optical microscope (Optika DM-15, Italy) equipped with a camera, and the different measurements were made with a software (Opmias Ver1.0, 2001-2008). Six hundred fields of view corresponding to 300 mg of pollen were made for each station at a rate of 60 per individual. We calculated the total number of pollens in the 600 microscopic

Photo 2.
Cedrus atlantica Manetti branch density in the High Atlas Mountains of central-eastern Morocco.
Photo M. Bendriss Amraoui.

Table III.
P value of multiple comparison Tukey test of five parameters of pollen of the seven populations of *Cedrus atlantica* studied.

	PTL	NGP	NPT	%	Starch	Amylase
Zerrouka - Ras elma	0.000*	0.000*	0.970	0.000*	1.000	1.000
Zerrouka - Moudemam-2	0.000*	0.000*	0.020*	0.000*	0.997	0.992
Zerrouka - Moudemam-1	0.000*	0.000*	0.000*	0.000*	0.855	0.526
Zerrouka - Seheb	0.000*	0.000*	0.000*	0.000*	0.014*	0.965
Zerrouka - Ait Oufella	0.236	0.000*	0.000*	0.000*	0.49	0.716
Zerrouka -Ait Ayach	0.000*	0.000*	0.000*	0.000*	0.524	0.888
Ras elma - Moudemam-2	0.903	0.991	0.228	0.752	0.998	0.967
Ras elma - Moudemam-1	0.000*	0.000*	0.000*	0.652	0.878	0.42
Ras elma - Seheb	0.000*	0.036*	0.000*	0.000*	0.017*	0.908
Ras elma - Ait Oufella	0.000*	0.000*	0.000*	0.000*	0.524	0.599
Ras elma - Ait Ayach	0.000*	0.000*	0.000*	0.997	0.566	0.793
Moudemam-2 - Moudemam-1	0.000*	0.000*	0.000*	0.029*	0.992	0.845
Moudemam-2 - Seheb	0.000*	0.003*	0.000*	0.000*	0.072	1.000
Moudemam-2 - Ait Oufella	0.000*	0.000*	0.000*	0.000*	0.831	0.960
Moudemam-2 - Ait Ayach	0.000*	0.000*	0.000*	0.356	0.908	0.998
Moudemam-1 - Seheb	0.000*	0.000*	0.535	0.006*	0.346	0.928
Moudemam-1 - Ait Oufella	0.000*	0.000*	0.000*	0.000*	0.995	1.000
Moudemam-1 - Ait Ayach	0.000*	0.000*	0.000*	0.945	1.000	0.983
Seheb - Ait Oufella	0.000*	0.000*	0.000*	0.000*	0.802	0.991
Seheb - Ait Ayach	0.035*	0.000*	0.000*	0.000*	0.151	1.000
Ait Oufella - Ait Ayach	0.000*	0.000*	1.000	0.000*	0.999	1.000

PTL: Pollen tube length's; NGP: Number of germinated pollen per microscopic field; NPT: number of pollen total per microscopic field; %: Germination frequency of pollen; * Statistically significant at the level of 5%.

fields per station (Nt), the total number of pollens germinated in the 600 microscopic fields per station (Ng). The frequency of pollen germination was calculated as the pollen germinated number ratio to the total of the pollen grains (germinated pollen + un-germinated pollen) × 100. The density of germinated or total pollen per microscopic field in each station is calculated, respectively, according to the ratio Ng or Nt on the 600 microscopic fields. The mean (± 1 µm) pollen tube length was determined from the pollen tubes of all germinated grains. A pollen grain was considered to have germinated when the pollen tube length was greater than or equal to the grain diameter. We determined descriptive statistics; for pollen tube length we calculated the mean, the maximum, the minimum, the standard error, and the coefficient of variation. For pollen starch reserve content (mg/g of pollen), the values were obtained by the standard range equation: $y = 1.0336x - 0.0269$ with $R^2 = 0.99743$; we only determined the mean and the standard error. The mean ± the standard error for amylase activity was expressed as mg maltose/min/g pollen.

Using Excel 2007 software, we defined similar semi-quantitative classes of pollen tube length at an amplitude of 100 µm for all stations, taking into account all pollen tube length values. In order to make the pollen tube length values continuous, we presented them as continuous classes to avoid a value being taken into account twice, the last value being 1,300 µm. For each station, the size of each class of values is determined by the number of times each class is represented in the station. The frequency of each class was calculated by the ratio of the number of each class to the sum of the numbers of all classes.

Statistical analysis

Differences between the different geographical sites were calculated using the Tukey test at a significance level of 5% on the mean values of the pollen characteristics. Linear regression analyses were carried out between the pollen characteristics and the station parameters (station, temperature, precipitation and humidity). All data were statistically analysed with IBM SPSS Statistics 20.0 software.

Table IV.
Pollen production and germination in the stations. Density = average total or germinated number of pollen per microscope field; Nt: total number of pollen found in the 600 fields; Ng: total number of germinated pollen found in the 600 fields; germination frequency = Ng/Nt × 100.

	Pollen	Zerrouka	Ras elma	Moudemam-1	Moudemam-2	Seheb	Ait Oufella	Ait Ayach
Density	Total	8.98 ± 0.332	8.32 ± 0.272	21.05 ± 0.771	6.64 ± 0.222	22.36 ± 0.761	16.97 ± 0.454	17.05 ± 0.444
	Germinated	1.31 ± 0.025	0.35 ± 0.021	0.60 ± 0.047	0.38 ± 0.024	0.22 ± 0.018	1.67 ± 0.044	0.81 ± 0.018
Germination	Nt	5,388	4,992	12,630	3,984	13,416	10,182	10,230
	Ng	787	213	359	232	133	1,003	487
	%	14.60	4.26	2.84	5.82	0.99	9.85	4.76

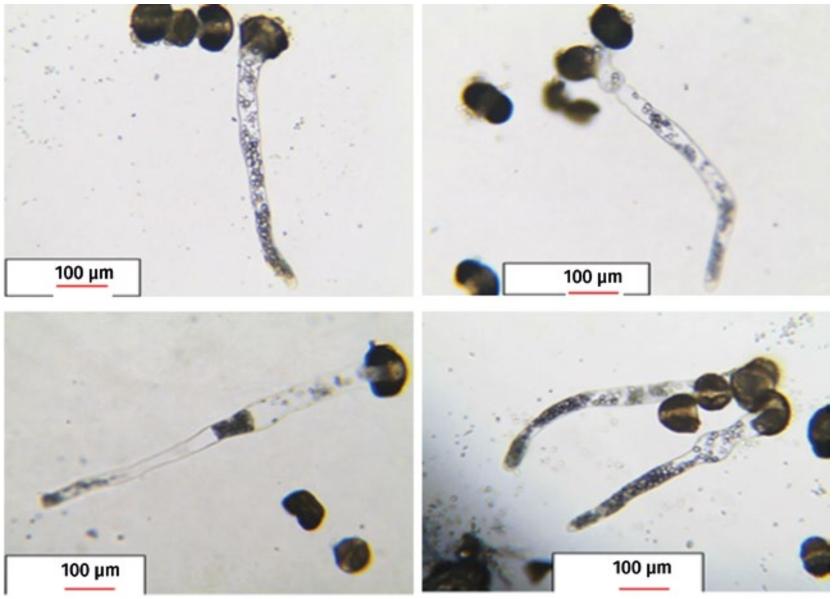

Figure 2.
Germinating *Cedrus atlantica* M. pollen (x 100).

The existing starch reserves in pollen before germination are significantly different between Seheb, Zerrouka, and Ras elma and similar for all other sites. The populations showed no significant difference in pollen amylase activity (tables III and V). The mean value of pollen tube length is variable from 258.14 to 531.33 µm in, respectively, the populations of Seheb and Moudemam-1, with a variable maximum of 611.76 µm in Seheb to 1,255.56 µm in Moudemam-1, giving the pollens from these populations a high fertilizing power in contrast to the other stations. These values dropped to 343.23 µm in the population of Moudemam-2, ranged from 166.34 to 291.05 µm in the populations of Ait Oufella and Ait Ayach, and ranged between 154.25 and 330.97 µm in the populations of Zerrouka and Ras elma. These length values significantly distinguish the populations of all stations except those of Zerrouka and Ait Oufella and those of Ras elma and Moudemam-2. The values of the coefficients of variation show that there is a large dispersion of the order of 28.61 to 50.21% around the average length of the tubes of the populations (figure 2; tables III and V).

The pollen tube class that groups all lengths between 100 and 200 µm is the most represented with a percentage of 33.45%, followed by the class [200-300[with 21.91%, then the class [300-400[with 17%, and finally the class [0-100[with 13.63%. The populations of the stations of Ait Oufella and Zerrouka and, to a lesser degree, Ait Ayach and Ras elma dominate by the classes of the shortest pollen tube [0-100[to [300-400[µm on the other stations. The classes [400-500[and [500-600[dominate at

Results

The results obtained show that the number of total pollen as well as the number of germinated grains differ between the cedar stations. The averages of total pollen density per microscope field (NPT) significantly distinguish the seven populations according to location except between Zerrouka – Ras elma, Ras elma – Moudemam-2, Moudemam-1 – Seheb, and Ait Oufella – Ait Ayach (table III). The densities of germinated pollen (NGP) also differentiate all the populations from each other except those of Ras elma and Moudemam-2. In the same sense, the number of total pollen grains (Nt) varies enormously between the populations, with maximum values in Moudemam-1 and Seheb, intermediate values in Ait Oufella and Ait Ayach, and minimum values in Zerrouka, Ras elma, and Moudemam-2. In contrast, the frequency of pollen germination (%) decreased progressively from the Zerrouka population to those of Ait Oufella, Moudemam-2, Ait Ayach, Ras elma, Moudemam-1, and Seheb. This frequency is significantly different between all sites except between Ras elma and Moudemam-1, Moudemam-2 and Ait Ayach; and between Ait Ayach and Moudemam-1 and Moudemam-2 (tables III and IV).

Table V.
Statistical description of starch reserves (mg/g pollen), amylase activity (mg maltose/min/g pollen), and mean pollen tube length (µm) of *Cedrus Atlantica* pollen from different study stations (n = 133 to 1,003)

Statistics		Stations						
		Zerrouka	Ras elma	Moudemam-1	Moudemam-2	Seheb	Ait Oufella	Ait Ayach
Starch		1.19 ± 0.3	1.17 ± 0.3	2.35 ± 0.27	1.85 ± 0.1	5.81 ± 1.4	4.03 ± 0.09	3.4 ± 1.75
Amylase		4.08 ± 0	4.20 ± 0.1	3.75 ± 0.2	4.30 ± 0.8	3.91 ± 0.4	4.68 ± 0.2	4.58 ± 0.7
Length	Moy	154.25	330.97	531,33	343.23	258.14	166.34	291.05
	Min	38.18	108.77	47.87	79.39	29.82	32.14	67.91
	Max	484.54	568.99	1,255.56	578.83	611.76	435	607.07
	ES	2.74	7.13	11.37	6.44	10.79	2.63	3.94
	CV	49.93	31.47	40.55	28.61	48.23	50.21	29.91

ES: Standard error
CV: Coefficient of variation

Ras elma, Ait Ayach, Moudemam-1 and 2; the class [600-700[is only present in Moudemam-1, Seheb, and Ait Ayach, while the highest classes [700-800[to [1,200-1,300[except [1,100-1,200[exist only at Moudemam-1 (table VI).

In order to see if there are relationships between all pollen indices and climatic factors, we used a linear regression analysis. Our results detected a significant link between pollen tube length, pollen production, pollen germination percentage, and the site, precipitation, and humidity in September. However, for the starch variable, a significant link was only found with the site, and for the amylase activity, no significance was found with the explanatory parameters (table VII).

Discussion

The study of the pollen produced by the seven populations shows that the male sexual phenotype and the male tendency of *C. atlantica* are parameters intrinsically linked to geographical location. A close link between the amount of pollen released by plants and temperature has long been established by several authors (Khanduri and Sharma 2002; Clot 2003; Matsumoto et al. 2003; Khanduri and Sharma 2009; Ejsmond et al. 2011; Ejsmond et al. 2015; Sharma and Bhondge 2016). According to Besancenot and Thibaudon (2012) and Zhang et al. (2013) a warmer climate has a high probability to anticipate flowering dates, to lengthen the pollen season, and to increase pollen concentrations. Recently, Monnier et al. (2020) reported that higher temperatures, by affecting the physiology of the plant, lead to an increase in pollen production. Several other authors have reported that a warmer climate increases pollen production in most woody species, angiosperms and gymnosperms, especially in catkin trees (Gehrig and Clot 2021; Glick et al. 2021; Adams-Groom et al. 2022; Thibaudon and Besancenot 2022). In contrast, Ejsmond et al. (2011) found a reduction in pollen production at high temperatures compared to low temperatures. These observations suggest that pollen formation is species dependent. On the other hand, several authors have reported that when temperatures rise, most species produce pollen with a low surface/volume ratio, allowing them to resist desiccation pressure and evapotranspiration (Aylor 2003; Aylor et al. 2005; Cruden 2009; Nepi et al. 2010; Ejsmond 2015).

In the sites of Ait Oufella and Ait Ayach, where a hottest and least rainy summer in July-August not exceeding 15 mm; characteristic of an absolute aridity during the period of formation of the sexual organs of the cedar in summer; we find a weak release of pollen in these stations compared to Moudemam-1 and Seheb, where the temperature is lower with heavy monthly precipitation during the months of May to September. These facts show that the variation in pollen formation in *C. Atlantica* recorded between our populations here may be due essentially to variation in rainfall, as these stations differ slightly in temperature but greatly in rainfall. These findings are consistent with those on *C. deodara* that show high pollen productivity when significant rainfall precedes flowering (Khanduri and Sharma 2009). On the other hand, the regression analysis has shown a relation between pollen production, rainfall, and humidity only in pollen phase maturation (September), suggesting that the climatic differences between our sites during June, July, and August from 2015 to 2019 were probably not sufficient to induce variation in pollen production and had little influence on this parameter. This observation shows that the variation in pollen production obtained in our study was due to the geographical situation effect, as found for Zerrouka, Ras elma and Moudemam-2. This trend implies a combined effect of many complex factors (genetic, physiological, and climatic) on the variation of the number of pollens released (Khanduri and Sharma 2009).

Table VI.
Numbers and frequencies of pollen tube length classes.

Classes (µm)	Stations								
	Zerrouka	Ras elma	Moudemam-1	Moudemam-2	Seheb	Ait Oufella	Ait Ayach	Total	Frequency%
[0-100[	203	0	2	2	12	214	5	438	13.63
[100-200[	393	24	26	15	39	510	68	1075	33.45
[200-300[	151	62	23	63	34	183	188	704	21.91
[300-400[	32	76	53	89	32	85	179	546	17
[400-500[	8	34	58	50	10	11	40	211	6.56
[500-600[	0	17	60	13	5	0	6	101	3.14
[600-700[	0	0	48	0	1	0	1	50	1.55
[700-800[	0	0	47	0	0	0	0	47	1.46
[800-900[	0	0	29	0	0	0	0	29	0.90
[900-1000[	0	0	10	0	0	0	0	10	0.31
[1000-1100[	0	0	2	0	0	0	0	2	0.06
[1100-1200[	0	0	0	0	0	0	0	0	0
[1200-1300[	0	0	1	0	0	0	0	1	0.03
Total	**787**	**213**	**359**	**232**	**133**	**1,003**	**487**	**3,214**	**100**

However, it has been reported that the productivity, the interval of production, and the release of pollen strobili depend on year and population in *C. deodara* (Khanduri and Sharma 2009) and other species (Allison and Treseder 2008). Our results do not agree with the suggested environmental condition dependences on the pollen observed on many species (Ejsmond et al. 2011; Ejsmond et al. 2015; Griener and Warny 2015; Jardine and Lomax 2017), but revealed specific responses of *C. atlantica* to geographical location and are in line with the data of Smith (1923) who noted "irregularity" with the development of pollen, and Bell et al. (2017, 2018a) who found no significant relationships between climate, soil nutrient availability, and pollen size for Atlas cedar.

In the stations of Ras elma, Zerrouka, and Moudemam-2, which have low pollen production, the germination rate is very variable, whereas in those of Moudemam-1 and Seheb, where the production was relatively high, the pollen germination was low, suggesting a great variation in the size and water state of pollen. Furthermore, the reduction in pollen fertility recorded in the fresh humid locations, particularly in the Seheb population, was linked to the high sensitivity of pollen to the level of humidity in this site, as showed by the regression analysis (table VII) and as reported by several authors for well-hydrated sites (Aylor 2003; Aylor et al. 2005; Nepi et al. 2010). This observation contrasts with the results of Ejsmond et al. (2011), who obtained a low germination rate when pollen was produced under water deficit conditions. This remark may be explained by the relatively high starch content in the pollen of Seheb and its deficiency in starch catabolism caused by the low digestibility and water absorption of starch due to its dense composition, as reported by MacNeill et al. (2017). Despite the low carbohydrate reserves of the pollen from the cold subhumid site compared to the fresh humid site, the pollen used exogenous sucrose supplied at 0.29 M in the medium to germinate more than the pollen from the fresh humid site populations. This observation was confirmed by relatively similar amylase activity in all populations and indicated that pollen sucrose consummation is probably involved in the inhibition of germination in the fresh humid site, as reported by Takaso and Owens (1995a) who have found that sucrose supplementation improved germination in *C. deodara*.

The elongation of the pollen tube is very heterogeneous between our populations but remains opposite to the germination rate. For example, in the population Moudemam-1 site where germination is low, the value of the length of the pollen tube is high from 600 to 1,300 µm, and vice versa for the populations of Zerrouka and Ait Oufella, which dominate by the classes of the shortest pollen tube from [0-100[to [100-200[in the populations of Ras elma, Moudemam-2, and Ait Ayach, whose values of the germination and the elongation of the pollen were intermediate with, respectively, 4.26 to 5.82% and 100 to 700 µm.

Table VII.
Model summary of the regression analysis.

Model		Unstandardized coefficients		Standardized coefficients	t	Significance	R
		A	Standard error	Bêta			
PTL	(Constant)	-1,992.538	85.428		-23.324	0.000*	0.617
	Station	78.156	4.403	1.089	17.751	0.000*	
	P September	-6.081	1.200	-0.274	-5.066	0.000*	
	H September	4,432.140	100.574	1.438	44.069	0.000*	
NGP	(Constant)	11.224	0.381		29.426	0.000*	0.466
	Station	-0.358	0.019	-0.791	-18.948	0.000*	
	P September	-0.028	0.005	-0.202	-5.502	0.000*	
	H September	-15.666	0.474	-0.817	-33.070	0.000*	
NPT	(Constant)	-72.781	6.131		-11.871	0.000*	0.362
	Station	5.143	0.304	0.745	16.945	0.000*	
	P September	0.343	0.081	0.163	4.217	0.000*	
	H September	104.710	7.615	0.358	13.751	0.000*	
%	(Constant)	162.606	9.727		16.716	0.000*	0.319
	Station	-7.219	0.482	-0.670	-14.991	0.000*	
	P September	-0.356	0.129	-0.108	-2.755	0.006*	
	H September	-212.269	12.081	-0.465	-17.570	0.000*	
Starch	(Constant)	87.610	227.086		0.386	0.703	0.633
	Station	1.302	0.601	1.063	2.166	0.039*	
	T May	-3.874	7.856	-2.200	-0.493	0.626	
	P September	0.058	0.180	0.142	0.320	0.752	
	H September	-71.652	227.264	-1.490	-0.315	0.755	
Amylase	(Constant)	3.056	3.390		0.901	0.389	0.607
	Station	0.01	0.168	0.045	0.059	0.954	
	P September	0.054	0.045	0.804	1.192	0.261	
	H September	-2.072	4.210	-0.224	-0.492	0.633	

PTL: Pollen tube length's; NGP: Number of germinated pollens per microscopic field; NPT: number of pollens total per microscopic field; %: Germination frequency of pollen; P: Precipitations; H: Humidity; * Statistically significant at the level of 5%.

These variations show that the growth of the pollen tube, which was found to be linked to site, rainfall, and humidity, was also conditioned by the pollen germination rate, whatever the station, suggesting the existence of a compromise between these two processes for resources. This trade-off, in parallel with the effects of site, rainfall, and humidity recorded above on production and germination, translates into overall differences in the ecological requirements of reproduction between our populations. Moreover, this pollen resource-dependent growth has also been reported in several studies (Cruzan 1990; Cruden 2009; Johri and Vasil 1961; Ejsmond et al. 2015; Vasil 1974; Baker 1983; Cruden and Lyon 1985; Lau and Stephenson 1994). Indeed, an increase in pollen reserves was found to be necessary to obtain a large pollen tube (Ejsmond et al. 2011). Similarly, Cruzan (1990) on *Erythronium grandiflorum* and Takaso and Owens (1995b) on *C. deodara* found that pollen resources are sufficient for self-growth in the ovary and that sucrose supplementation improves germination by 11% and pollen tube by 85 µm. These data show the existence of competition between germination and elongation for pollen reserves and suggest that the differences between our populations were due to variations in germination and elongation process in terms of priority of pollen resource use. These findings agree with the study of Astija and Musdalifah (2018), who found a regulation of pollen germination and tube elongation in tomato by cell wall invertase through sucrose hydrolysis in medium containing sucrose only, but not in glucose and fructose. This recalled the control of pollen tube tip growth by a Rop GTPase-dependent pathway that leads to tip-localised calcium influx (Roger and Li 1999) and suggested studies on the effect of medium composition on germination and tube elongation of *C. atlantica* pollen.

In the case of *C. atlantica*, as the period of sexual organ production (Khanfouci 2005) coincides in summer with an increase in temperature, CO_2, and radiation (June to August), the pollen benefits from a significant flux of carbon (Aussenac and Finkelstein 1983; Ziska et al. 2003; Wayne et al. 2002; Stinson et al. 2006; Zhang et al. 2013) due to the increase in solar intensity and temperature. Despite this, the summer temperature rise does not increase the pollen tube, starch supply, or pollen amylase activity in populations of the cold subhumid and semi-arid localities where the heat rises more in the summer compared to the fresh humid sites. On the other hand, it reduced the pollen tube of the Ait Oufella population of the semi-arid site and the Zerrouka population of the cold subhumid site, as well as the starch stock of the pollen of the latter population. These observations show that pollen tube elongation in *C. atlantica* is not dependent on endogenous pollen starch resources but is still sensitive to site and, to a lesser extent, to precipitation and humidity in the month of September, as revealed by the regression analysis. This contrasts with studies in which water deficit conditions induce a low germination rate but yield long pollen tubes depending on pollen volume (Cruden 2009; Ejsmond et al. 2011; Aylor 2003; Aylor et al. 2005; Nepi et al. 2010) and in which desiccation pressure caused by high temperatures increases pollen reserves (Ejsmond et al. 2015).

The existence of great variability in the sensitivity of germination and pollen tube growth to intense solar radiation which can produce effects in interaction with CO_2 and temperature on pollen, has been shown by several studies (Feng et al. 2000; Koti et al. 2005; Llorens et al. 2015; Zhang et al. 2014). Similarly, other authors have shown that a mutation in chlacone synthase, a key enzyme in the synthesis of UV-B absorbing phenolic compounds, which can manifest itself with an alteration of the cell membrane by strong irradiation, decreases the viability and length of the pollen tube and blocks pollen germination in *Petunia* and *Cucumis melo* L. (Taylor and Jorgensen 1992; Cuny and Roudot 1991). This effect was found to depend on the radiation dose and pollen size. In contrast, radio resistance was found to be inversely proportional to pollen size in apple, pear and melon (Cuny and Roudot 1991; Jinks et al. 1981). Furthermore, it has been shown by Bell et al. (2018b) that at the geographical localities of the Middle Atlas where our populations are located and from which our pollens were collected, a longitudinal East-West gradient of UV-B flux occurs during the months of July and August, which returns to the expected North-South latitudinal gradient in September. According to this study by Bell et al. (2018b), a wave of radiation has been affecting our populations of Moudemam-1, Moudemam-2, and Seheb sites in the Azrou region from June to September, whereas those of Zerrouka and Ras elma sites in the Ifrane region are only slightly affected in July and August, and those of Ait Oufella and Ait Ayach sites in the Itzer and Tounfite regions are affected in September, after pollen development. The low germination rate found here in our populations of fresh and humid sites is consistent with the long 4-month exposure of this region to high UV-B radiation, which, by inducing enzyme mutation or cell membrane alteration, may block carbon catabolism, as found here in the pollen of Seheb. This slowing of germination in these populations by radiation could be the cause of the development of a long pollen tube by the germinating pollen. On the other hand, the high germination rates noted in the populations of the cold subhumid site Zerrouka and the semi-arid site Ait Oufella agree with the short duration of exposure to UV-B radiation in these two sites. This instability in cedar pollen viability observed here corroborates the variability in pollen grain size observed by Bell et al. (2018b) in *C. atlantica*. These authors found that populations of *C. atlantica* M. exposed to UV-B in the summer to protect the viability of their pollen significantly accumulate UV-B absorbing phenolic compounds such as p-coumaric acid and ferulic acid. The possible cause of this instability is the development of a certain summer radio resistance inversely proportional to pollen size, as has been developed by several species (Cuny and Roudot 1991; Jinks et al. 1981). This radio resistance would be triggered in *C. atlantica* pollen by the accumulation of p-coumaric acid and ferulic acid in the sporopollenin, responsible for the decline of resources and subsequently the reduction of germination and the increase of the pollen tube, as observed here in the Moudemam-1 station. These factors likely allow us to find links between pollen traits and climate only in September.

Photo 3.
Cedrus atlantica Manetti male cone in the High Atlas Mountains of central-eastern Morocco.
Photo M. Bendriss Amraoui.

Photo 4.
Cedrus atlantica Manetti seedling in the High Atlas Mountains of central-eastern Morocco.
Photo M. Bendriss Amraoui.

Conclusion

In this study on *Cedrus atlantica* in the High Atlas Mountains of central-eastern Morocco, there is significant ecological variation in pollen production, germination, and elongation among geographical localities. Our results suggest an extrinsic control of *C. atlantica* characteristic reproduction by site, precipitation, and humidity in September. However, these data on the effect of location on pollen remain fragmentary and call for further studies to better elucidate the effect of climate in interaction with radiation, pollen size, and carbon reserves on the pollen viability and tube length of *C. atlantica* for an efficient conservation of the genetic heritage of Moroccan cedars.

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Access to data
The data used to produce this study can be accessed with an agreement of the corresponding author.

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