doi: 10.25750/1995-4301-2022-3-135-141

Host by strain association study of rhizospheric actinobacteria on two Algerian date palm cultivars

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Extreme ecosystems such as the Algerian Sahara can be a source of untapped microorganisms that produce novel bioactive compounds against fusarium wilt disease. Effective control of fusarium wilt agent *Fusarium oxysporum* f. sp. *albedinis* relies on a thorough understanding of host-by-strain relations. Achieving this understanding can be highly beneficial, particularly for extensive multidimensional experiments. This paper investigates the qualitative and quantitative distribution of the actinobacteria in the rhizosphere (endorhizosphere and pneumatodes) of two date palm cultivars, one resistant (Takerbucht) and one susceptible to fusariosis (Aghamu). Consequently, 199 actinobacterial isolates were recorded; 13 species were identified, 6 were identified in root tips, and 10 in pneumatodes. The highest actinobacterial densities were recorded in the rhizospheric soils of the susceptible cultivar. However, the dominant species are present in the roots of the resistant ones. Differences in the composition of genera and species were found between cultivars. Actinobacteria are mainly represented by the genera *Streptomyces* and *Nocardioides*, which are respectively related to healthy and diseased date palm cultivars. Numerically, the most important species are related to *S. chartreusis*, *Nocardioides albus* and *S. gannmycicus*. Consequently, correspondence analysis facilitated the visual representation (associations patterns) of host-by-strain data and confirmed the aforementioned findings.

Keywords: Actinobacteria, saharan oases, date-palm, endorhizosphere, Pneumatodes, host by strain association.

УДК 579.64

Исследование ассоциации хозяев по штаммам ризосферных актинобактерий на двух алжирских сортах финиковой пальмы

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Экстремальные экосистемы, такие как Алжирская Сахара, могут быть источником неиспользованных микроорганизмов, которые производят новые биоактивные соединения против фузариозного увядания. Эффективная борьба с возбудителем фузариозного увядания *Fusarium oxysporum* f. sp. *albedinis* основана на исследовании отношений между хозяином и патогеном. В данной статье исследуется качественное и количественное распределение актинобактерий в ризосфере (эндоризосфера и пневматоды) двух сортов финиковой пальмы, устойчивого (Takerbucht) и восприимчивого к фузариозу (Aghamu). Было зарегистрировано 199 изолятов актинобактерий. Выявлено 13 видов, 6 в кончиках корней и 10 – в пневматодах (листьях). Наибольшая плотность актинобактерий отмечена в ризосферных почвах восприимчивого сорта. Однако доминирующие виды присутствуют в корнях устойчивых. Между сортами обнаружены различия в составе родов и видов. Актинобактерии в основном представлены родами *Streptomyces* и *Nocardioides*, которые относятся соответственно к здоровым и больным сортам финиковой пальмы. Численно наиболее важные виды родственны *S. chartreusis*, *Nocardioides albus* и *S. gannmycicus*. Таким образом, анализ соответствий облегчил визуальное представление (паттерны ассоциаций) данных по штамму хозяина и подтвердил вышеупомянутые выводы.

Ключевые слова: актинобактерии, сахарские оазисы, финиковая пальма, эндоризосфера, пневматоды, ассоциация хозяев за штаммами.

Actinobacteria, formerly known as actinomycetes, are a group of microorganisms commonly found even in the soils of extreme ecosystems, such as the Saharan soils of Algeria that are permanently exposed to challenging climatic conditions. These soils are ecosystems worth of being explored because of their significant biodiversity [1, 2].

Actinobacteria are embroiled in the ecology of these extreme habitats, as they are involved in several transformation processes of complex biopolymers (lignocellulose, hemicellulose, pectin, keratin, chitin) as well as being recommended as potential biocontrol agents, such as certain species of Streptomyces, which can produce effective antibiotics against phytopathogenic fungi such as *Fusarium oxysporum*, *Pyrenochaeta lycopersici*, *Sclerotium rolfsii*, *Sclerotinia sclerotiorum* and *Botrytis cinerea* [3–6].

In-plant pathology, host-by-pathogen or genotype-by-strain association are particular cases of genotype-by-environment interactions studies. This is especially true for host-by-strain interactions/associations in which there are clear race differentiations such that a host genotype can be described as resistant or susceptible according to a specific/unique interaction pattern. These patterns of associations are generally challenging to characterize because of the complexity of generated data that frequently span on multiple dimensions [7].

A genotype-by-strain association study on actinobacterial species distribution was conducted to characterize species associated with healthy and diseased date palm cultivars. The association pattern was assessed on healthy/resistant and diseased/susceptible cultivars affected by *Fusarium oxysporum* f. sp. *albedinis* (Killian et Maire) [8], which is a significant threat to date-palm oases located in south-western Algeria and the M'zab region [9–12]. Actinobacterial species distribution was assessed at two different potential penetration points of *F. oxysporum* f. sp. *albedinis*, namely on young root tips (endorhizosphere) and pneumatodes, which are complex respiratory structures that form on older roots.

Materials and methods

Study site. The study site is an oasis with a typical Saharan climate located in southwest Algeria (28°00′N, 0°30′W) in the territorial division of Adrar (south-western Algeria). The experiment was carried out on a 160 × 20 m plot composed of 133 date palms belonging to the cultivars Takerbucht (resistant) and Aghamu (susceptible) to fusarium wilt (Bayoud disease) caused by *F. oxysporum* f. sp. albedinis. Thirty percent of the susceptible date palms were affected by this disease in study area.

Rhizosphere sampling. Five plots, separated from each other by approximately 25 m were delimited. Each plot consisted of three date-palm trees arranged in a triangle. These consisted of one resistant Takerbucht palm tree and two susceptible Aghamu trees where one was healthy (no symptoms) and the second showed typical symptoms of fusarium wilt. For the latter, the disease was confirmed after isolation of *F. oxysporum* f. sp. *albedinis* from the rachis.

Isolation and enumeration of actinobacteria from the endorhizosphere and pneumatodes. Roots were collected at 25–40 cm depth from all around the date-palm trees. Two types of structures are considered: (i) young roots with exuding root tips and (ii) old roots with whitish sleeves at the base of their branches (pneumatodes).

Young roots tips and aged roots carrying pneumatodes were washed and disinfected with sterile distilled water and 3.5% aqueous calcium

hypochlorite solution. Both were cut (2 cm long), ground separately, filtered; and from the resulting suspension, decimal dilutions were made.

The enumeration in colony forming units (CFU) per gram of dry roots was carried out after 7–15 days of incubation. The actinobacteria were isolated on Petri dishes by the mean of suspension-dilution method [13] and spread on the "chitin-agar" medium of Lingappa and Lockwood [14].

Identification of actinobacteria. Actinobacterial species and genera identification was based on macromorphological cultural characteristics (colour of aerial and/or substrate mycelium and diffusible pigments), micromorphological structures (spore production, number of spores and arrangement, straight to flexuous, hooked, looped or spiral spore chains disposition) as stated in the Bergey's manuals [15].

We determined the configuration of the isomer (LL or DL) of diaminopimelic acid, as well as the presence of glycine [16], characteristic sugars [17] and the presence of parietal mycolic acids on cell walls [18]. In addition, several determination keys were checked out [8, 15, 19–21].

Twenty-three (23) biochemical tests (carbohydrate assimilation as sole carbon source) were determined as described by [22].

Statistical analysis. All data were analyzed in R for Windows v4.1.0 [23] using the R-Studio GUI v1.4.1717. Multivariate genotype-by-strain data were analyzed using correspondence analysis using abstract and product terms using FactoMineR, Factoextra and Corrplot [24–26].

Results and discussion

Quantitative distribution of actinobacteria. Enumeration results in Figure 1 showed a large variability in bacterial density between the five lots, ranging from 0.1 to 62 · 10^4 CFU/g root and 1.5 to 83.3 · 10^4 CFU/g in pneumatodes. This variability is even observed within the same cultivar, whether healthy or diseased (i. e., diseased Aghamu: 0.33 to 62 · 10^4 CFU/g root and 4.17 to 83.3 · 10^4 CFU/g in pneumatodes). This heterogeneity can be related to the uneven distribution of the organic matter (1.1, 2.1, 3.2, 4.3 and 6.3% respectively in lot D, E, A, C and B). Thus, the relatively small quantity and nature of the organic matter, along with a heterogeneous amendment with N-P-K fertilizers typically combined with organic fertilizers, results in a quantitative variability between the investigated plots and the proliferation of non-yeast-like bacteria at the expense of actinobacteria.

The comparison of the distribution of actinobacteria regarding penetration points areas indicates that their density is much higher in the pneumatodes than in the endorhizosphere, whether in diseased Aghamu, healthy Aghamu or Takerbucht. This can be explained by the loose anatomical structure of the pneumatodes compared to young roots [27, 28]. This flexible structure allows easy entry and adhesion of rhizospheric microflora and pathogens such as *F. oxysporum* f. sp. *albedinis*.

Overall, few actinobacterial species were able to colonize the interior of the roots in the five lots. Nevertheless, an exception can be seen in root tips of healthy and diseased Aghamu (lots A and B), which hosted more actinobacteria than the pneumatodes did. This exception is due to the exudation process, as it was found that susceptible cultivars exudate a large amount of easily assimilable carbohydrates, proteins, lipids and mineral salts. Whereas resistant cultivars secret complex substances such as organic acids and phenolic compounds, which inhibit phytopathogenic soil microorganisms. This process induces an adaptation of the local microflora that becomes typically associated with specific parts of the rhizosphere (Fig. 2 and 3). The same observation has been also reported by many authors [29, 30].

Qualitative distribution of actinobacteria. This distribution is based on macromorphological, micromorphological and physiological criteria. A total of 199 actinobacterial isolates belonging to 13 species were identified. Six species were identified in root tips, and 10 in pneumatodes. Two species (*S. narensis* and *S. coeruleor*) are not represented in figure 2, and were excluded from subsequent analyses due to their rarity (1 occurrence/5 lots). All the recorded species belong to the genus Streptomyces (> 75%) or Nocardioides (about 25%). The latter is less frequently isolated than Streptomyces, which are among the most widespread telluric genera worldwide (Fig. 2). This dictum has been noticed by other authors [31]. Indeed, in culture media, Streptomyces and Nocardioides grow much faster than other actinobacteria, suggesting a higher competitive ability.

Isolated *Streptomyces* are characterized by the presence of an aerial mycelium that produces long chains of non-mobile spores (straight to flexuous, hooked, looped or spiralled) carried by sporophores and a non-fragmented substrate mycelium. Their cells contain the LL isomer of diaminopimelic acid (DAP), glycine and sugars

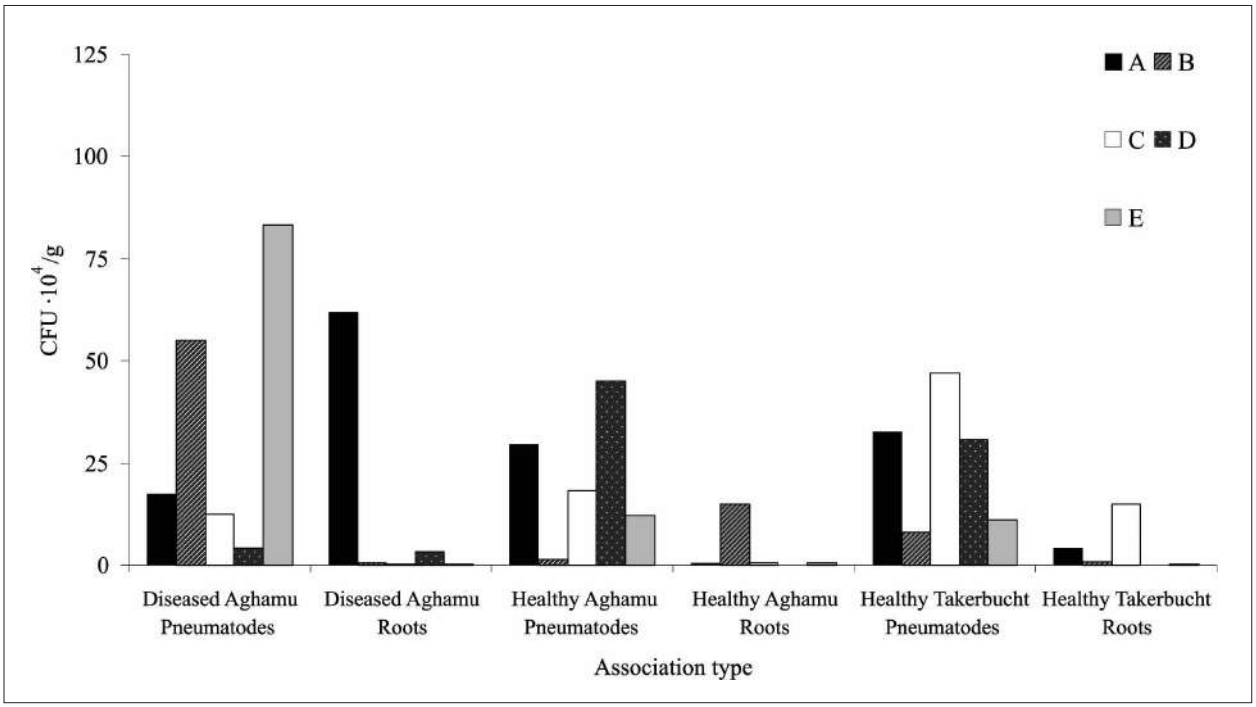

Fig. 1. Actinobacterial density (10^4 CFU per gram of dry root) at the endorhizosphere and pneumatode of the cultivars Aghamu and Takerbucht

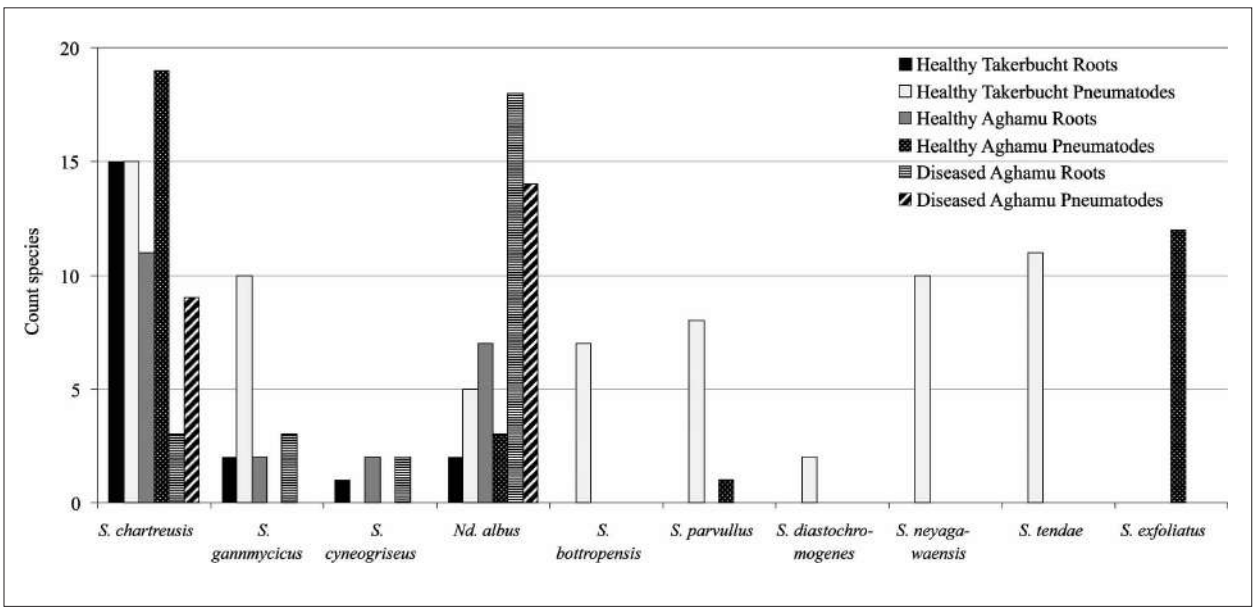

Fig. 2. Species distribution of the 197 isolates identified on pneumatodes and endorhizosphere in healthy and diseased cultivars

such as ribose, glucose and galactose; mycolic acids are absent. The isolates of *Nocardioides* are characterized by an aerial mycelium and a substrate mycelium with short filaments that fragment into non-mobile elements. Their cells contain the LL-isomer of DAP, glycine, ribose, glucose and galactose; mycolic acids are also absent.

The dominant species are *S. chartreusis* (36.54%) and *N. albus* (24.87%). In the present study, *S. chartreusis* is equally distributed between healthy cultivars (83.32%). This percentage decreases sharply in the susceptible cultivar Aghamu when diseased (16.66%). For *N. albus*, the results are inverted. This species is present at 14.28% in the resistant cultivar Takerbucht,

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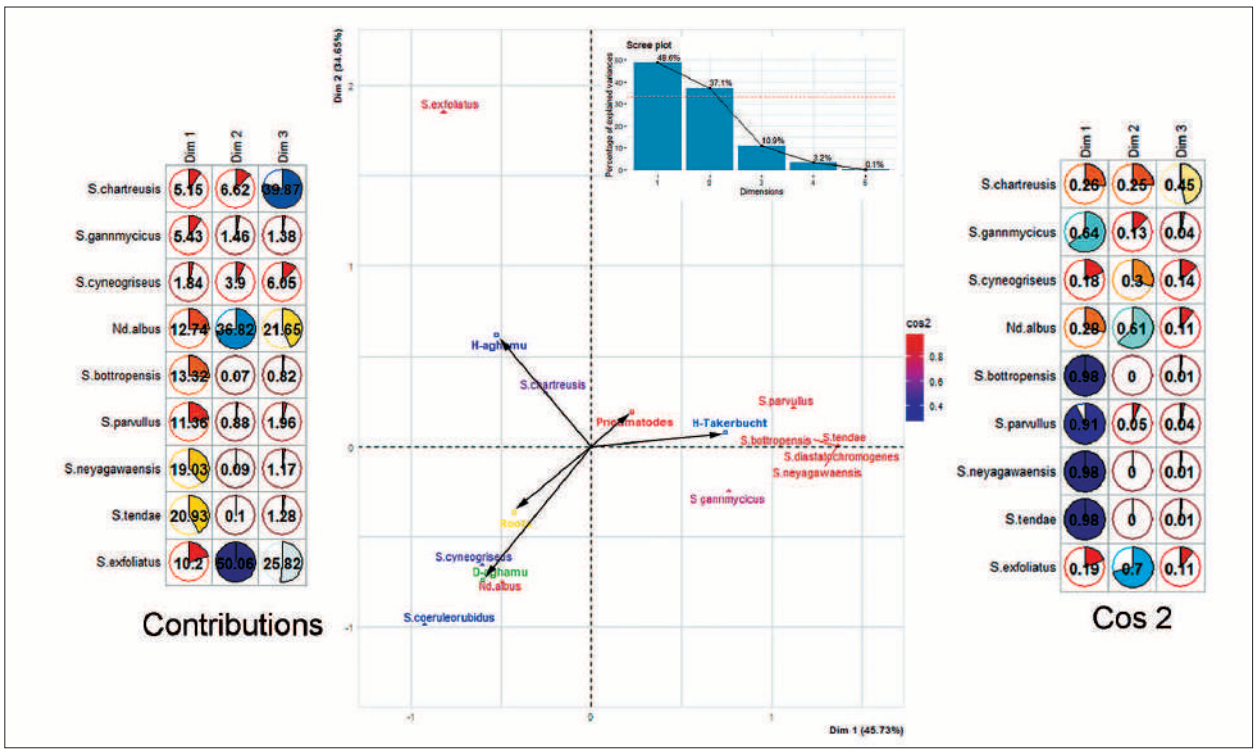

Fig. 3. Correspondence analysis biplot of species score and Cultivar's health state/penetration point. Cultivar groups: Dim 1 [healthy Takerbucht], Dim 2 [healthy Aghamu] Dim 3 [diseased Aghamu] and penetration point groups: 1 [endorhizosphere], 2 [pneumatodes]

20.4% in healthy Aghamu and 65.3% in diseased Aghamu; this species is ubiquitous and is present in all sampled lots.

The species *S. gannmycicus*, primarily associated with pneumatodes of the resistant cultivar Takerbucht, constitutes 8.62% of the total isolates. The rest of the species: *S. parvulus*, *S. bottropensis*, *S. tendae*, *S. diastatochromogenes*, *S. eyagawaensis*, *S. cyneogriseus*, *S. coeruleorubidus* and *S. exfoliatus* share the fourth rank of the most dominant species and may be specific to one or other part of the rhizosphere or be even quite rare (i. e. *S. narensis* and *S. coeruleor*).

The species *S. chartreusis* and *S. gannmicicus* are two species associated with the healthy state of both cultivars. Indeed, *S. chartreusis* is a non-specific (ubiquitious) species present on all sampled lots and *S. gannmicicus* is a species predominantly found on pneumatodes. *In vitro* confrontation tests, highlighted the antagonistic activity of several isolates against *F. oxysporum* f. sp. *albedinis* (data not shown). These findings, may explain the infield direct (antibiosis) and indirect (attachment/penetration site/point occupancy) biocontrol of fusarium wilt populations [32].

Correspondence analysis results. Applying correspondence analysis "CA" on the data in figure 1 (6 rows and 11 columns, with 2 explanatory variables "cultivar's health state and penetration points) results in figure's 3 contributions and representation quality given by the Cos 2 colour scale. Each actinobacterial strain (active variable) cultivar's health state and penetration points (supplementary variables) is represented by two scores for Dim 1 and Dim 2, respectively. When the scores of Dim 1 and Dim 2 are projected on the plane, each active and supplementary variable is displayed as a point on the biplot (Fig. 3, see color insert V).

The inertia of the first dimensions shows if there are strong relationships between variables and suggests the number of dimensions that should be studied. The first two dimensions of analysis express "80.37%" of the total dataset inertia; that means that the plane explains 80.37% of the rows (or columns) cloud total variability. This percentage is high, and thus the first plane represents an essential part of the data variability; From these observations, it is probably not helpful to interpret the 3rd dimensions (Fig. 3; Scree plot). Correspondence analysis results demonstrate an association between cultivar's health state and penetration point area variables with a raw score per order (Chisq = 227.33, p-value = 0.001) [25]. However, no explicit penetration point-related pattern is present (Wilk's $\lambda = 0.69$). Instead, distances between individuals on the plane seems to be best separated by the cultivar's health state variable (Wilk's $\lambda = 0.35$; Fig. 3). At this stage, results suggest that subsequent analysis should consider cultivar's health state as a factor but not penetration point structure. These findings should be taken with precaution as more evidence must be brought by analogues confirmatory studies [33].

Row and columns score contributions (Fig. 3) indicate that the first dimension represents the latent variable cultivar's phytosanitary health state which can either be healthy (Upside) or diseased date-palm (Downside). The second dimension represents the penetration point structure where associated species can be either linked to roots (left side) or pneumatodes (Rightside); the two latter are set in opposition on the biplot (Fig. 3).

Overall, three distinct clusters of isolate groups are present: cluster 1 consists of *S. parvulus*, *S. bottropensis*, *S. tendae*, *S. diastatochromogenes*, *S. neyagawaensis* and *S. gannmycicus*; cluster 2 consists of the isolate *N. albus*, *S. cyneogriseus*, *S. coeruleorubidus* and cluster 3 consists of two isolated groups, which are *S. exfoliatus* and *S. chartreusis* (Fig. 3). Among all actinobacteria, red or nearly red represented species are well projected on their respective dimension ($\cos^2 > 0.7$) (Fig. 3). Thus, all members of cluster 1 are well projected on Dim 1 and are all equally associated (species clustering together; no long vector) with the pneumatodes of healthy Takerbucht.

The unique *Nocardioides* isolated group is the only well-projected species among cluster 2 on Dim 2 and is associated with diseased Aghamu roots rather than pneumatodes. For cluster 3, *S. exfoliatus* is best projected on Dim 2, where it is strongly related to pneumatodes of healthy Aghamu even if it is plotted farthest. Finally, although *S. chartreusis* is a frequently encountered species (isolated from 4 among 5 lots), this species group is associated unambiguously with pneumatodes of healthy date-palm cultivars.

Conclusion

In the present host-by-strain association study, information on actinobacterial genera and species distribution in date palm rhizosphere are highlighted. Indeed, correspondence analysis allowed us to gain more insight through dimensionality reduction and graphical representation

of various isolate group association patterns on date-palm cultivars and their endorhizosphere and pneumatodes. Overall, differences were observed between cultivars resistant and susceptible cultivars (healthy or diseased), particularly in the distribution of some dominant actinobacterial species in the endorhizosphere. Globally, a negative relationship is observed between the two dominant genera (*Streptomyces* and *Nocardioides*), as we have noticed an apparent decrease in the percentage of *Streptomyces* from Takerbucht to healthy then diseased Aghamu, in favour of the *Nocardioides* genus, which is present at an exceptionally high percentage in diseased Aghamu. The rate of *Streptomyces* also decreases significantly in diseased Aghamu pneumatodes (compared to healthy Aghamu and Takerbucht). These findings are confirmed by the correspondence analysis biplot, where specific association patterns are emphasized. Further investigations should focus on the role and mechanisms of action of dominant rhizosphere species against the fusarium wilt pathogen *F. oxysporum* f. sp. *albedinis*, by considering their antagonistic capability (molecular characterization of secondary metabolites such as antibiotics and antifungals) for an integrated pest management strategy to limit Bayoud disease progression in Saharan oases.

This work is dedicated to the memory of the deceased Nasserdine Sabaou and Ahmed Moustiri, who were among the pioneers and influential researchers who studied the microflora of Algerian Sahara oases. These two exceptional people of great kindness and dedication contributed to the training of many professionals and enlightened the path of the following generations of researchers, may they rest in peace.

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