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Contents

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Abstract : An extremely rare conifer with hardly more than 230 spontaneous individuals, the Saharan Cypress (*Cupressus dupreziana*) is undoubtedly the most emblematic plant species and one of the rarest in the immense Sahara Desert. This tree has a very restricted distribution. It is located in a mountainous massif of the central Sahara in the southeast of Algeria. Given its extreme rarity and a very limited regeneration, it was estimated that the tree was in imminent danger of extinction. But is this true witness of more favourable past environments really doomed to disappear or will its extraordinary biological adaptations help it to get through the current climate and anthropogenic crises?

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Abstract : Vegetative propagation by cuttings of the Saharan Cypress is a difficult, but not impossible task. The author explains how to proceed and the time it requires to have a successful result. Comparison is made with another *Cupressus* species where the cuttings produce roots much more easily.

Abstract : *C. dupreziana* constitutes one of the most remarkable relics of the plant world, and the existence in the mountains of the central Sahara of an endemic cypress has aroused the interest of biologists for more than a century. The history of its discovery as well as the discussions over its taxonomic position are reviewed.

Abstract : A report on an experimental plantation of *C. dupreziana* established in 1984 in the South of France. The mortality is exceptionally high and the growth very limited because of the shallow soil and competition with local plants.

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Cover photo: *Cupressus dupreziana* near Tamghit, Tassili n'Ajjer, Algeria. 2005.12.14.
© Ph. & Y. Orsini. "Tree in majesty, superb trunk." P. Perret.

Bull. Cupressus Conservation Proj. 12 (1): 3-17 (31.12.2023) **F. Médail**[1]

The extreme resistance of the Saharan Cypress (*Cupressus dupreziana* A.Camus)

An extremely rare conifer with hardly more than 230 spontaneous individuals, the Saharan Cypress (*Cupressus dupreziana* A.Camus) is undoubtedly the most emblematic plant species and one of the rarest in the immense Sahara Desert. This tree, whose most beautiful specimens reach 22 m in height and 12 m in circumference, has a very restricted distribution (Maps 1 & 2). It is located in a mountainous massif of the central Sahara, the Tassili n'Ajjer plateau near Djanet in the south-east of Algeria. Long remaining unknown, this cypress has fascinated many botanists and explorers since the mid-nineteenth century. Given its extreme rarity and a very limited regeneration, several of them quickly estimated that the tree was in imminent danger of extinction. But is this true witness of more favourable past environments really doomed to disappear or will its extraordinary biological adaptations help it to get through the current climate and anthropogenic crises?

Fig. 1: Standing in the middle of the desert, this majestic tree seems to be a mirage. The Saharan Cypress keeps the memory of a Sahara that was green... but for how much longer? *Cupressus dupreziana* on the Tassili n'Ajjer, old individual in a sandy wadi in Aladoumen, expedition of December 2005.
(Photo © Ph. & Y. Orsini.)

A presence that has remained mysterious for a long time

The existence of the only Saharan conifer long remained an enigma for naturalists. The first European explorers, including the geographer Henri. Duveyrier (1840-1892) during his famous mission of 1861-1863, could not identify the tree which was used for the wood of the frames and the doors of the houses, and locally named tarot (pronounced "*taroot*") by the Tuareg. In his book *Les touareg du Nord: exploration du Sahara*, Duveyrier indicates: "the forest that produces this essence seems considerable, because all the woods used in the constructions of Rhât and Djânet come from it." But having only a "reported board sample", he doubtfully assigned this mysterious

[1] Professor, Aix-Marseille University, Mediterranean Institute of Biodiversity and Ecology (IMBE).
Original article published in French in 2019 in the journal **Espèces**, here with the addition of several new photographs.

Fig. 2: Saharan Cypress, pruned, Tamghit. (Photo P. Simonneau 1957-1958.)

specimen to the Arar (*Tetraclinis articulata*), another conifer endemic to the middle mountains of North Africa still widely used in marquetry and cabinetmaking, and in the manufacture of various objects sold in the Moroccan souks. Duveyrier also reports that the Tuareg extracted tar from it and that the resin was used to make sonorous the strings of local violins or *rebâza*.

It was not until 1924 that Captain Maurice Duprez met two living trees about ten meters high and a third dead tree, by chance, during a Meharist mission in the Tamghit valley (or Tamrit), located east of the Djanet oasis (south-eastern Algeria). During the Tunis mission to Chad, in 1925, the forest inspector Louis Lavauden finally brought back the first samples that allowed the French botanist Aimée Camus to describe this new species. Then, during a scientific mission carried out in 1949, Claude Leredde was able to collect a greater number of *tarot* cones which seemed

Fig. 3: *Cupressus dupreziana* cones. (Photo © Ph. & Y. Orsini.)

morphologically different to Professor Henri Gaussen, from the University of Toulouse, since he described a new taxon, *Cupressus lereddei* Gaussen. A morphological analysis of these new harvests showed that these cones, although larger, were in fact within the range of variation already known from *Cupressus dupreziana*.

Current distribution and ecology

The Saharan Cypress is distributed over an area of 750 km², in an area of about 120 km long and 6 km wide on average, located in the southwestern part of the Tassili n'Ajjer plateau near Djanet, between the Tiddedj wadi in the north and in Ghaldjiwen in the south. The distribution area is divided into two large groups, the Tassili Hedjrit region, and the Madak-Tazolt region (Maps 1 & 2, pp. 16-17). The existence of the species in the Hoggar massif has been assumed several times, but the remnant of the imposing trunk observed in 1953 by Pierre Quézel in a wadi near Tin Tarabine during his mission for the Institut de recherché sahariennes (Saharan Research Institute) corresponds in fact to an acacia (*Faidherbia albida*) according to the dendrological analysis carried out by Mr. Michel Thinon (CNRS France) during the 2000s.

For several decades, censuses of individuals of the Saharan Cypress have given rise to various estimates and interpretations. The first detailed population analysis was that conducted by Jean-Paul Barry and his collaborators in 1965, during a mission for the Institute of Saharan Research. They counted and mapped 83 individuals in their monographic study published in 1970. In 1972, the forester Saïd Grim drew up an almost complete inventory listing 230 living and 153 standing dead trees, an assessment very close to that conducted in 1997-2001 by two Algerian researchers Fatiha Abdoun and Mohamed Beddiaf who recorded 233 living individuals. This suggests that the cypress survived the last extreme aridification episode of the 1970s-1980s.

Fig. 4: Saharan Cypress, Tassili n'Ajjer, Tamghit. (Photo © F. Médail.)

The species is found over an altitudinal range between 1,430 m and 1,830 m, with an average altitude of 1,700 m. The average rainfall is of the order of 30 mm per year. Cypress individuals occupy the beds of sandy wadis (37% of individuals), rocky beds with sandy veneers (31%), sandstone slab cracks (22%) and, more rarely, the ridges (8%) and the edges of temporary pools or *gueltas* (2%). In the sandy wadis of the Tamghit valley, the cypress dominates a plant community formed by two low shrub species, *Deverra scoparia* and *Pulicaria crispa*, and the grass *Stipagrostis pungens*. After the rains, it is not uncommon to meet mats of a bulbous plant close to the colchicae, the *Androcymbium gramineum*. In the more rocky biotopes, the cypress meets with several plants of Mediterranean affinity such as Saharan Myrtle (*Myrtus nivellei*), Laperrine's Olive (*Olea europaea* subsp. *laperrinei*), a lavender *Lavandula antineae* and Tripartite Sumac (*Searsia tripartita*, Anacardiaceae). But the cypress does not individually form a particular plant grouping in terms of floristic composition, nor a "forest" as has been argued by some ancient authors.

Fig. 5: Saharan Cypress, Tassili n'Ajjer, sandy wadi in Aladoumen with *Deverra scoparia*, mugwort and launea. (Photo © Ph. & Y. Orsini.)

A remnant of the "Green Sahara"?

The Saharan Cypress is the vicariant[2] of the Atlas Cypress (*Cupressus atlantica*), a tree endemic to the High Atlas (Morocco) and located 1,700 km from its Saharan congener. These two taxa have sometimes been considered as two distinct varieties of *Cupressus dupreziana*, but a phylogenetic study has just confirmed that they are indeed two entities that can be distinguished at the rank of species (Sekiewicz *et al.* 2018). The results show that the differentiation between the two cypresses occurred about two million years ago (early Pleistocene), while the separation between this African lineage and the Mediterranean lineage (which includes the Mediterranean Cypress, *Cupressus sempervirens*) dates back about ten million years (late Miocene). This diversification must be explained by the isolation of the cypress populations following the intense palaeo-environmental modifications induced by the widespread aridification of the Sahara which occurred about three million years ago, then by the alternation of wet and dry periods.

[2] Vicariant: relating to the geographical separation of an initial distribution area of an ancestral species into one or more entities that will gradually differentiate to form related taxa.

Wood samples taken from the *tarot* doors of old houses of Ghât and Barkat (in Libya) have made it possible, by dendroclimatic[3] analysis of the rings and Carbon-14 dating, to provide indications on the palaeo-environments of the eastern part of Tassili n'Ajjer since the Middle Holocene. Major phases of drought that occurred around 5900-5750 and 5100 years before the present were followed by wetter periods, and the current conditions of very high aridity began only about 500 years ago in this region. Thanks to palynological analysis of Holocene sediments, Cupressaceae pollen most probably attributable to Saharan Cypress – as the only Saharan representative of this family – have been found in regions of the Libyan Sahara (Acacus and Messak Sattafet) adjacent to Tassili n'Ajjer. They are evidence of a more eastern extension of the species during the humid phases of the Holocene, around 8,000 and 7,000 BC. The current populations therefore form the last relics of a formerly larger distribution.

An exceptional strategy of persistence

The *tarot* could probably be maintained until now in the Tassili n'Ajjer thanks to the individuals present in the mountains, at the edge of a few wadis which guarantee additional humidity compared to the very arid environment of the reg[4] and the rocky slopes nearby. Its extensively developed root system is inserted deep into the crevices of the rock, from where it can withdraw substantial moisture. In the mountains, where the cypress is distributed, the climate is more favourable than in the extremely arid Djanet plain, and the occult precipitation (fog, dew) must provide a surplus of moisture absorbed by the foliage. But in the absence of any microclimatic study on its ecological niche, it is not possible to estimate the importance of this factor in the survival and regeneration of the species.

This cypress is also characterized by considerable longevity: the individuals studied by F. Abdoun and collaborators have an age between 600 and 2,400 years, and they show very reduced growth of their rings, between 0.07 and 0.3 mm per year in old cypresses. On the other hand, young individuals show vigour comparable to that of other cypress species, and the radial growth of their trunk can reach 2.23 mm per year. But the most extraordinary thing remains its unique reproductive strategy in the world, of the “surrogate mother" type (see Appendix A).

Fig. 6: Saharan Cypress wood door of an old house in Ghat, Libya. (Photo © Ph. & Y. Orsini.)

Threats and conservation

The historical analysis of the distribution of this cypress shows, since the mid-nineteenth century, a decline of about 100 km towards the south of the area, attested by the presence of dead wood in at least two northern localities (wadis Ahloun and Djerat).

3 Dendroclimatic: relating to the retrospective study of the relationships between climatic parameters and the analysis of tree rings over long periods.

4 Reg: generally flat surface covered with pebbles of variable size and shaped by the wind. It derives from a skeletal soil abraded by wind action.

The species was also present in the region called Edehi from where it must have disappeared between the 1920s and 1950s. This retraction must be attributed in large part to the intense exploitation of cypress wood by the inhabitants of the Djanet and Ghât oases who used it in carpentry and cabinetmaking. Since 1972, twenty trees have died, a loss of 8% in thirty years, but two juveniles have been discovered, proof that germinations remain possible even if they are exceptional.

Due to its limited distribution, the reduced number of individuals and the very low regeneration, the cypress therefore remains a very threatened and vulnerable species. It is further threatened by anthropogenic impacts, with most of the trees bearing traces of pastoral pruning, and are browsed to the height of a Dromedary Camel's head. In addition, a recurring threat has emerged for over a decade, linked to the increase in transit, between Djanet and Ghât, by sub-Saharan migrants who illegally use tarot as firewood.

If a rescue plan for the species was defined in 2006, the political instability affecting the Sahelo-Saharan region has so far thwarted its concrete application on the ground. The Algerian government created in 1972 a controlled reserve of 3,000 km² in Tassili n'Ajjer in order to guarantee above all the protection of the rock engravings of the Tamghit plateau. Then, the Tassili n'Ajjer National Park was established, but with the objective of preserving the archaeological heritage; its official name has also become since 2011 "Tassili Cultural Park". In fact, current *in situ* actions in favour of the preservation of this cypress remain minimal. However, the cultivation of *C. dupreziana* in vitro and the micropropagation techniques are now well established (Lábusová *et al.* 2020), and this increase the chance of preservation of its genetic stock.

Fig 7: Mouflon and jelly-fish, the rich bestiary of the "Green Sahara" in the Middle Holocene; rock engraving in Tassili n'Ajjer, Tamghit.

December 2005.
(Photo © F. Médail).

Despite these threats, it is difficult to classify this cypress as a relic destined to disappear with the aridification of the Saharan climate, a phenomenon that seems neither linear nor inevitable. The Saharan Cypress has a life cycle rooted in long time: there is no need to reproduce every year when it can cross without damage – or almost – centuries, even millennia. The *tarot* seems to be rather well adapted to current environmental conditions and it continues to regenerate spontaneously *in situ*. But the pressures of man and his livestock must be moderated, and this is the aspect that remains the most worrying. It remains to undertake precise and regular monitoring of the species, both demographically, ecologically and environmentally, and to set up an effective protected area in order to safeguard in its ultimate refuge this extraordinary biogeographic witness of a distant "green Sahara".

Appendix A

A reproduction of the "surrogate mother" type

In seed plants, sexual reproduction is the most frequent reproductive system. The diploid[5] embryo is of two-parent origin and it results from the fertilisation of a haploid female gamete by a haploid male gamete. In the rarer cases of reproduction by classical or "maternal" apomixy (encountered in about 35 families of angiosperms), there is the production of a diploid embryo of uniparental origin, derived from maternal tissue. But at the beginning of the 2000s, a Franco-Italian team led by Christian Pichot (INRAE Avignon) has highlighted a hitherto unknown reproductive process in Saharan Cypress: atypical meiosis which systematically leads to the production of diploid (unreduced) pollen. Reproduction therefore takes place by paternal apomixy, that is to say the production from the diploid pollen of embryos of solely paternal origin in the maternal tissues, inside the female gametophyte (the embryonic sac) which brings only the nutritive substances. The embryogenic capacity of the diploid pollen of the Saharan cypress has been demonstrated in the context of interspecific pollination with Mediterranean Cypress (*C. dupreziana* pollinating *C. sempervirens* L.). This mechanism therefore allows the development without fertilization of the embryo which feeds on the tissues of the "surrogate mother". This atypical reproductive system may explain the very low proportion of viable seeds, generally less than 10%, which contributes to the low natural regeneration observed *in situ*. The analysis of the genetic diversity of the Saharan cypress also highlights a weak differentiation between populations and individuals, but there is an accumulation of different mutations on each chromosome of a pair.

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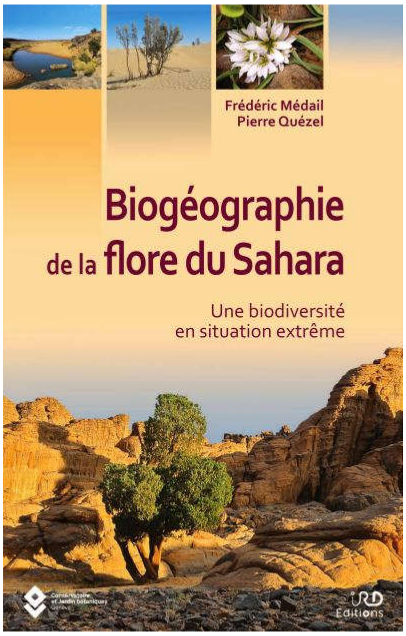

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[5] Diploid: which has 2n chromosomes, as opposed to haploid which has n chromosomes.

Fig. 8: *Cupressus dupreziana* another individual in the sandy wadi in Aladoumen. (Photo © Ph. & Y. Orsini)

Fig. 9: Aerial view of the Tassili n'Ajjer looking northwest, showing the oasis of Djanet on the left, the cliffs running east and north of the town and the plateau which shelters the few remnant *Cupressus dupreziana* trees. Compare with maps 1 & 2, p. 16-17. (Photo © F. Médail.)

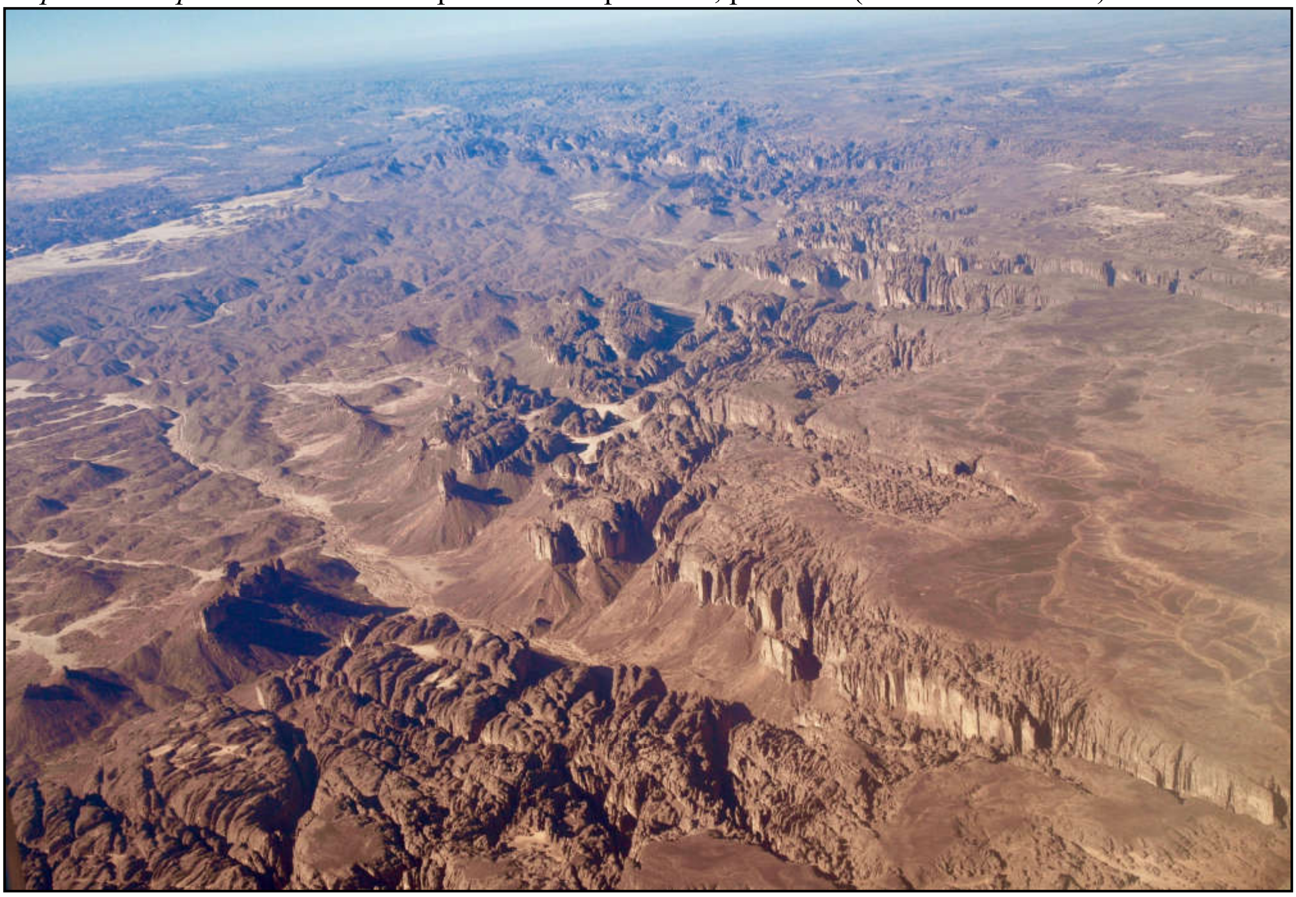


Fig. 10: *Cupressus dupreziana* in Tamghit. (Photo © F. Médail.)

Fig. 11: *Cupressus dupreziana* in Tamghit. (Photo © F. Médail.)

Fig. 12: *Cupressus dupreziana* in Tamghit. (Photo © Ph. & Y. Osini.)

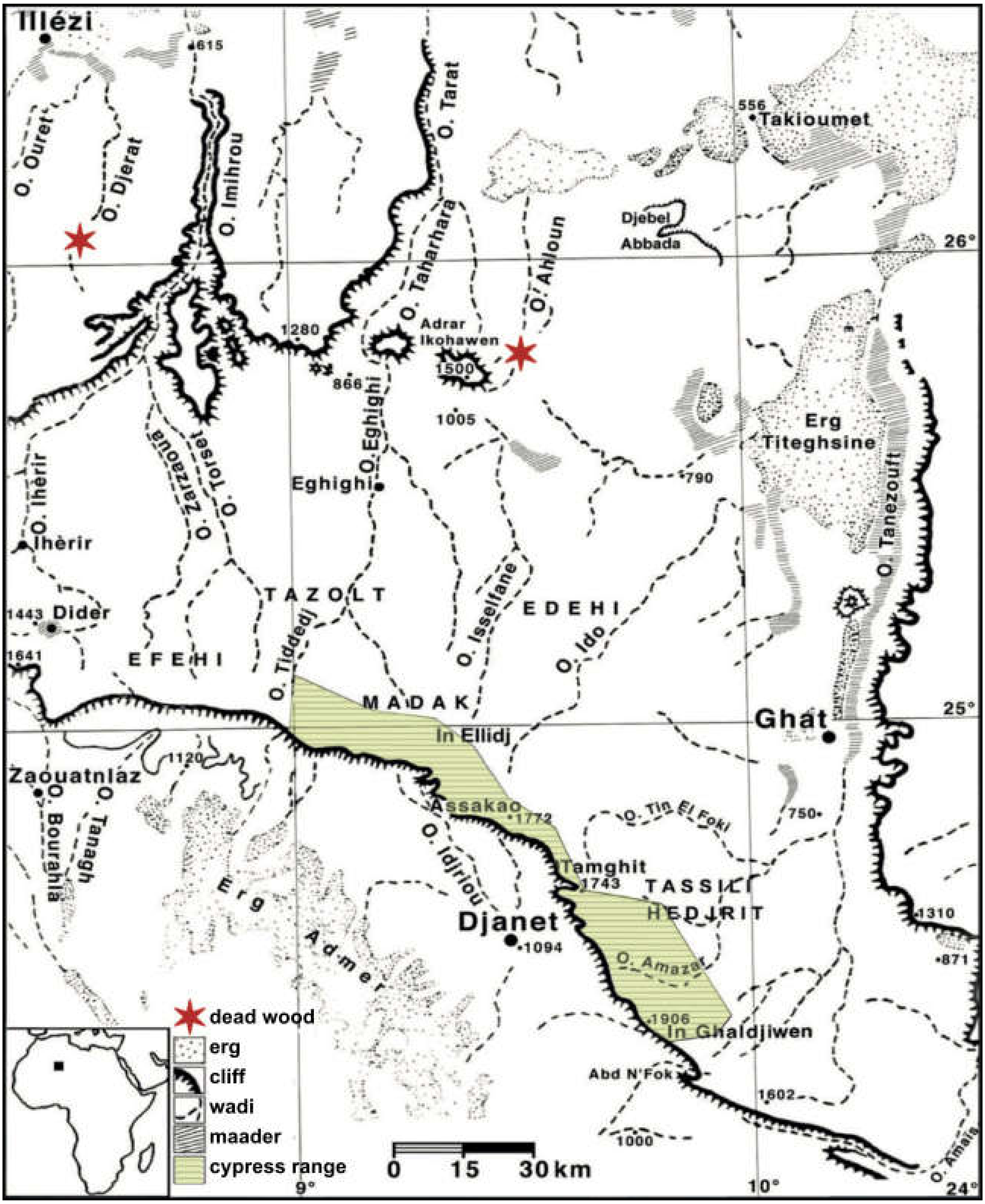
Fig. 14 (p. 13): *Cupressus dupreziana* in Tamghit. The presence of the photographers shows the real size of this centuries-old tree. (Photo © Ph. & Y. Orsini.)

Fig. 13: *Cupressus dupreziana* in Tamghit. (Photo © Ph. & Y. Orsini.)

Fig. 15: *Cupressus dupreziana* in Tamghit. (Photo © Ph. & Y. Orsini.)

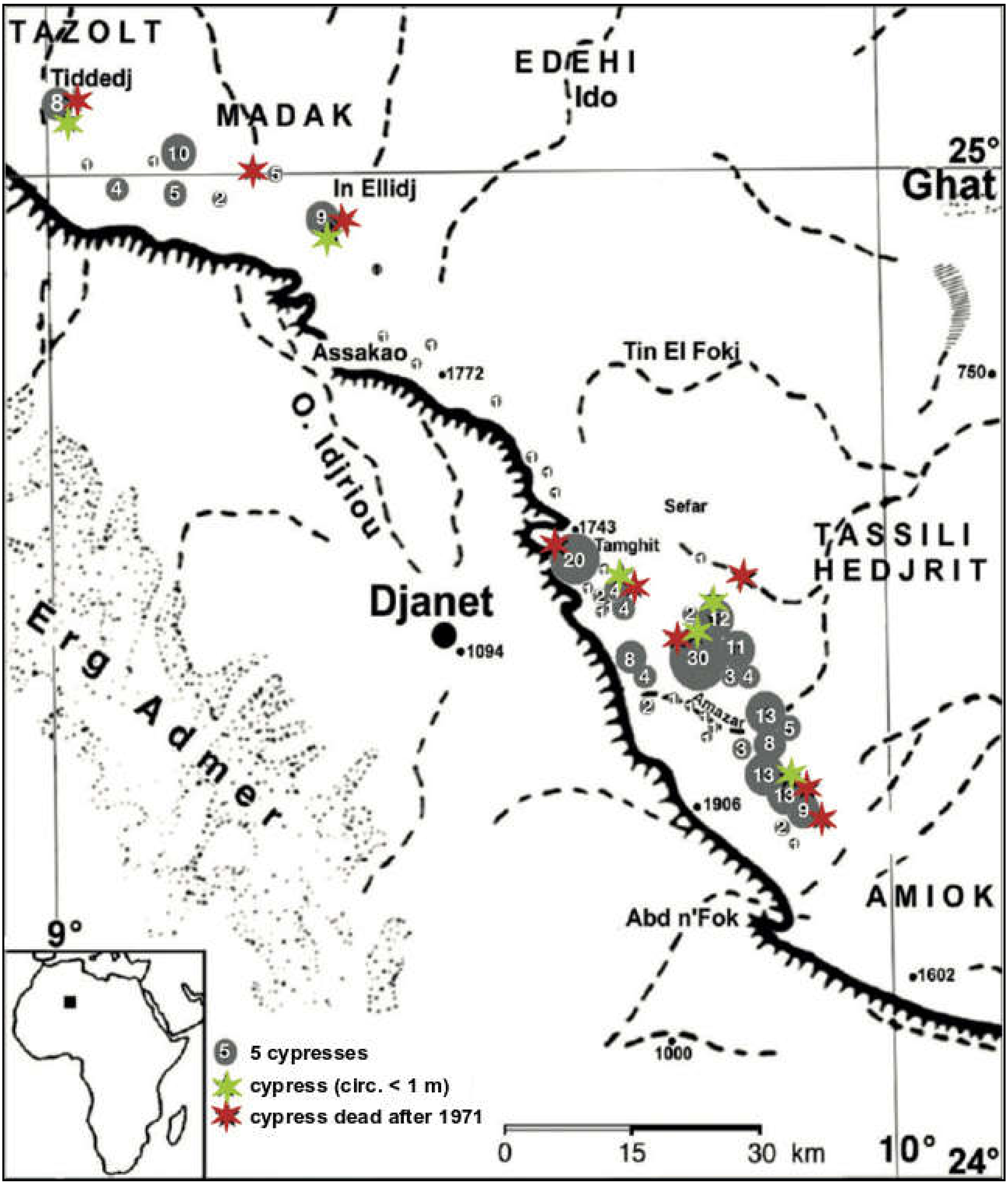
Fig. 17 (p.15): *Cupressus dupreziana*: huge pruned trunk. (Photo © F. Médail.)

Fig. 16: *Cupressus dupreziana* in Tamghit with a Kel Tamasheq. (Photo © Y. Orsini.)



Map 1: Current distribution range of *Cupressus dupreziana* (green hatching) in Tassili n'Ajjer (southeastern Algeria) and location of dead individuals (red stars) present beyond the current area (modified after Abdoun & Beddiaf 2002).

Erg: sand desert, usually with dunes.
Maader: flood zones in the main bed of the wadis.
Wadi: river valley with a temporary stream.



Map 2: Detailed map of the distribution range of *Cupressus dupreziana* showing for every locality the number of specimens (grey rounds) as well as the dead trees (red stars) and the younger ones (green stars) (modified after Abdoun & Beddiaf 2002).

Characterisation of French seed sources of *Cupressus dupreziana*, the only plant species with male apomictic reproduction known to date

Introduction

The Saharan Cypress (*Cupressus dupreziana* A.Camus), also known as Duprez Cypress or, more locally, Tarout by the Tuaregs ("Tree of thirst" in Tamahaq), is the only conifer in the Sahara. In its natural range, it can exceed 20 m in height and 12 m in circumference. The species is strictly endemic to the Tassili N'Ajjer plateaux in Algeria, where altitudes range from 1,500 to 2,000 m.a.s.l. and average annual rainfall does not exceed 30 mm (Abdoun 2002). The presence of conifers in the middle of the desert was suspected as early as 1860, when the English explorer H.B. Tristram suggested on his return from an expedition that "judging from the woodwork of the Tuareg saddles, there is also a species of hard resinous wood probably related to the junipers" (Tristram 1860). An observation that would later prove relevant insofar as the genera *Juniperus* and *Cupressus* are phylogenetically close, and both included in the family Cupressaceae.

The most recent inventory, carried out between 1997 and 2001 by Fatiha Abdoun and Mohamed Beddiaf, recorded 233 living trees, including a dozen young individuals, unevenly distributed over a strip 120 km long and around 6 km wide. Their study reveals numerous remnants of the species (trunks, branches, etc.), testifying to a population that was once much higher than the 165 dead trees recorded in 1972 (Grim 1982). Pollen of the genus *Cupressus* discovered during sediment analyses indicates an occupation of the species over 1,000 km from living trees, from neighbouring Libya (Mercuri *et al.* 1998) to northern Chad (Quezel 1978), at a time when the humid phases of the Holocene (8,000 to 4,000 BC) formed a much richer biome than today, commonly known as the "Green Sahara".

While the oldest living specimens have been estimated to be over 2,000 years old, the desertification phenomenon attributed to the region began only 500 years ago and probably forced the cypress population to persist only at high altitudes, where a few seasonal streams provided an additional source of moisture to the extremely arid environment of the reg[2] and surrounding rocky slopes: "Its root system inserts itself deeply into rock crevices from which it can draw substantial moisture." (Médail 2019). The lack of knowledge about the physiology of this cypress and the climatic conditions it faces mean that it cannot be said to be able to subsist on the frequent fogs and dews of the Tassili plateau (Dubief 1999), nevertheless it is accepted that most conifers are able to absorb atmospheric moisture through their foliage (Oren & Sheriff 1995).

Its decline, estimated at 8% over a 30-year period (Abdoun & Beddiaf 2002), led the IUCN to place Saharan Cypress on the critically endangered species red list. Natural regeneration of 2-3 trees per century is not enough to maintain the population without effective protection. Indeed, the last representatives are subject to numerous pressures, mainly linked to pastoral pruning, but also and above all to the increasing cutting of wood for bivouacs by Tuaregs, clandestine migrants and tourist camps who come to admire the rock engravings in the region (Abdoun & Beddiaf 2002, Werner & Bubriski 2007). The plan to safeguard the species drawn up in 2006 has unfortunately never come to fruition, due to a lack of political stability (Médail 2019).

However, the Saharan Cypress's extreme resistance to drought is not the only reason for its success. Even more exceptionally, in the 2000s, a research team led by C. Pichot revealed the existence in this species of a sexual reproduction process that had never been observed in plants (Pichot *et al.* 2001). Normally, after meiosis, the male reproductive cell of spermaphytes has only one set of chromosomes, which, after fusion with the female reproductive cell, also haploid, gives the embryo a biparental genetic heritage. However, by observing the unusual size of pollen grains in *Cupressus dupreziana* (38 µm, the largest of all cypress species) and analyzing them by flow cytometry, the researchers discovered a high production of unreduced gametes (around 75%). By tracing the origin of this genetic singularity, an exceptional occurrence of meiotic anomalies was revealed, which in this species seem to have become the norm (El Maâtaoui & Pichot 2001). These anomalies affect the production of healthy gametes and

[1] Original document published in French, cf. p. 31, thesis for a master title at the Perpignan University Via Domitia.
[2] Reg: stony desert

may explain the very low germination rate (less than 10% of seeds are normally formed). In some cases, however, they result in a diploid pollen grain, which, after penetrating the ovule, generates an embryo of exclusively paternal origin. Here, the female gametophyte is dedicated solely to the development of the embryo and its supply of nutrients. In other words, no genes are transmitted by the female way. The Saharan Cypress generates clone-like embryos from the "father" developing thanks to the "surrogate mother" ability. Perhaps the most surprising consequence of this male apomixis is that *C. dupreziana* ovules also allow the development of all-paternal embryos from pollen produced by another species, *Cupressus sempervirens* L. (Pichot *et al.* 2008). So, depending on the pollinating species around it, a seed harvested from a Saharan Cypress can just as easily give rise to a diploid Saharan Cypress seedling as to a haploid and sometimes homozygous diploid *C. sempervirens* cypress by doubling the initial set of chromosomes. A few cases of interspecific triploids have also been detected. Cultivation trials carried out by INRAe between 2000 and 2005 showed that, out of 1169 cypress trees from 4 *ex situ* collections, the proportion of *C. dupreziana* seeds resulting in a seedling of the same species varied from 30% to 50%. The others turned out to be mostly homozygous *C. sempervirens* cypresses, regularly expressing strong morphological anomalies (Nava 2008). The variability in full-seed rate and the production of *C. dupreziana* versus *C. sempervirens* embryos remain to be explained.

The present study continues the characterisation of the reproductive system of Saharan Cypress, by specifying in greater depth the resources that can be mobilized for this species. To this end, an experiment was set up to study seed lots and produce seedlings from a larger number of French provenances. The two objectives are to analyze i) the germination capacity of the seeds produced, and ii) the proportion of *C. dupreziana* or *C. sempervirens* embryos, depending on the origin of the stand and the surrogate mother. The aim is also to determine the stage of development of the seedlings at which confusion, on a morphometric basis, between the two species is no longer possible. This work also provided an opportunity to resume the work carried out by C. Laguerre, by updating the inventory of the species on a national scale (C. Laguerre 2006).

Materials and Methods

Plant material

Trees sampled: in order to assess the variability of seed characteristics according to origin, seeds were collected following a stratified sampling plan at 2 levels: sites and mother trees within sites. Cones were collected from October 2022 to February 2023 from 55 trees aged between 14 and 58 years, representing 12 French sites, all located in south-eastern France (Fig.1). For each of these trees, 20 cones had their seeds removed before being weighed and measured. Seeds were stored in a cold room at a temperature of 5°C.

Seeds and germination: in total, around 135,000 seeds were collected by drying the cones before being sorted and weighed (total batch weight, sampling of 4 x 100 seeds per batch, determination of weight per 1000 seeds), then immersed in a 2% dilute acetic acid bath for 90 seconds (Fig. 2a). This treatment based on the literature on seed aseptization (ITAB 2013, Venail *et al.* 2017, Piyatida Inpitak & Udompijitkul 2022) was adjusted to the size and permeability of *C. dupreziana* seeds.

The germination test was split into two series, from 17 February to 13 May 2023 for the first, and from 14 April to 14 June 2023 for the second. In each series, seeds from the same "mother" were distributed in 3 petri dishes of 25cm², thus constituting 3 repetitions. The dishes were first cleaned and then immersed for 1 hour in a 1/10° solution of 2.6% chlorine bleach. Each box contained a sheet of blotting paper sterilized by moist heat under pressure (autoclave), on which a predefined quantity of seeds was evenly distributed (Fig. 2b). Flexible forceps, pillboxes and beakers were regularly disinfected by dry heat for one hour at 140°C, and sterile gloves were used throughout seed handling.

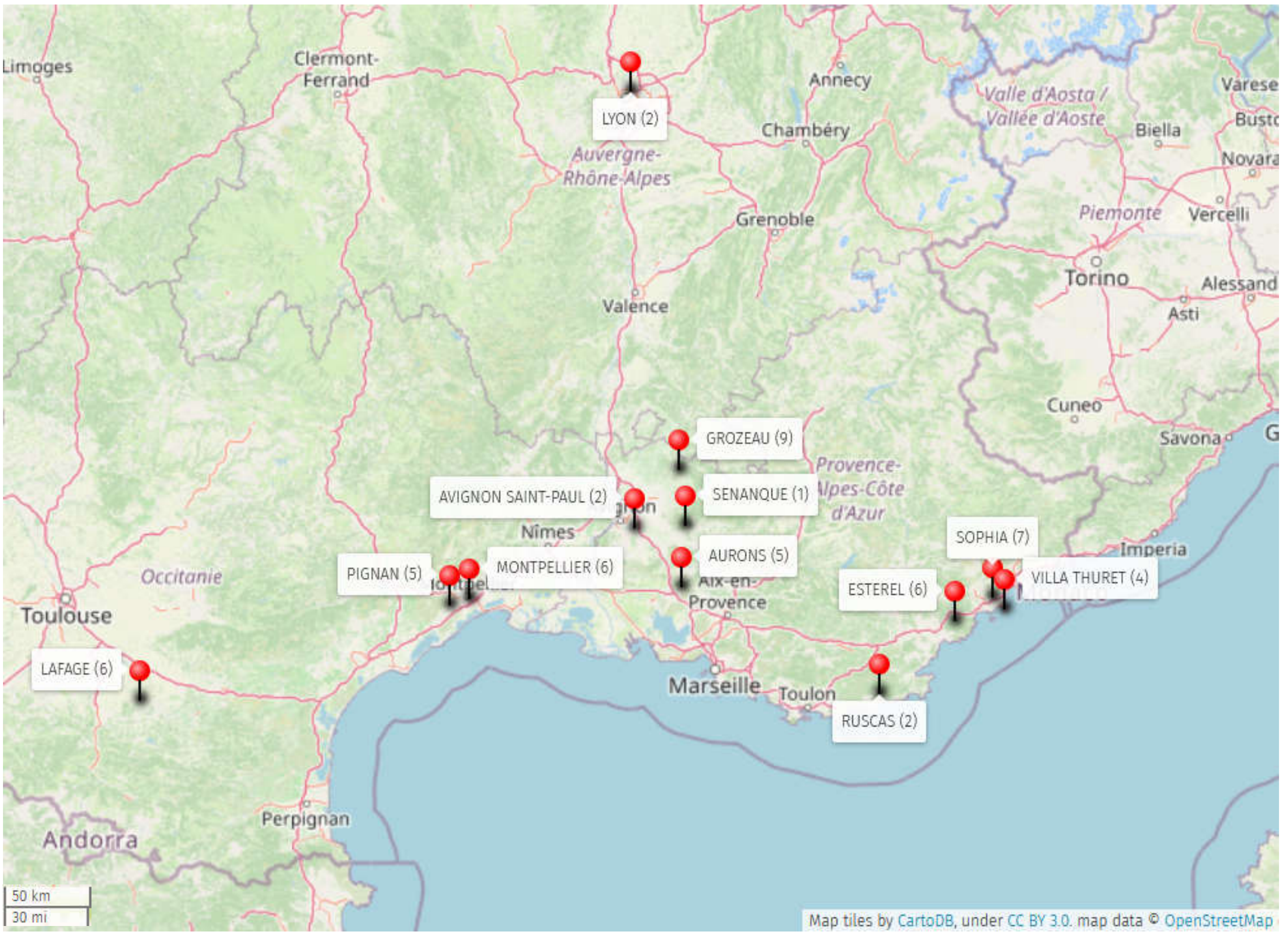


Fig. 1: Tree sites sampled (number of cypress trees sampled)

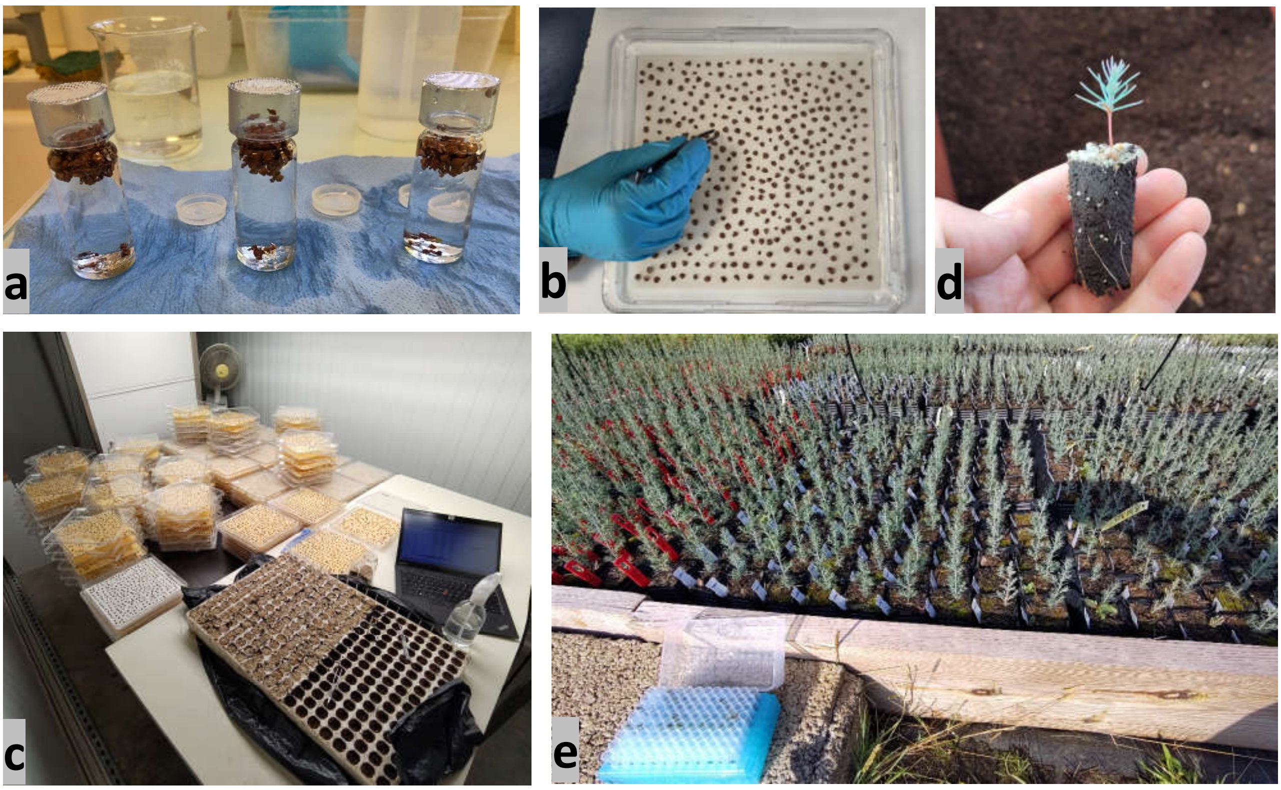


Fig. 2a-e: Experimental procedure. **a** Aseptisation of seeds. **b** Installation of seeds in petri dishes. **c** Sowing of seeds in soil. **d** Size of seedling before transplanting into 600cm³ containers. **e** Sampling of seedlings for genotyping.

Of the 55 batches included in this experiment, 10 showed clear-cut holes of around 1mm in diameter on their seeds, suggesting the presence of insect larvae in the seeds.

The 6 petri dishes containing the seeds of a mother tree were set up in different locations: two climate-controlled chambers (Fig. 2c) (average humidity: 70.3%; avg. T°: 20.6°C; min. T°: 10.4°C; max. T°: 25.5°C; LED lighting 12h/day) and a laboratory (average humidity: 52.8%; avg. T°: 18°C; min. T°: 13.5°C; max. T°: 25.3°C; natural lighting). Humidity and temperature were recorded by HOBO Pro V2 at 5-minute intervals. The blotting papers were kept moist throughout the experiment by adding distilled water using a spray bottle. In order to characterize the seeds in terms of size and quantity, the 343 petri dishes were photographed before germination according to a standardized protocol. The dishes were placed under a plexiglas box surrounded by an LED strip for uniform illumination of the seeds. Photos were taken with a Fairphone 4 smartphone equipped with a 48MP sensor, positioned at the top of the plexiglas box and leading to a resolution of 14 µm.

Regular monitoring of the germination enabled precise evaluation of the radicle emergence date, with daily resolution. Each germinated seed was assigned a unique number, ensuring traceability throughout the experiment. The germinated seeds were transferred to germination plates comprising 285 wells, and the seedlings were raised in a culture chamber for around 2 weeks before being transferred to the Naudet nursery in Lambesc (Bouches du Rhône). The seedlings were then raised in a greenhouse for around 4 weeks, then transplanted at the appropriate time (Fig. 2d) into 600 cm^3 containers and acclimatised to outdoor conditions.

Measured characteristics

Seed size: petri dish photographs were analyzed using scripts executed by the GRASS and QGIS software packages. These scripts enabled precise clipping of the seeds and automatic recording of the geometry and surface area of each seed in a PostgreSQL database.

Cotyledon colour: given the bluer appearance of foliage in adult *C. dupreziana* individuals, a colorimetric analysis of cotyledons was set up to assess whether the pigment variation observed in seedlings could be used to deduce species. To this end, 8 germination plates with 285 wells were photographed every 3 days for 6 to 15 days. Images were captured using a tripod-mounted Canon EOS 450D 12MP camera. The seedlings were photographed in a darkroom where no outside light could alter their hue and using the camera's flash to ensure uniform exposure for each shot (V: 1/80, f: 5.6). Colorimetric analysis and image processing were carried out using PostgreSQL, GRASS and QGIS software.

Species assignment of the seedlings

Phenotyping: we observed the morphological characteristics of the seedlings after they had all reached an age of over 40 days. Identification focused on phyllotaxis, seedling growth and leaf length and shape. A second person, a *Cupressus dupreziana* specialist, took part in this exercise on half of the plants produced, to mitigate operator bias. This collaborative approach enabled us to achieve 98% cross-validation of observations.

Genotyping: the results obtained by observation were further strengthened by a sampling approach dedicated to genotype determination on around 10% of the seedlings produced. Semi-random leaf sampling was carried out throughout the production (Fig. 2e) on 100 seedlings identified as *C. dupreziana*, 100 seedlings identified as *C. sempervirens* and 154 seedlings for which visual identification remained uncertain. Our genetic analyses therefore involved 354 individuals, to which 23 controls were added. For this study, DNA from the samples was extracted from the leaves (50 mg) using QIAGEN DNeasy 96 plant kits, before being amplified by PCR. Genotyping was carried out on a HITACHI 3730xl DNA Analyzer capillary sequencer using microsatellite markers developed for *C. sempervirens* by Sebastiani *et al.* (2005) and already used by INRAe for seedlings from *C. dupreziana* mothers (Nava *et al.* 2009) : CYP 174 (800 nm), CYP 257 and CYP 258 (700 nm), CYP 293 (800 nm).

Environmental characterisation of sites

Meteorology: the trees sampled are planted along an altitudinal gradient that ranges from 27 m (Montpellier, Hérault) to 410 m (Ruscas, Var), at sites up to 400 km apart. As a result, it seemed appropriate to integrate the climatic conditions of each site into our analysis, focusing in particular on those associated with the pollination period of the harvested cones (January-February 2021). To do this, we used the monthly temperature and rainfall data available on the meteociel.fr website, from the weather stations closest to the sites studied (average distance: 16.7 km; maximum distance: 40 km).

Distance to the sea: to complete our database, we also included in our model the distance separating the mother trees from the Mediterranean Sea. This factor is designed to capture the effects of atmospheric humidity, marine air masses and the influence of local microclimates. These data were estimated using the uMap website.

Statistical analysis

Germination and proportion of *C. dupreziana*: we chose to withdraw from our study the data from these 3 maternal progenies: Thuret J2007 for the uncertain nature of the species of the mother tree and its abnormally high germination results, Grozeau 48/303 for the low quantity of initial seeds and the total absence of germination, and Lafage 1, for which the seeds come from cones pollinated one year earlier than the others (2020 and not 2021).

All analyses were performed using Rstudio statistical software. Germination rates and proportions of *C. dupreziana*, expressed as binomial data, were analyzed using generalized linear regression (GLM) with the logit link function (log(p/(1-p)). We assessed the effects of factors (site of origin, mother, series, place of cultivation) and variables (seed size, germination rate, distance from the sea, age of mothers, temperature and rainfall) using deviance analyses (ANOVA function with chi-square test on the GLM model). The data (germination rate and proportion of *C. dupreziana*) were also analyzed using a linear model built according to the following design:

glm(cbind(germination$Nbgermees,germination$Nbnongermees)~dateplantation+tmax01+distmer+serie+labo%in%serie+Prov+Mere%in%Prov, data=germination, family=binomial)

To improve the fit with a more normal distribution, we then worked on the square root of the germination rate, which better conformed to the assumption of normality required for statistical analyses.

Cotyledon colorimetry: we trained a model to predict species based on cotyledon colour. A pre-processing phase normalised our data, taking into account the intensity level of red and green, as well as the proportions between red, green and blue (RGB). Then, the distribution of values indicating the discriminative power of the model was estimated by bootstrapping (1000 replicates with 70% of data for model calibration and 30% for model validation). For each run, the linear discriminant analysis model was used in the form:

lda(espece~green+red+BGratio+BRratio+RGratio, data = train).

Results

Seed germination

Aseptisation of the seeds and environment was very effective, despite the appearance of mycelia at the end of the process (with no impact on germination). A few larvae of Cecidomyiidae, probably in the genus *Contarinia* that grows in cypress seeds in southeastern France (Boivin & Auger-Rozenberg 2016), were observed in around 10 seeds from the Antibes region. Around 0.5% of germinated seeds contained two embryos (Fig. 3c-d), whose natural disappearance of one of the two radicles in the more or less short term systematically left room for a single individual. Several radicles also showed an abnormal appearance (shape, colour, truncated apex), often associated with a slower growth rate (Fig.3 e-h). As none of them survived, genetic analysis of these seedlings could not be undertaken. Nevertheless, according to Nava (2008), these morphological anomalies inherit from "genetic defects naturally present in *C. sempervirens* and here revealed due to the haploid or diploid state probably homozygous". This inbreeding depression could explain the phenotypic aberrations observed for numerous *C. sempervirens* radicles (Fig.4 b-d) as well as the high juvenile mortality rate (25.9% of the germinating embros, most of them dying before transplanting at 6 weeks).

Germination analysis

The overall germination rate was 4.55% (4889 from the 103772 seeds), ranging from 0.38% to 10.99% between mothers.

All the climatic data recorded during the pollination period were highly correlated. We only retained the maximum daily average temperature of January 2021, this variable proving to be the most representative of them all (Fig. 5a). The principal component analysis graph (Fig. 5b) shows the distribution of sampled sites according to pollination weather conditions (Tmax01), distance of sites from the sea (DistMer), and the year in which the mothers were planted (DatePlantation). These include the two plantations of different ages at the Grozeau site (GROZEA), represented by the formation of distinct clusters.

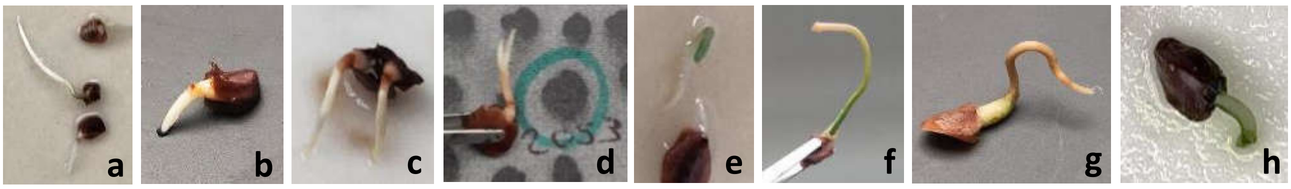


Fig. 3a-h: Observation of different types of germination. **a-b** Reference radicles. **c-d** Seeds containing two embryos. **e-h** Various anomalies observed during the germination phase.

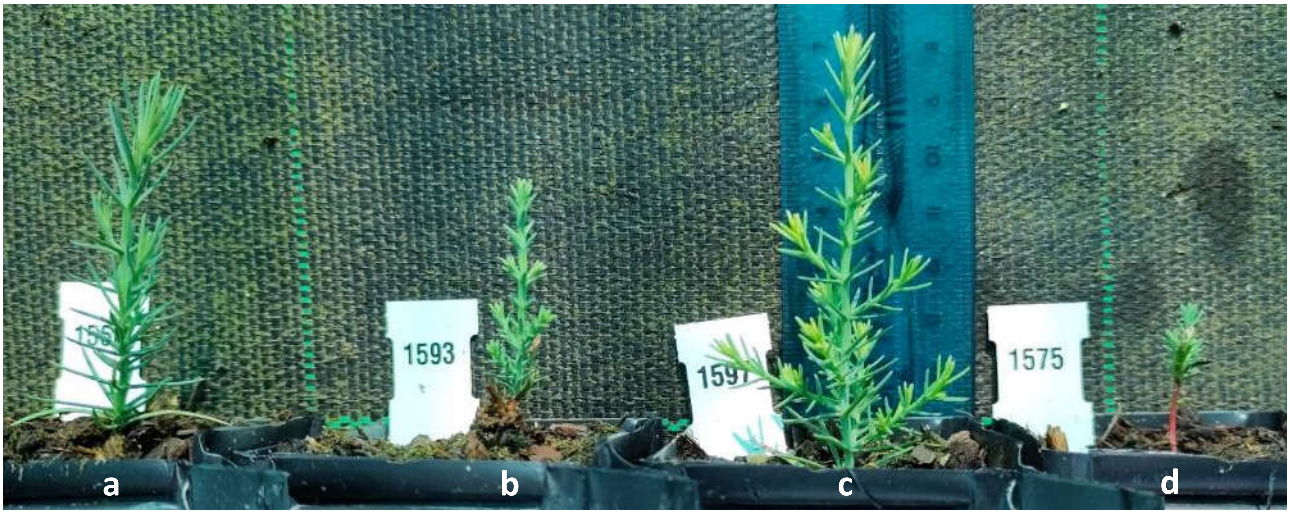
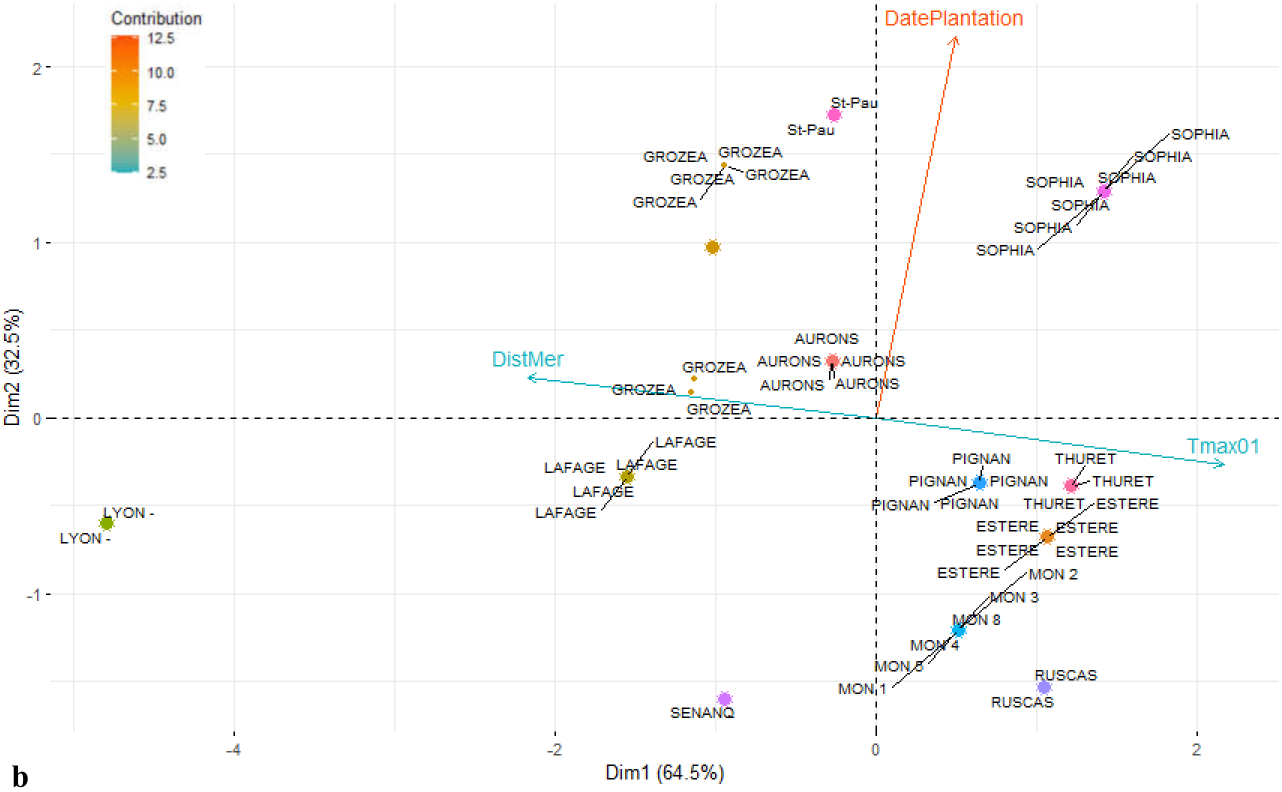


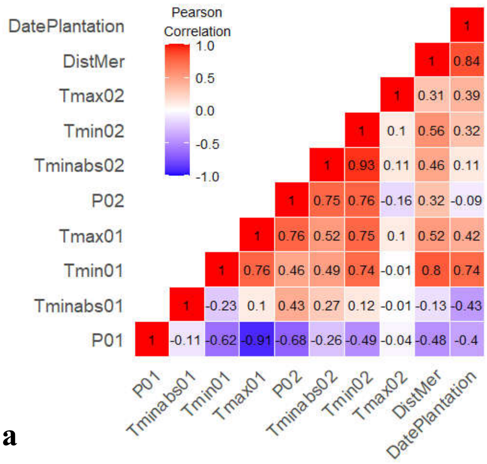
Fig. 4a-d: Phenotypes of seedlings from *C. dupreziana* seeds germinated on the same day.
a *C. dupreziana* seedling. **b-d** *C. sempervirens* seedlings.

Analysis of variance-covariance: results (cf. Table 1, p. 24) show a strong impact of the Mother and Provenance factors, as well as a significant correlation with the maximum temperature during the pollination period and the distance of the sites from the sea. However, by reversing the order of the variables "tmax01" and "distmer", "distmer" loses its significance (Table 1a, c), suggesting that despite the strong correlation between the two variables, climatic conditions during pollination (tmax01) have a greater impact on germination than mere distance from the sea. We also note the limited influence of mothers' age (DatePlantation) and the absence of any effect of growing location (labo). The significant influence of the series contrasts with that of growing location and could be linked to slightly different seed watering methods and temperature cycles.



b

Fig.5 a-b: Analysis of covariates
a by Pearson correlation **b** by projection (PCA)
With : **P01:** Precipitation for January 2021, **P02:** Precipitation for February 2021, **Tmax01:** Average of maximum T°C for January 2021, **Tmax02:** Average of maximum T°C for February 2021, **Tmin01:** Average of minimum T°C for January 2021, **Tmin02:** Average of minimum T°C for February 2021, **Tminabs01:** Absolute minimum T°C for January 2021, **Tminabs02:** Absolute minimum T°C for February 2021, **DistMer:** Distance to the sea, **DatePlantation:** Planting date of mother trees.



a

Table 1a-c: Results of the analysis of variance of the effect of variables and factors on germination according to their sequence of integration in the model **(a b c).**

a

	Df	F value	Pr(>F)	
dateplantation	1	0.290	0.590578	
distmer	1	175.412	< 2e-16	***
tmax01	1	42.368	4.43e-10	***
serie	1	12.024	0.000623	***
Prov	8	36.250	< 2e-16	***
serie:labo	4	0.402	0.807042	
Prov:Mere	34	4.618	7.30e-13	***
Residuals	238			

b

	Df	F value	Pr(>F)	
tmax01	1	211.905	< 2e-16	***
distmer	1	0.427	0.513971	
dateplantation	1	5.738	0.017372	*
serie	1	12.024	0.000623	***
Prov	8	36.250	< 2e-16	***
serie:labo	4	0.402	0.807042	
Prov:Mere	34	4.618	7.3e-13	***
Residuals	238			

c

	Df	F value	Pr(>F)	
dateplantation	1	0.290	0.590578	
tmax01	1	217.653	< 2e-16	***
distmer	1	0.127	0.722253	
serie	1	12.024	0.000623	***
Prov	8	36.250	< 2e-16	***
serie:labo	4	0.402	0.807042	
Prov:Mere	34	4.618	7.3e-13	***
Residuals	238			

Generalised linear model: applying the deviance analysis on a binomial GLM model (germinated seeds – non germinated seeds), we find results broadly similar to our previous data analysis (cf. Table 2). On the other hand, the effect of mothers' age on germination becomes highly significant after tmax01 and distmer have fully expressed their share in the variability. The "distmer" variable remains significant whatever its position in relation to "tmax01", although the latter retains a stronger effect on germination when placed before "distmer" in the model (Table 2a, 2c). We should also mention the p-value associated with growing location (labo), which acquires statistical significance here despite its low value.

Table 2a-c: Results of statistical analysis based on the generalized linear model evaluating the influence of variables and factors on the germination process according to their sequence of integration in the model **(a b c).**

a

	Df	Dev.Res.	Dev	Pr(>Chi)	
NULL			2282.13		
dateplantation	1	0.92	2281.21	0.337735	
distmer	1	720.54	1560.67	< 2.2e-16	***
tmax01	1	12.90	1547.76	0.000328	***
serie	1	19.61	1528.15	9.494e-06	***
Prov	8	683.82	844.33	< 2.2e-16	***
serie:labo	4	8.28	836.05	0.081767	.
Prov:Mere	34	343.28	492.77	< 2.2e-16	***

b

	Df	Dev.Res.	Dev	Pr(>Chi)	
NULL			2282.13		
tmax01	1	655.70	1626.43	< 2.2e-16	***
distmer	1	57.88	1568.54	2.780e-14	***
dateplantation	1	20.78	1547.76	5.156e-06	***
serie	1	19.61	1528.15	9.494e-06	***
Prov	8	683.82	844.33	< 2.2e-16	***
serie:labo	4	8.28	836.05	0.08177	.
Prov:Mere	34	343.28	492.77	< 2.2e-16	***

c

	Df	Dev.Res.	Dev	Pr(>Chi)	
NULL			2282.13		
dateplantation	1	0.92	2281.21	0.33773	
tmax01	1	677.44	1603.77	< 2.2e-16	***
distmer	1	56.01	1547.76	7.223e-14	***
serie	1	19.61	1528.15	9.494e-06	***
Prov	8	683.82	844.33	< 2.2e-16	***
serie:labo	4	8.28	836.05	0.08177	.
Prov:Mere	34	343.28	492.77	< 2.2e-16	***

Analysis of *C. dupreziana* proportion in seedlings

Due to the loss of identity for some seedlings, the dataset was reduced to 4631 individuals. Based on Nava's work, dead individuals were assigned to *C. sempervirens*.

Analysis of covariance: using the same methodology as for germination rate, we tested the individual impact of covariates on *C. dupreziana* rate by modifying their order of integration in the model. The results (cf. Table 3) show a very strong effect of the age of the mothers and a significant influence of temperature during pollination (tmax01), a variable highly correlated with distance from the sea. However, the latter (distmer) has less impact on the proportion of *C. dupreziana* than Tmax01, probably due to its lesser consideration of the species compared with the Tmax01 variable.

Table 3a-c: Results of the analysis of variance of the effect of variables and factors on the rate of *C. dupreziana* according to their sequence of integration in the model (**a b c**).

a

	Df	F value	Pr(>F)	
dateplantation	1	41.381	7.33e-10	***
distmer	1	30.928	7.50e-08	***
tmax01	1	13.928	0.00024	***
serie	1	0.755	0.38581	
Prov	8	13.270	1.08e-15	***
serie:labo	4	0.722	0.57767	
Prov:Mere	34	3.530	7.69e-09	***
Residuals	227			

b

	Df	F value	Pr(>F)	
tmax01	1	27.912	2.97e-07	***
distmer	1	4.700	0.0312	*
dateplantation	1	53.625	4.19e-12	***
serie	1	0.755	0.3858	
Prov	8	13.270	1.08e-15	***
serie:labo	4	0.722	0.5777	
Prov:Mere	34	3.530	7.69e-09	***
Residuals	227			

c

	Df	F value	Pr(>F)	
dateplantation	1	41.381	7.33e-10	***
tmax01	1	43.727	2.67e-10	***
distmer	1	1.128	0.289	
serie	1	0.755	0.386	
Prov	8	13.270	1.08e-15	***
serie:labo	4	0.722	0.578	
Prov:Mere	34	3.530	7.69e-09	***
Residuals	227			

Generalised linear model: as expected, the results obtained with GLM (Table 4) do not fundamentally change the conclusions obtained with ANOVA. Planting date and temperature at pollination remain the variables with the greatest influence on the rate of *C. dupreziana*, and there is a strong correlation between tmax01 and distmer. We observe that the influence of the series effect takes on a considerable magnitude, which we attribute to the increased complexity of the identification of seedlings in series 2 due to their youth, and to the fact that this identification was carried out by a single observer.

Table 4a-c: Results of statistical analysis based on the generalised linear model evaluating the influence of variables and factors on the rate of *C. dupreziana* according to their sequence of integration in the model **(a b c).**

a

	Df	Dev.Res.	Dev	Pr(>Chi)	
NULL			855.14		
dateplantation	1	62.353	792.79	2.871e-15	***
distmer	1	38.750	754.04	4.817e-10	***
tmax01	1	8.296	745.74	0.003973	**
serie	1	32.175	713.56	1.409e-08	***
Prov	8	267.164	446.40	< 2.2e-16	***
serie:labo	4	5.658	440.74	0.226165	
Prov:Mere	34	150.996	289.75	< 2.2e-16	***

b

	Df	Dev.Res.	Dev	Pr(>Chi)	
NULL		277	855.14		
tmax01	1	276	838.86	5.468e-05	***
distmer	1	275	838.52	0.5589	
dateplantation	1	274	745.74	< 2.2e-16	***
serie	1	273	713.56	1.409e-08	***
Prov	8	265	446.40	< 2.2e-16	***
serie:labo	4	261	440.74	0.2262	
Prov:Mere	34	227	289.75	< 2.2e-16	***

c

	Df	Dev.Res.	Dev	Pr(>Chi)	
NULL			855.14		
dateplantation	1	62.353	792.79	2.871e-15	***
tmax01	1	46.929	745.86	7.361e-12	***
distmer	1	0.118	745.74	0.7315	
serie	1	32.175	713.56	1.409e-08	***
Prov	8	267.164	446.40	< 2.2e-16	***
serie:labo	4	5.658	440.74	0.2262	
Prov:Mere	34	150.996	289.75	< 2.2e-16	***

Prediction of germination and species ratio within seed lots

The generalised linear model is not only better suited to non-normed data and different sample sizes than analysis of variance, but in its binary form (sprouted seeds – unsprouted seeds; *C. dupreziana* – *C. sempervirens*) it also enables more accurate predictions to be simulated, using a link function to relate the independent variables to the probability of success (germinated seed or *C. dupreziana*).

Reliable confidence intervals of the germination rates and *C. dupreziana* proportions were estimated in the estimation space of the binomial model, before reprojecting them in the initial space by the inverse function (exp(x)/(1+exp(x)).

The estimates show the clear segregation of germination rates attributable to mother trees and their provenance (Fig. 6). The contrast is particularly visible: on the one hand, at the "Grozeau" site (northern edge of Vaucluse), where germination rates are moderate but stable and relatively uniform, and on the other hand at the "Pignan" site (south-east of Montpellier), where despite a more pronounced "mother" effect, the overall germination rate is the highest (9.4%).

With regard to the proportion of *C. dupreziana*, the cluster effect is less marked than for germination, but nevertheless very distinct (Fig. 7). Mothers sampled in the Esterel massif and at Pignan show by far the lowest variability, but also the highest overall proportions of *C. dupreziana*, with average rates of 76.2% (from 71.9% to 80.8%) and 72.8% (from 64.7% to 79.5%) respectively. The Villa Thuret site (3 seed trees) comes close to these values (71.9%). It is interesting to note that all 3 sites are less than 10 km from the sea, and therefore benefit from a particular climate. Moreover, the trees on these sites are among the oldest (Esterel: 42 years, Pignan: 39 years, VT: 38 years). Age effect is particularly notable for Sénanque, where the oldest mother (58 years) produces the highest proportion of *C. dupreziana* (86%). Conversely, the only mother to have produced only *C. sempervirens* seedlings is at the Grozeau site (age: 36 years, distance to sea: 100 km), although the results for the latter are not very representative (only 4 germinated seeds). Overall, the graphs in figures 6 and 7 indicate a positive correlation between germination rates and *C. dupreziana*, which was confirmed by a correlation coefficient of 0,46. However, this correlation is not linear but "triangular" (Fig. 8), demonstrating that high germination rates are always associated with high proportions of *C. dupreziana*.

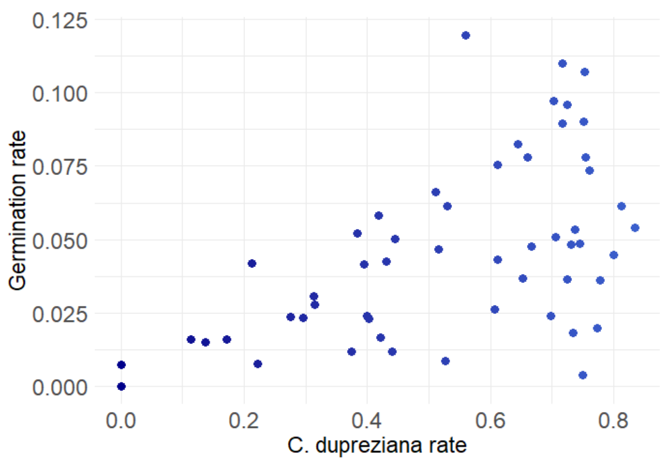


Fig. 8: Correlation between germination and seedling rates of *C. dupreziana* (per "mother")

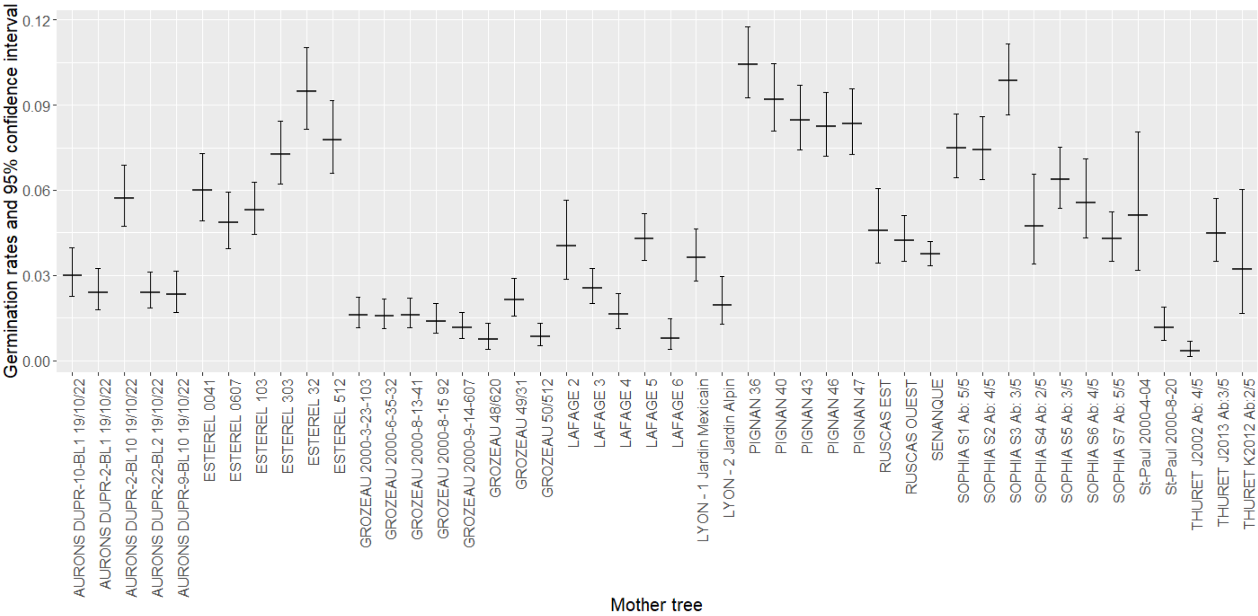


Fig. 6: Estimation of germination rates by "Mother" with 95% confidence intervals

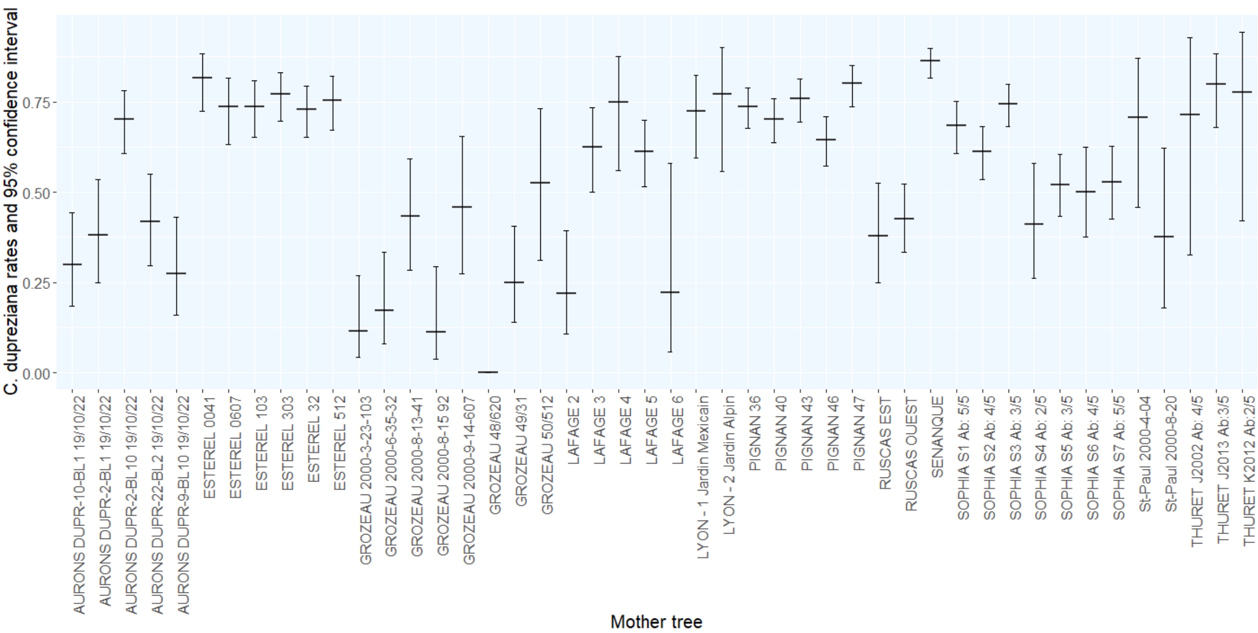


Fig. 7: Estimated rates of *C. dupreziana* produced by "Mother" with 95% confidence intervals

Seed characterisation by species: the stage of development allowing species identification was assessed on seed and seedlings characteristics. Although slightly correlated to species, seed size (estimated for 2167 seeds) cannot be efficiently used for this purpose.

The colorimetric analysis of cotyledons was realised through a linear discriminant analysis on to two subgroups, one encompassing all the photos (Group 1 - 339 cotyledons), the other focusing solely on the last seedling stage before transfer to the nursery (Group 2 - 130 cotyledons). Colour and colour ratio were used as discriminant variables. The linear combination of these variables led to little distinction between species, with cotyledon colours tending to harmonise with seedling age. Difference was mainly due to the green value, higher in *C. dupreziana*. Based on 1000 bootstrap estimates, the probability of correct attribution to a species was around 0.7, ranging from 0.6 to 0.8.

Discussion

The results of our analyses, carried out on over 100,000 seeds, show that germination rates and the proportion of *C. dupreziana* versus *C. sempervirens* produced are very significantly correlated with the mother trees and their provenance. The differences observed between them are probably linked, not to their genome, but to their conditions of exposure to pollen. In the case of germination rates, the variability between sites depends mainly on the climate at the time of pollination, whereas *C. dupreziana* rates seem to be more influenced by the age of the mothers. In this respect, it is interesting to note that the Esterel massif, one of the largest and oldest concentrations of Saharan Cypress in France, had an overall germination rate in 2001 ranging from 0.22% to 3.9%, with an average *C. dupreziana* rate of 23% (Nava 2008). In 2023, germination rates for the same provenance range from 2.3% to 11.9%, with an average proportion of *C. dupreziana* reaching 76.2%. It is highly probable that tree maturation may explain this phenomenon. The increase of pollen production with age leads to greater pollination of individuals, and therefore higher germination and *C. dupreziana* rates. With a view to mass reproduction of the species, this would suggest directing seed harvesting to the oldest trees and, if possible, checking that they are well pollinated (from mid-January to mid-February) 1.5 years before harvest, by observing the colour of the foliage of trees whose pollen turns the young cones at the end of the needles yellow.

With regard to the phenotypes of *C. dupreziana*, and still with a view to large-scale seedling production, it seems difficult to identify with certainty the species of seedlings before they have reached their first month, although more or less pronounced morphological anomalies in seedlings remain a good indicator of *C. sempervirens*. We thought it would be interesting to pursue this research using near-infrared spectroscopy (NIRS). This rapid, easy-to-use technique is now widely used in the agricultural industry to determine the internal structure of seeds and ensure they are free of defects (Pansare *et al.* 2012, Nicolaï *et al.* 2014). We initiated studies in this direction, the conclusions of which are still to come.

Studying and propagating the Saharan Cypress has at least three major benefits. Firstly, to preserve in *ex situ* conditions a species on the verge of extinction in its native range. Although its exceptional characteristics have enabled it to survive the centuries in extreme conditions, its disappearance from the desert is now a serious concern. On the other hand, its integration into French forests would offer a promising prospect of evolving into ecosystems better adapted to future environmental conditions. In the absence of any adaptive evolution, however, this cypress would have to be planted sporadically, as a companion species or as an ornamental. The establishment of monospecific stands over large areas could present risks, particularly in the event of parasitic attack. Finally, its unique "surrogate mother" strategy opens up a vast field of research into gymnosperms, their genetic variability and the expression of recessive genes. The production of haploid lines is already being used to select non-pollinating ornamental cultivars to prevent allergy to Cupressaceae pollen. These lines are also being used as part of the sequencing of the green cypress genome (INRAe 2023) and could eventually be extended to the production of cultivars selected for their rapid growth or resistance to pathogens.

C. Laguerre pointed out at the end of her dissertation that France is now home to four times more specimens of this cypress than the Tassili n'Ajjer plateau (Laguerre 2006). An update of his inventory brought this number to seven, with over 1,500 trees, most of them located in the south-east of France (Appendix 1). If we consider that the survival of this species seems to be closely dependent on human action in its favor, this increase is a source of encouragement, all the more so as it does not take into account the 3139 individuals from our production and presently in nursery. We regret, however, that these trees are not fully representative of the relict population. The updated inventory and the work of L. Nava indicate that most of the seeds used in *ex situ* collections come from Tamrit, the most easily accessible region of the natural range. Although this species has a quasi-unique genome, variants have been detected in samples from the north of the natural area (Nava 2008). Knowledge of its genetic heritage is lacking, and it would be essential to remedy this by mobilising all the resources of the natural area, which could easily be achieved by collecting seeds or grafts from the 233 trees still alive.

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Appendix 1

National inventory

From 2006 to 2008, Laguerre and Nava (Nava 2008) drew up a fairly exhaustive inventory of French Saharan Cypress resources, identifying 1,026 trees throughout mainland France. In order to monitor the evolution of this resource, it now seemed appropriate to update the inventory by checking the persistence of known trees and adding new individuals. To do this, a survey was carried out among those already identified and extended to over 190 arboretums, as well as the main public bodies, associations and private collectors. A file was created containing all the information relating to the trees inventoried, including their altitude, age, the substrate on which they grow, as well as the origin of the information and the contact details of the owners.

The census revealed the disappearance of around fifty trees, particularly in the Carpentras and Montfavet communes. However, plantings by several private owners, arboretums and the rediscovery of former FCBA experimental plots have increased the overall number of representatives of the species in France, which we were able to estimate at 1,564 individuals.

Figure 9 illustrates their distribution, with the sites used as a basis for this study highlighted in red.

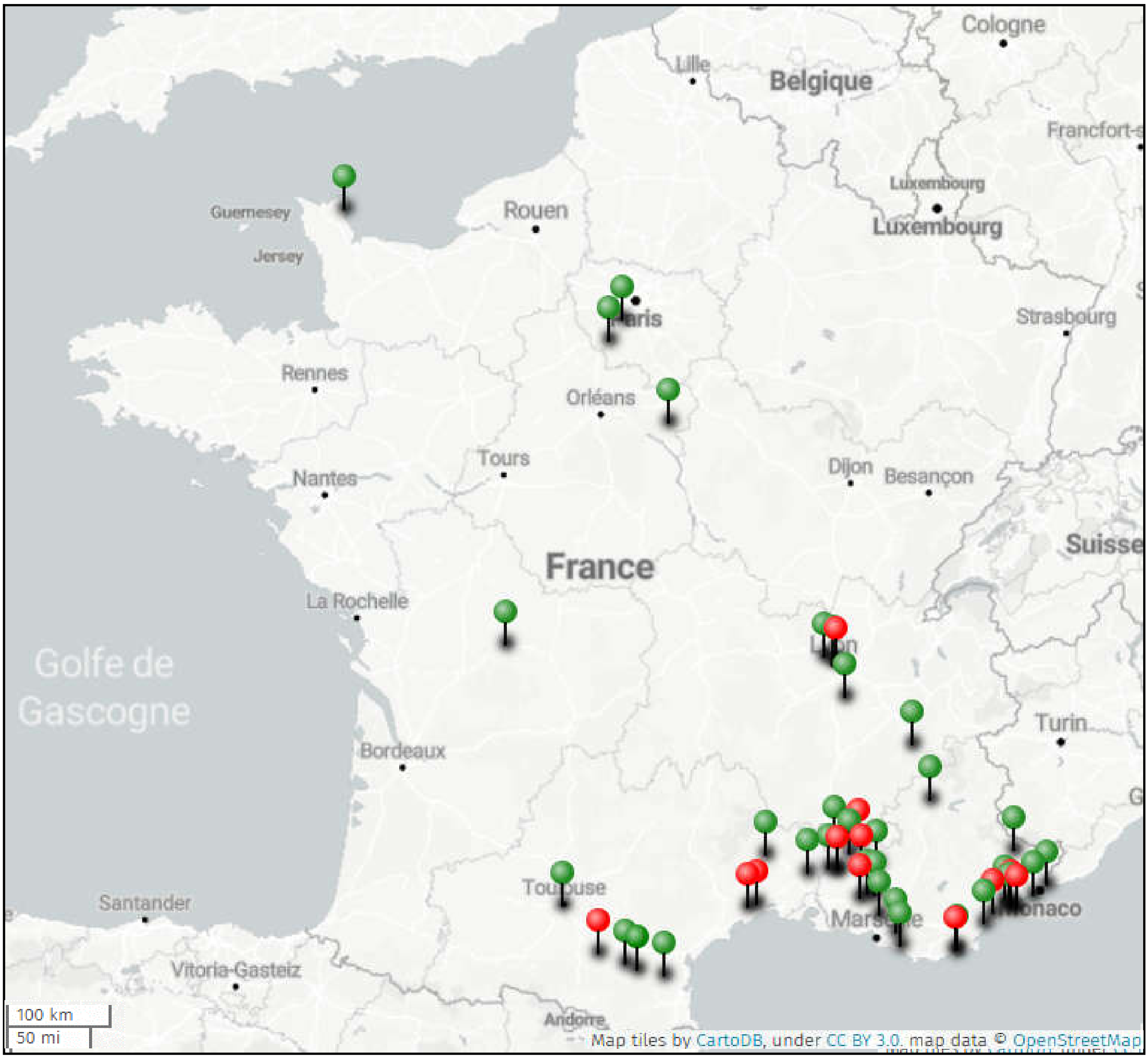

Fig. 9: Distribution of French *C. dupreziana* resources (sampled sites in red)

Université de Perpignan Via Domitia

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Master Biodiversité, Ecologie, Evolution
Parcours "Biodiversité et Développement Durable"

Caractérissation des sources de grains françaises de *Cupressus dupreziana*, unique espèce végétale à reproduction apomictique mâle connue à ce jour

Jacques Francioly

Academic year 2022-2023
Under the direction of Christian Pichot
French National Research Institute for Agriculture, Food and the Environment
RU 0629 Ecology of Mediterranean Forests

Propagation of *Cupressus dupreziana* A.Camus, Saharan Cypress

Cupressus dupreziana in situ

This cypress is endemic to the Tassili n'Ajjer National Park, which is a sandstone mountainous massif in south-eastern Algeria and in the central Sahara. It grows between 1430 m and 1830 m altitude, mostly on exposed mountain ridges, on fractured rocks, ravines or in very hard accessible bottoms of valleys and with 30 mm estimated annual rainfall. Average summer temperatures are between 20°C and 30°C, in winter between 1°C and 13°C, with possible frosts down to -7°C[2]. In cultivation the conifer can resist temperatures down to at least -15°C.

It can reach 16-20 m high in the wild. Some specimens with a 1.3 m wide trunk and 7-12 m wide crown are thought to be more than 2000 years old.

Fig. 1: *Cupressus dupreziana in situ*. © Messaoud Ramdani.

Although this plant is protected in Algeria and situated in a National Park, its conservation status is in constant decline. Right now its IUCN Red List category is "Critically Endangered", which means the species is "therefore considered to be facing a very high risk of extinction in the wild"[3].

C. dupreziana is amongst the most threatened conifer tree species in the world.

The total population in Algeria is less than 250 individuals (233 according to the most recent survey, Abdoun & Beddiaf, 2002: 618), with "a predicted 25% decline within the next generation (ca. 25 years)" (IUCN 2013). Its habitat is indeed very degraded and scattered on 46 sites and less than 250 km^2 (120 km in length and between 6 and 15 km wide) (IUCN 2013). Its main threats are

[1] Florence BILLIART-DURET, Botanist-gardener, ex-responsible of the outdoor propagation unit at the Lyon Botanical Garden, France.
[2] Source Abdoun and Beddiaf 2002.
[3] The IUCN (2013) considers the Saharan Cypress only at the variety rank which is not accepted here, see Appendix.

the goat overgrazing, trampling of the habitat by tourists (at least 1000 per year) and by animals, seed collection, and firewood cutting (branches and roots). In the past the trees were destroyed by logging. Fires and climate changes also have a disastrous effect on the species, although it is adapted to the very dry conditions of the Tassili Plateau.

In addition to these, a very poor natural regeneration of the species has been observed, with only five cases of successful spontaneous seedlings observed in one century. It seems that the groundwater has decreased a lot, preventing any regeneration[4]. This species would be a relic of a more humid period that occurred before desertification. But in the early 2000s, two young trees were found *in situ* in the old population of *C. dupreziana*.

The species name *dupreziana* is in honour of a French soldier, Captain Maurice Duprez (1891-1943). In 1924 Maurice Duprez commanded the Saharan Company of Ajjer from Fort Charlet in Djanet. During an expedition to the Tamrit Plateau he discovered the Tassili Cypress and he wrote to René Maire (1878-1949) professor of botany at the Alger Science University to give him his observations about the tree, named "Tarout" by the locals. From the information given by Captain Duprez, Louis Lavauden (1881-1935), a Tunisian forest guard, who took part in an automobile expedition from Tunis to Tchad brought back home samples of the conifer to Aimée Camus (1879-1965). This botanist, who was a specialist in the genus *Cupressus* (Camus 1914), named the new species *C. dupreziana*. In 1926 Aimée Camus published that new species of *Cupressus* in her article "Un cyprès nouveau du Tassili (*Cupressus dupreziana*)".

C. dupreziana ex situ in Lyon

At the Lyon Botanical Garden (France), there are 3 specimens of *Cupressus dupreziana.* We first thought that they had been introduced in 1961 by Marc Lafferrère, who was a French botanist and also the director of the gardens "les Cèdres" in Saint-Jean-Cap-Ferrat. He studied a lot on that species, and had for mission, in 1961, to find a maximum amount of *C. dupreziana* to map its distribution in Algeria. He also collected a lot of seeds in the wild and distributed them to different gardens in Algeria, Tunisia and France.

That was thought to be how Lyon Botanical Garden first got seeds from Mr Lafferrère in 1961, but unfortunately, according to Dr Paul Berthet, who was the Director of the garden from 1964 to 2000, those seeds did not germinate.

Fig. 2: Captain Duprez. Photo given by J.-L. Champion, Maurice Duprez's grand-niece's husband (http://europeana1914-1918.eu/fr/contributions/12322).

[4] Source World Conservation Monitoring Centre, 1999, quoted by Earle 2023.

Fig. 3: Captain Duprez was astonished by this conifer due to its foliage and its growth habit that was unusual in that area. © F.Billiart-Duret.

Fig. 4 (p. 35): *Cupressus dupreziana* grafted on *C. arizonica* at the Mexican garden in Lyon Botanical Garden. © F.Billiart-Duret.

Fig. 5: *Cupressus dupreziana* in the arboretum of the Lyon Botanical Garden. © F.Billiart-Duret

Fig. 6 (p. 37): *Cupressus dupreziana* behind the Alpine garden, Lyon Botanical Garden. © F.Billiart-Duret.

While writing this article and thanks to the monograph on *C. dupreziana*, I found out that the three specimens in Lyon Botanical Garden were in fact grafted on *Cupressus arizonica*, and also from cuttings. The cuttings and scions had come from trees planted in Lebanon (Barry *et al.* 1971).

According to Dr Berthet, the scions and cuttings were collected by the Abbe R. de Tarade, who sent them to the Lyon Botanical Garden. They were collected in the Jesuits High School of Jamhour in Lebanon, where the Abbe R. de Tarade had planted two Tassili cypress trees in 1953, whose seeds came from Tassili, collected by Mr Claude Leredde, a French botanist.

At that time the botanical garden also received seeds from the Abbe R. de Tarade, who collected them on those two cypress trees. They were sown in May 1969 in Lyon.

Dr Berthet confirmed that one of our *Cupressus* was grafted, the one in the "Mexican garden", because he actually participated to the grafting on *C. arizonica* rootstocks.

The grafting method was pretty particular, like an approach graft, where the scion and the rootstock still have their root system until the graft union occurs, the scions of *C. dupreziana* here were branches that were dipped in a tube filled with water. The aim was to maintain them alive for a longer time, while the grafting was done between the upper part of the scions and the rootstock plants, which were Arizona Cypress in containers.

Our two other specimen are smaller than the one in the Mexican garden. These ones come from seeds that were sown in May 1969 at the botanical garden and were collected on the 2 Cypress trees from Jamhour, Lebanon.

Other specimens from these seedlings were sent to gardens, such as the Arboretum des Barres, in Nogent-sur-Vernisson in Autumn 1973, but they are not present there anymore.

In 2019 samples of our three cypress trees were sent to an Italian researcher working on *C. dupreziana*.[5] Thanks to the genetic studies he made, the results were that our three trees have the same genotype as the main genotype found on 82 trees studied *in situ* in Tassili.

Propagation of *C. dupreziana*

For a long time, we thought that there were hybridisation risks with other cypresses of the Parc de la Tête d'Or, especially with *C. sempervirens*, which was why we would rather propagate the species by cuttings here at the Lyon Botanical Garden.

After publishing my article in our revue "Sauvages et cultivées", that D. Maerki, specialist of conifers, contacted me about it and told me that the cypress could not hybridise[6].

Indeed, the species has a very peculiar method of reproduction, called paternal apomixes. That is effectively a vegetative propagation. "It is the only species in the plant kingdom known to reproduce by cloning its male genetic material through a process known as male apomixis. (…) Male cloning requires an additional step unique to the Saharan cypress: Pollen, carrying the male cells, enters the tree's ovule, but instead of combining with the female cells, it divides internally to become a viable seed genetically identical to itself" (Werner & Bubriski 2007).

That way, every new plant is a perfect clone.

Pollen is able to develop alone without any fecundation and create an embryo. The ovule is useful to stock reserves for the embryo.

Male gametes contained in pollen are also able to form an embryo by themselves in the ovule of *Cupressus sempervirens*, this one acting like a "surrogate mother".

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[5] Dr. Gianni Della Rocca, Istituto per la Protezione Sostenibile delle Piante (IPSP-CNR), Institute for Sustainable Plant Protection, Italy

[6] *Editor's Note:* cf. the research lead by C. Pichot, El Maâtaoui *et al.* A list of these articles is available here.

This was good news, because it meant that the seeds I collected from our *C. dupreziana* here at the Botanical Garden would not produce hybrids, and that we would be able to give the seedlings as real clones of the plants coming from Tassili.

For 3 years we have been trying here to make cuttings of *C. dupreziana* after a request made to Gilles Dutartre (a French botanist who was responsible of the seed bank at that time), by a member of the Duprez family, Mr Nicolas Duprez. This man wanted to offer to each member of his family, a specimen of *C. dupreziana.*

Propagation by tip cuttings is the best way, but is a pretty long process. The tree itself grows very slowly and its young stems are often very frail.

Several tries have been done, with cuttings made in February or March. I usually kept them at least for one year in sand in a warm frame, until I could see signs of new growth. That is why it is a long process compare to other species of cypress or other genera. When the cuttings were divided, ⅓ to ½ had a few roots, ¼ to ⅓ had only made a callus but no roots and less than ¼ to ⅓ died (Figs 9 & 10, p. 40).

One year I waited 1 year and 4 months before dividing them and the roots were pretty well developed. They took advantage of the warm months of spring to grow in sand (Fig. 11, p. 41).

To me, sand is the best substrate to use for cuttings because it is well drained, avoiding the risks of mould because of the humidity, it gets warm faster and allows a good root system to develop.

In comparison I made cuttings of *Cupressus cashmeriana* in 2014, at the same time as I made cuttings of *C. dupreziana*, and in less than 3 months, they showed signs of growth and had a perfect root system. I divided them and got 80% success (Figs 7 & 8).

Figs 7 & 8: Cuttings of *Cupressus cashmeriana* with a very good root system after less than three months. © F.Billiart-Duret.

Fig. 9: Rooted cuttings of *Cupressus dupreziana* after one year that they were made. © F.Billiart-Duret.

Fig. 10: Same batch of cuttings but they only made calluses after one year. © F.Billiart-Duret.

Fig. 11: Rooted cuttings of *Cupressus dupreziana* after 16 months that they were made. © F.Billiart-Duret.

I also sowed seeds of our grafted Saharan Cypress and got a very good success rate (more than 90%). The plants grew also faster than the ones from cuttings.

In 2015 we were happy to have propagated by cuttings 15 new plants that would join the gardens of Maurice Duprez's family over the next year. A good way to preserve *ex situ* a so rare species!

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Appendix[7]

The Saharan Cypress was described at species rank as *Cupressus dupreziana* (Camus 1926). In 1950, Gaussen described a new cypress from Morocco, also at species rank, as *Cupressus atlantica*. The two species ranges are separated by more than 1800 km of desert, and have distinctive morphological characteristics. Moreover there is a specific barrier to hybridisation between the two taxa, because of the diploid pollen of *C. dupreziana* (see Appendix A, p. 9 in this issue & link in footnote #8, p. 38). In 1998, Silba reduced *C. atlantica* to the variety rank which was accepted by Farjon (2005). There was no scientific reason to reduce the rank of *C. atlantica* to a variety or a subspecies. The ranks must be defined precisely; this was never the case with either Silba or Farjon, the former changing a list of varieties to subspecies without explanation, the latter working mainly with dead and dry herbarium material and without statistical analysis. Here at the *Cupressus* Conservation Project, we have adopted the definitions proposed by Christensen (1987: 384):

> The species concept used in the present work is morphological, and mostly in line with Rothmaler (1944) and Du Rietz (1930). The taxonomic ranks used are defined as follows:
>
> Forma of a variety, subspecies or species occurs sporadically within the distribution area of the taxon of higher rank to which it is referred and differs from that taxon in a single character.
>
> Varietas of a subspecies or species is to some extent allopatric and forms local, distinct populations as well as mixed, integrating populations within the distribution area of the subspecies or species. They differ from each other in usually more than a single, distinct character.
>
> Subspecies of a species are both regionally and locally allopatric. They differ from each other in several, distinct characters, but intergrade in overlapping areas.
>
> Species of a genus differ from each other in numerous, distinct characters and have a characteristic distribution area of their own. Where closely related species meet occasional hybridization and introgression may occur.

[7] Editor's note.

Historiography of the Saharan Cypress
- Tarout - سرو صحراوي - +O+ (TRT)
Cupressus dupreziana A.Camus 1926, endemic species of Tassili n'Ajjer (central Sahara) in danger of extinction

1860.

The British traveler and naturalist, the Reverend Henry Baker Tristram (known particularly for his work in ornithology), having stayed in Algeria and explored the South from 1856 to 1860, concluded the existence of a conifer in this region of the central Sahara, a conifer probably close to the genus *Juniperus* (Tristam 1860: 236) after observing wood used in the manufacture of utensils by the Touareg of the Hoggar:

"To judge from the woodwork of saddles and the handles of weapons which I obtained from Touareg, manufactured in the Dj. Hoggar, there is also a species of hard resinous wood, probably allied to the junipers."

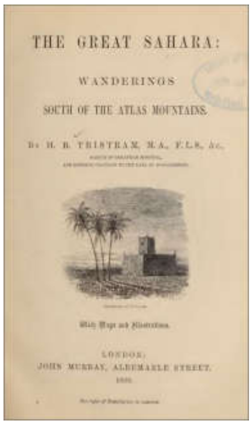

Fig.1: *The Great Sahara* by H.B.Tristram

1863-1864.

According to information collected from indigenous populations, and after examining the wood used in framing and carpentry, the explorer and geographer Henri Duveyrier, who traveled the Sahara from 1859 to 1863, confirms the existence of this resinous tree, called tarout in Tamashek, and which he identifies with *Thuya articulata* Vahl (Duveyrier 1863: 9-10):

"A rather important fact of botanical geography to note is the presence of the olive tree (*Olea europaea*) in Tessaoua, near Mourzouk, but especially that of *Thuya articulata* on the highest points of Tassili n'Ajjer and Ahaggar, about sixty kilometers north of the Tropic of Cancer. This green tree, which constitutes real forests, reaches gigantic proportions there.

Duveyrier will take up his observations and develop his extrapolations (Duveyrier 1864: 210-211):

"The forest which produces this species seems considerable, because all the wood used in the constructions of Rhât and Djânet comes from there.

The dimensions of the boards, the colour, the fineness and the solidity of the wood, are reminiscent of *Thuya*.

Fig. 2: H. Duveyrier, from a photograph.

The name taroût, a Berber form of the word *'ar'ar* used in the Tell to designate the *Thuya articulata*, leads me to identify, provisionally, the taroût of the Touareg with the *'ar'ar* of the Arabs.

This tree provides a resin (…)

Tar is extracted from it.

These two facts support the identification of the tarout with *Thuya articulata*." (**A**)[2]

---

[1] Extract from Barry *et al.* 1970, completed by B. Belin 2015 & 2023.

1878-1920.

These data and hypotheses of Tristram and Duveyrier guided the research of explorers and inspired phytogeographers for sixty years. Grisebach (1877) and Drude (1897), extrapolating exaggeratedly from the few data they had, also admitted the existence of a coniferous forest on the Tassili plateau and on the summits of Hoggar. E. von Bary, C. de Motylinski, R. Chudeau, N. Villatte, L. Diels, H. Geyr von Schweppenburg, successively travelled through these mountainous regions of the central Sahara without bringing anything that could confirm the hypotheses of Tristram and Duveyrier. The work of the latter was then strongly criticised, and his indications relating to the tarout were doubted, particularly by Diels (1917), and further by Geyr von Schweppenburg (1920).

1924.

Infantry Captain Maurice Duprez, of the Saharan Company of Ajjer, then commanding the Djanet Annex, had the privilege in 1924 of being the first European "traveler" to see this conifer whose explorers and phytogeographers had until then only suspected the existence in both regions of the Tassili n' Ajjer and the Hoggar. Two years later he notified his discovery to Professor René Maire, of the Faculty of Sciences of Algiers, by a "Note dated February 27, 1926" which the latter published in 1933 (Maire 1933: 49):

"During one of my mehari[3] tours in the Tassili n'Ajjer, in 1924, in the part which is to the east of the small oasis of Djanet and to which the Touareg gave the name Tassili Edehi, I discovered one day in a small wadi called Tamerid a tree whose green appearance and more than abnormal size for the country did not fail to attract my attention. This conifer, because undoubtedly I was dealing with a specimen of that species, was not isolated, since by continuing my investigations in the same wadi I soon discovered a second one, then the dead stem of a third. Not having my camera, I was unable to photograph this curious sample of vegetation in the dark aridity of this sandstone plateau. However, I took with me a small branch and a few drops of dried resin that I found at the foot of the tree. I had the disappointment when I arrived in Djanet to see my branch crumble into almost impalpable dust. All I had to do was hope that my wanderings across the Sahara would bring me back to the same area. In the meantime, I asked the natives about what seemed to me to be a Conifer and here is the information I managed to gather:

The "Tarout", because this is the name that the natives of the country give to this tree, is known to the Ajjer Touareg, but also, and one could say above all, to the Kel Djanet, farmers of the oasis of the same name. In fact, these natives have been using the wood of this tree for a very long time to build the doors of their homes. This wood, very soft, can be worked quite easily by the rudimentary tools of the local natives."

1925.

"Tunis-Chad Mission", reconnaissance mission – equipped with specially built Citroën-Kegresse half-tracked vehicles – with the view to link southern Tunisia by a military ring road starting from the Gabès oasis and reaching the heart of Central Africa "by constantly remaining in French territory" [sic! (B.B., 2016)]. Head of Mission: Lieutenant-Colonel Victor-Paul Courtot, Director of the Military Office of the general Resident of France in Tunisia. To mark the complementarity of the French authorities of Tunisia and Algeria in this project, it was decided that Captain Duprez, ensuring command of the Annex of the Ajjer of the Saharan Company, will join the mission at Fort de Polignac.

Thanks to the instructions of Captain Duprez, the general Inspector of Water and Forests Louis Lavauden, general Forest Guard in Tunisia, responsible for the scientific part (botany, zoology, geology) of the mission, found again the conifer of Oued Tamerit (Lavauden 1926: 541):

"We were able [...] to find and approximately identify the tree in question, which in the Tamahek language bears the name *Tarout*. It is not *Callitris articulata* (Vahl) Link [= *Thuya articulata* Vahl],

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[2] See endnotes numbered A, B, etc. pp. 48-49.

[3] Mehari = *Camelus dromaderius*.

as Duveyrier thought, but a tree that [according to the indications of Philibert Guinier, Director of the National School of Water and Forests (ENEF) of Nancy, to whom the samples had been submitted] we provisionally reported as *Cupressus sempervirens* L. forma *horizontalis*."

1926.

From cones, seeds and fragments of branches collected by Lavaudan [and entrusted by Guinier to various specialists], the botanist Miss Aimée Antoinette Camus, Laureate of the Institut de France (Academy of Sciences), author of a world monograph of the genus *Cupressus* (1914), established that the Tamerit cypress was specifically distinct, and names it *Cupressus dupreziana* (**B**) in homage to the one who discovered it (Camus 1926: 101):

"This Cypress belongs to a distinct species, not yet described. I dedicate it to Mr. Captain Duprez, commander of the Djanet annex, who indicated to Mr. Lavauden the precise locality where this endangered *Cupressus* grows. It once formed a real forest of which today only one living individual remains."

1933.

Shortly after Duprez and Lavauden, the famous geologist Conrad Killian [the first to have affirmed from geological data the existence of oil in the Saharan subsoil] in turn observed the Tassili Cypress and also collected information on the probable presence of a dead cypress trunk in the Hoggar. Having shared his observations with R. Maire, he subsequently reported them – at the same time as the "Note dated February 27, 1926" from Captain Duprez – considering that the cypresses of Tassili and Hoggar are identical (Maire 1933: 48-49):

"***Cupressus dupreziana*** A. Camus — Stony beds of the wadis of the lower Mediterranean altitude level. Tassili n'Ajjer: sandstone mountains between Djanet and Ghat, in Wadi Tamerid and Wadi Amezar, particularly in places called Tin Beradjen, Tin Bellelé!, Tin Lezit, 1700-1900 m (Duprez, Lavauden, Kilian).

Hoggar: a large dead trunk still exists in Oued Tin Tarabine, around 1700 m, according to information given to C. Kilian by Khamma ag el hadj Mohammed, from Aït-Telouaïn.

Geographical area – Endemic to the mountains of the central Sahara.

This tree was used for the constructions of Djanet and Ghat, which led to its extreme rarity. Its branches are also very sought after as a febrifuge (Kilian)".

1949-1950.

The "Scientific mission to Tassili n'Ajjer" of the Saharan Research Institute (IRS) of the University of Algiers (1949). Head of the Mission: Francis Bernard, Professor of zoology.

Claude Leredde, botanist from the Faculty of Sciences of Toulouse, collected around two hundred cones during his first botanical exploration mission of Tassili. On examination, the cones appear to be different from those collected by Lavauden in 1925 and used to describe the species *Cupressus dupreziana* A.Camus. There are none that are smaller than 19 mm and several exceed 24 mm; in width they are 16 to 20 mm; most have 12 scales. Then Professor Henri Gaussen, of the Faculty of Sciences of Toulouse, described the species *Cupressus lereddei* (**C**) specifying (Gaussen 1950: 55):

"Or Miss A. Camus had in her hands a sample of an exceptional tree, there was only one, and this tree alone deserves the name *dupreziana*, that of M. Leredde being of a different species; or the two types belong to the same species and Miss A. Camus had the misfortune of describing an aberrant tree as a type. In any case, her diagnosis does not apply to the Leredde tree (…). As the rules do not allow a published diagnosis to be modified and, on the other hand, it is not impossible that there are two species in Ajjer, I describe the Leredde species."

1952.

The first volume of the "Flora of North Africa (Morocco, Algeria, Tunisia, Tripolitania, Cyrenaic and Sahara) was published by † Dr René Maire, Member of the Institut de France, Professor at the University of Algiers, published by Marcel Guinochet, successor to René Maire in Algiers, and Louis Faurel, "Prince of Algerian botany" (B.B., 2016). There is only the description of *Cupressus dupreziana* A.Camus, as R. Maire (1949 †) had no knowledge of the description of *Cupressus lereddei* by Gaussen. (**D**)

The same year, Gaussen expressed some doubts as to the existence of two species of cypress at Tassili n'Ajjer, and specifies when speaking of the specimens studied by Miss A. Camus (Gaussen 1952: 509): "It is probable that the first studied sample was a poorly built runt", but it does not, however, completely exclude the possibility of a distinct *Cupressus dupreziana* and a *Cupressus lereddei*.

1954.

During a botanical itinerary in the Hoggar Massif carried out in November 1953, Pierre Quézel, Professor at the Faculty of Sciences of Algiers (successor to Mr. Guinochet), found a dead trunk in the bed of Oued Erherhi on the Tazrouk-Tin Tarabine track, which he declares was a cypress, which in indigenous tradition passes for the last tarout of the Hoggar, and upstream of this, dead trunk and in the same wadi, a large branch, which he also declares was of cypress. Concerning the dead trunk, Quézel notes in various publications: "There is no doubt that this tarout or the one that Kilian reported on the faith of the natives... / individual, whose age could not exceed eight to ten centuries, vegetated at 1100 meters of altitude... / enormous trunk, more than six meters high, and at its base 'a diameter of 2.60 meters..." As for the branch, he provides some additional details: "We found in this same Oued Erherhi, about ten kilometers upstream, brought by the floods, a large branch of cypress in excellent state of conservation, dead for several decades, while the dead trunk still in place downstream has not been alive for at least a century." (**E**)

Quézel admits the possible existence of living individuals in the Hoggar Massif, and considers that: "It is infinitely probable that the Tassili Cypress is identical to that of Hoggar; however it will be impossible to affirm this as long as living individuals, if any remains, will not have been seen." (1954, Contribution to the flora of North Africa. IV: Contribution to the flora of Hoggar, and various publications).

[It eventually turned out that it was not a cypress trunk and not a cypress branch, nor a conifer, nor a gymnosperm, but an *Acacia* species (B.B., 2016) (**F**)]

1957.

The synonymy "*Cupressus dupreziana* A.Camus, 1926 = *Cupressus lereddei* Gaussen, 1950", is admitted by Leredde (1957):

"It is certain that the original diagnosis of Miss Camus for *Cupressus dupreziana* does not correspond for the cone to those collected in the same station and very probably partly from the same tree... It corresponds to a cone that is at least miniature and moreover abnormal. Following the advice of the eminent Dutch taxonomist Professor Joseph Lanjouw of the University of Utrecht [Lanjouw 1956], Professor Gaussen, who did not think he could modify a diagnosis, did me the honor of associating my name with this magnificent tree by giving an exact description. But the new rules of nomenclature allow the modification of the original diagnoses when an obvious error was recognized."

1961.

Gaussen himself confirms the existence of a single species of cypress at Tassili n'Ajjer, and puts an end to the controversy sparked by the famous relic of the Algerian Sahara (Gaussen 1961: 98) (**G**):

"In the article in Le Monde des Plantes where I created the species *lereddei*, I noticed that the original diagnosis of Miss Camus relating to *Cupressus dupreziana* indicated a cone of 12–18 × 10–15 mm with ten scales. However, the samples brought by Leredde (several hundred) were 19–24 × 16–20 mm and with twelve scales. The question was still poorly understood, if there could be two species in these little-explored regions, but I said: "or both types belong to the same species and Miss Camus had the misfortune of describing an aberrant tree as a type". This happened in 1949 and at the International Botanical Congress (IBC) in Stockholm in 1950 the taxonomists I had consulted agreed on the intangibility of Miss Camus's diagnosis, so I published the species *lereddei*. Since then, Mr. Leredde made a second trip to Tassili and was able to ensure that there was indeed only one species and that the standard sample of Miss Camus was an anomaly. The new rules of nomenclature adopted after the Stockholm IBC allow modifications to the original diagnosis and it is obvious that the *Cupressus dupreziana* A.Camus binomial has priority." (**H**)

Gaussen (1961: 99) provides the first details regarding the germinative capacity of the seeds: "It is possible that the germination capacity varies depending on the years, but the seeds reported by Leredde germinated in Toulouse (…) and, at least in certain years, the seeds are normal and have a notable germination capacity."

1965-1966.

"Mission of the Saharan Research Institute (IRS) & Botany Laboratory of the Faculty of Sciences - University of Algiers". December 1965 - January 1966. Head of Mission: Jean-Paul Barry. Guide to the Tassili n'Ajjer plateau: Aboutalen.

The 34 floristic surveys carried out in the Saharan Cypress plant group by J.-P. Barry & L. Faurel show the extreme poverty of the plant cover both in terms of species and individuals (93 species including a few rare therophytes).

We consider that various species are to a certain extent linked (Jaccard community coefficient / Czekanowski differential analysis) to the presence of *Cupressus dupreziana*, and that they constitute with it, in the sense of phytosociologists, the backbone of a true plant association.

From this point of view the most notable species would seem to be: *Olea laperrini* Batt. & Trab. / *Myrtus nivellei* Batt. & Trab. ssp. *nivellei* / *Globularia alypum* L. ssp. *arabica* (Jaub. & Spach) Maire / and perhaps: *Lavandula pubescens* Decne. ssp. *antineae* (Mayor) De Miré & Quézel / *Varthemia sericea* (Batt. & Trab.) Diels ssp. *incanescens* Maire / *Phagnalon saxatile* (L.) Cass. ssp. *purpurascens* (Sch. Bip.) Maire.

2001-2005.

A team from the Tassili National Park listed 233 living individuals in 2001 and a map of their natural area was established (Abdoun 2002; Abdoun & Beddiaf 2002). A comparison with an old inventory (Grim 1972, unpublished) showed a loss of 8%, dead by drying out or most often by cutting. The surprise was, however, the discovery of two young cypresses among the old ones, which makes its qualification as a relic obsolete. It reproduces *in situ* and some of its seedlings persist in the current hyperarid climate.

Research on the age of cypresses, carried out by the University of Arizona in Tucson (United States), begun in 1967. This led in 2002 to knowledge of the rate of growth in circumference. Radiocarbon dating of old subjects with a trunk diameter of more than one meter was carried out. Their ages vary between one and three thousand years (Abdoun *et al.* 2005).

2015.

While monitoring the state of the trees between 2014 and 2015, a reconstituted research team led to different wadis where six new individuals were observed and added to the total, but at the same time, several plants were found dead which kept the count around 233 specimens.

2023.

November: Several years without rain took their toll on cypress #1 (Grim inventory) as well as on the two young ones from Tamrit. But I found, elsewhere, other young trees that are doing well (Abdoun[4] pers. comm.).

The *C. dupreziana* constitutes one of the most remarkable relics of the plant world, and the existence in the mountains of the central Sahara of an endemic cypress has aroused the interest of biologists for more than a century. Unfortunately the observations made on this relict tree are scattered in works of very diverse nature, some of which are not easily accessible and often forgotten today. Furthermore, these elements are disparate and sometimes only of very relative

[4] F. Abdoun, Laboratoire d'écologie végétale et environnement, Faculté des sciences biologiques, Université des Sciences et de la Technologie Houari Boumediene, Bab Ezzouar, Alger.

value, because they often result from simple compilations and reminders of unverified facts. It was therefore extremely interesting that a critical synthesis was made, and that everything we know today with certainty about the Saharan Cypress was brought together in a single work. This was all the more desirable since, if *C. dupreziana* poses numerous biological problems, it seems likely to be of great silvicultural interest for future reforestation in arid regions.

The *C. dupreziana* appears to be inevitably doomed in its natural area, and it is all the more short-lived as any effective protection is impossible in this region, and the development of tourism represents an additional danger. It is fortunate that cultivation in botanical gardens or forest nurseries reassures us about the conservation of the species in the future.

Before it is too late, a formal assessment of the cypress populations of the Edehi plateau, much more precise than that provided in the "Essai d'une monographie du *Cupressus dupreziana*", could and should be drawn up. Due to the local topography and the difficulties of using aerial photographs, this would be a long and difficult job, requiring significant material resources but which the interest would amply justify.

Endnotes

A. The determination made by Duveyrier of the softwood of Ajjer therefore turned out to be false, but it can be explained very well given that the Thuya of Berberia, *Tetraclinis articulata* (Vahl) Masters 1892 [= *Thuya articulata* Vahl 1791 = *Callitris quadrivalvis* Vent. 1808 = *Callitris articulata* (Vahl) Link 1831], is one of the most widespread gymnosperms in the dry areas of North Africa, where no *Cupressus* was then known in the spontaneous state. On the other hand, Duveyrier, to identify the tarout of the Tassili n'Ajjer with the Thuya of Berberia, draws argument from linguistic reasons and also from the fact that the two species both provide a resin and a tar. It should be remembered that *Juniperus phoenicea* L., another conifer widely distributed throughout North Africa, from the coastal dunes to the last reliefs of the Saharan Atlas, is also called *'ar'ar* by the Arabs, and that on the other hand a resin and a tar are extracted from it, the latter widely used for the treatment of camel scabies.

B. Diagnosis of *Cupressus dupreziana* by Miss A. Camus (very brief, and not including any indication relating to the dimensions of the Tamerit cypress which Camus also assumed to be a unique specimen):

« *Cupressus Dupreziana* A.Camus *nov. sp. - Arbor procera. Rami compressi, foliis patulis 1,5-2 mm longis. Ramuli compressi, foliis parvis obtusiusculis 1 mm. longis. Fructus subovoideus, apice rotundatus, 12-18 mm. longus, 10-15 mm. diam. Squamae 10, planisculae, rugosae, mucronulatae. Semina compressa, pallida, 5-6 mm. longa, late alata.*

Tassili des Azdjers : entre Rhât et Djanet (Lavauden) ».

C. Diagnosis of *Cupressus lereddei* by H. Gaussen (even more brief than that of Camus):

"*Cupressus Lereddei* H. Gaussen : *Arbor habito Cupressi Duprezianae similis ; strobilis longioribus, circa 18-24 mm., 16-20 latis ; squamis 10-12 saepe 12*."

D. It should be emphasized that Maire's description is much more detailed than that of Camus and that it was obviously established on more consistent study materials. It indicates the dimensions reached by the species and in particular gives larger extreme dimensions for the cones, and a less strict number of scales, which makes it correspond to both *Cupressus dupreziana* sensu A. Camus and *Cupressus lereddei* sensu H. Gaussen (Maire 1952: 121-123):

"Tree that can reach 12 meters in height, with a trunk 4 meters in diameter, with *Juniperus phoenicea* habit, very dense branches, slightly glaucescent green foliage. Branches and ramules ± flattened in a single plane; branches with red-brown bark, then with gray-brown scaly rhytidomes, bearing in their young parts fairly spaced, opposite, decussate, oblong-acuminate leaves, long fused to the axis, and carrying in this un-keeled fused part several linear resin glands , parallel, ± glaucous-pruinose, with free ± spreading acumen; ramules covered with leaves closely appressed, imbricate, opposite decussate, ovate, obtuse, 1-1.5 mm, the facial ones flat, the lateral ones obtusely keeled on the back, all dull, provided with a single resin gland ± apparent. Cones carried by very short, solitary, ovoid or ellipsoidal ramules, 12-24 x 10-17 mm, light brown, dull or not very shiny; scales 10-12, with escutcheon wider than tall, radially rough, with rounded central laminar mucron, very short, barely projecting. Seeds cinnamon brown, ovate-suborbicular, ± flattened, 4-6 x 5 mm, broadly winged. (…)

Ravines of the central Sahara mountains; very rare. Tassili-n'Ajjer: plateau called Edehi, in Oued Tamerit! (Duprez, Lavauden, Kilian, Lhote), Oued Amezar! (Kilian), 1,700-1,900 m.

Endangered species, which is hardly represented by more than ten living individuals, whose seeds are usually sterile. Out of a hundred seeds examined, for a long time we were unable to find any containing a well-formed embryo and endosperm. However, in 1943, following heavy rains, Lieutenant d'Estienne d'Orves harvested a young seedling of C. Dupreziana from the edge of a guelta downstream from the surviving trees, and brought us seeds in the one of which we found an embryo. We then sowed the rest of the lot and obtained two plants which are currently growing in the Botanical Garden of the University of Algiers where they are developing perfectly. The young plant has 2 cotyledons, it is glaucous and has acicular young leaves similar to those of *C. sempervirens*. *C. dupreziana* would also have existed in the past in Hoggar and a dead trunk is still found in Oued Tin-Tarabine (Kilian, according to indigenous information).

Geographical area. – Endemic."

E. When we know the long persistence on the ground of dead wood, in place or felled, in the Saharan regions where no rot can practically occur, it is difficult to understand why Quézel can affirm that the trunk and the branch observed in the Oued Erherhi, on the Tazrouk-Tin Tarabine track, died at different times!

F. "According to the examinations carried out on the samples from Paris and on site - by Michel Thinon [Faculty of sciences and techniques of Marseille Saint-Jérôme, Botany and Mediterranean ecology department] -, what had been considered by Quézel to come from cypress (sample taken from Oued Tin Tarabine) turned out to be acacia." (Dubief 1999) [B.B. 2016.]

G. An observation made in the field (December 1965-January 1966) seems to us to be able to explain why two distinct species of cypress could be described at Tassili n'Ajjer, when in reality only one exists:

- At the time of our harvest, the cones were adherent to the branches and they almost all had a size and number of scales consistent with the description established in 1950 by H. Gaussen for *Cupressus lereddei*;

- Some cones, generally found on the ground, were significantly smaller, often had a reduced number of scales, and thus corresponded to the description given by Miss A. Camus for *Cupressus dupreziana*;

- These last cones were either parasitized by an insect that remained undetermined because the adults had already hatched and emerged, or aborted and containing only very poorly developed seeds which were themselves abortive;

- It is likely that the samples - or perhaps the single sample - from Lavauden described in 1926 by Miss A. Camus corresponded to cones of the second type, picked up on the ground.

H. *Cupressus dupreziana* A.Camus, 1926 (= *Cupressus lereddei* Gaussen, 1950).

Two subsequent combinations have been published, by John Silba (1981: 398) of the State University of New York, and by Alexey Vladimir Bobrov & Aleksander Pavlovich Melikyan (2006: 72) of the Moscow State University. "*Cupressus sempervirens* var. *dupreziana* (A.Camus) Silba" brought the Saharan Cypress to the status of a simple variety of the common Mediterranean Cypress, while in contrast, "*Tassilicyparis dupreziana* (A.Camus) A.V.F.Ch.Bobrov & Melikian" went so far as to create a new genus with a single species. Neither has had any widespread acceptance, and both are rejected here.

In creating the combination "*Cupressus dupreziana* A.Camus var. *atlantica* (Gaussen) Silba", Silba (1998) also created the autonym "*Cupressus dupreziana* A.Camus var. *dupreziana*", with this trinomial to distinguish the Saharan Cypress from the Moroccan Cypress or Atlas Cypress *Cupressus atlantica* Gaussen, 1926 when treating it as a variety of the Saharan Cypress.

I. Jean-Paul Barry, Professor at the Faculty of Sciences of Algiers, then at the Faculty of Sciences of Nice (Arid Regions Ecology Laboratory); Bernard Belin, Assistant to the Faculties of Sciences at the University of Algiers, then Researcher at the Overseas Scientific and Technical Research Office (Botanical and Plant Biology Section) in Paris; Jean-Claude Celles, Daniel Dubost and Pierre Hethener, Assistants of the Faculties of Sciences at the University of Algiers; Louis Faurel, Lecturer at the Faculty of Sciences of Algiers, then Deputy Director at the Pratical School of High Studies (Laboratory of tropical mycology and phytopathology) in Paris.

Accompanying the Mission on the Tassili n'Ajjer plateau: Georges Arbuz, Ethnologist (Cf. "The economic situation of Djanet in 1965", *Travaux de l'Institut de recherche sahariennes*, Algiers, 1966, Volume 25).

Post-mission collaboration: Marc Laferrère, Center for Scientific Studies of the Algerian Hydraulic Service.

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Cupressus dupreziana **- Quintillan**

Experimental plantation

During the 1970s and 1980s, several species of conifers were planted in the South of France as experiments to test their adaptability to the local climate. *Cupressus dupreziana* was one species of choice to face the Mediterranean climate with dry warm summers. It is also quite tolerant of frosts like the ones happening in the South of France. One such experiment was conducted close to Quintillan (Aude). The plantation was done in 1984 by AFOCEL, now FCBA. The idea was to test its suitability as a potential species for wood production on difficult sites.

The soil of the Quintillan site is shallow, acidic, on schist rocks. The south-western slope lies between 285 and 290 m. The main vegetation consists of *Arbutus unedo* and *Erica arborea* which strongly compete with the introduced cypresses. It is almost impenetrable.

One of the aims of this experimental plantation was also to establish a conservatory of 34 clones of *C. dupreziana*. The plants were reproduced either by cuttings or grafting. Unfortunately there is no documentation left of the origin of the plants (several were grafted from original material collected in the Tassili), nor a map of the plantation where the origin of all plants was referenced.

A previous report was carried in 2010, when it was noted that already 50% of the cypresses had not survived (that is 26 years after the plantation). No cleaning of the vegetation to suppress the competition occurred after the plantation. The site, isolated, is very difficult to access, especially during bad weather.

The site is currently left abandoned. A rough estimation of the surviving cypresses lies between 30 and 40. The number of trees originally planted is lost. The 2010 report says that the plants were established at 3 m distance in all directions on a surface of 675 m². Our estimation is that this surface is at least 1,000 m² larger, allowing the plantation of some 220 cypresses (instead of merely one hundred or less).

Fig. 1: An Aleppo Pine *Pinus halepensis* in the middle of the experimental field outgrew the surviving cypresses.
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Fig. 2: The tallest *Cupressus dupreziana* at the top of the slope and close to the dirt road. Every time the road is restored (for instance after strong rains), some soil is pushed to the side, allowing all plants along the road to grow better.

Fig. 3: The dense shrubs in competition with the cypresses.

Figs 4 & 5: The leaders of several cypresses show signs of dieback. The cause could be the last two very dry and hot summers.

Fig. 6: Some cypresses are hidden among the vegetation, being no taller than the surroundings shrubs and making it difficult to assess the number of surviving plants without a drone or without cleaning the field.

Fig. 7: On the west side of the field the soil is very shallow.

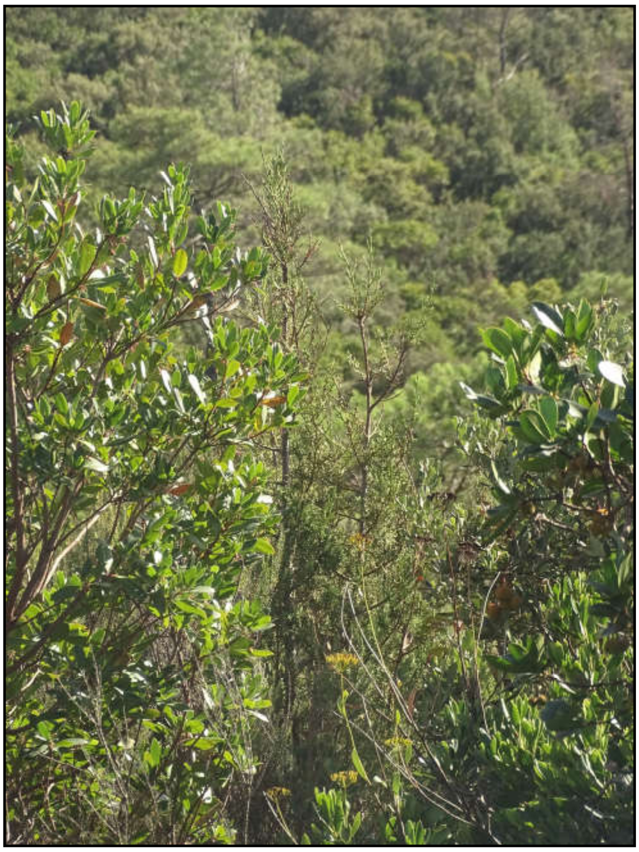

Fig. 8: Larger view from the southwest; the cypress in the foreground is the same as the one on Fig. 7.

Fig. 9: During strong rains, the water flows from the dirt road at the limit of the field and washes part of the soil away. *Juniperus* sp. in the foreground with *Erica arborea*.

Fig. 10: Another view of some of the tallest cypresses, not even 3 m high.

Fig. 11: East side of the field, with impenetrable vegetation (*Arbutus unedo* in foreground).

Fig. 12: For comparison, here is a second experimental plantation also in the Aude Department, planted in 1980, but on better soil at the bottom of a valley and without competition from other woody plants.