# Differential effects of the crustose *Diploschistes diacapsis* and the squamulose *Fulgensia bracteata* on the establishment of a Mediterranean grass species

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## Abstract

The interest of the scientific community in biological soil crusts has grown exponentially over the last decades. One of the scientific research interests is the study of the effect of these crusts on plant establishment. Findings in this topic have been controversial, and some differences were attributed to crust types. Biological soil crusts dominated by lichens are common components of *Stipa tenacissima* steppes in arid and semi-arid environments of the southern Mediterranean. In the current study, we conducted growth chamber experiments to investigate the differential effects of two lichen species with continuous crustose thalli (*Diploschistes diacapsis*) and with squamulose semicontinuous thalli (*Fulgensia bracteata*) on seed germination, root penetration, shoot emergence and seed viability of the tussock grass species *S. tenacissima*. Our results showed that under laboratory conditions, two distinct lichen species had significantly different effects on the establishment of *S. tenacissima*. Our findings clearly demonstrated that *D. diacapsis* significantly decreased germination, root penetration and shoot emergence of *S. tenacissima* compared to *F. bracteata*. This can be related to differences in morphological and physiological characteristics between crustose and squamulose lichens. Overall, we suggest that *D. diacapsis* and crustose lichens generally can act as natural barrier to the establishment of *S. tenacissima*.

*Key words:* *Diploschistes diacapsis*, *Fulgensia bracteata*, germination, root penetration, shoot emergence, *Stipa tenacissima*

## Résumé

L'intérêt de la communauté scientifique pour les croûtes biologiques a crû de façon exponentielle au cours des dernières décennies. Un des intérêts de la recherche scientifique est l'étude de l'effet de ces croûtes sur l'établissement de plantes. Les résultats obtenus à ce sujet restent controversés et certaines différences ont été attribuées aux types de croûtes. Les croûtes biologiques dominées par des lichens sont des composantes fréquentes des steppes à *Stipa tenacissima*, dans les environnements arides et semi-arides du sud de la Méditerranée. Dans cette étude, nous avons mené des expériences en chambre de croissance pour étudier les effets différentiels de deux espèces de lichens avec des thalles encroûtants continus (*Diploschistes diacapsis*) et avec des thalles squamuleux semi-continus (*Fulgensia bracteata*) sur la germination des semences, la pénétration des racines, l'émergence des pousses et la viabilité des semences de l'herbe en touffe *S. tenacissima*. Nos résultats montrent que, dans les conditions de laboratoire, deux espèces de lichens distinctes avaient des effets significativement différents sur l'établissement de *S. tenacissima*. Nos résultats montrent clairement que *D. diacapsis* diminue significativement la germination, la pénétration des racines et l'émergence des pousses de *S. tenacissima* par rapport à *F. bracteata*. Ceci peut être mis en rapport avec des différences de caractéristiques morphologiques et physiologiques entre les lichens encroûtants et squamuleux. En résumé, nous suggérons que *D. diacapsis* et les lichens encroûtants en général peuvent agir comme des barrières naturelles à l'installation de *S. tenacissima*.

## Introduction

Arid and semi-arid environments are characterized by spatial heterogeneity partially attributed to the presence of biological soil crusts (West, 1990; Belnap, Prasse & Harper, 2001) between vascular plants (Harper & Marble, 1988; Eldridge & Greene, 1994). These organisms consisting of bacteria, cyanobacteria, algae, mosses,

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liverworts, fungi and lichens grow on the top or within the top layers of the soil (Belnap, Büdel & Lange, 2003; Quiñones-Vera *et al.*, 2009). It has been reported that biological soil crusts enhance nutrient content of soils (Belnap & Harper, 1995; Belnap, 2002; Hawkes, 2003; Ghiloufi & Chaieb, 2014), increase soil stability (Veluci, Neher & Weicht, 2006) and protect the soil surface from wind and water erosion (Eldridge, 1998; Zhang *et al.*, 2006), which may contribute to the development of patchy vegetation patterns through an effect on seed germination and establishment (Deines *et al.*, 2007).

The interest of the scientific community in biological soil crusts has grown exponentially over the last two decades (Sancho, Maestre & Büdel, 2014). One of the scientific research interests is the study of the effect of these crusts on plant germination. In fact, seed germination representing a critical stage in the life cycle of vascular plants could be directly affected by the presence of biological soil crusts (Eckert *et al.*, 1986; Harper & Marble, 1988; Prasse & Bornkamm, 2000). Nevertheless, contradictory findings on the effect of biological crusts on seed germination were observed. Some authors reported positive (Mücher *et al.*, 1988; Danin *et al.*, 1989; Rivera-Aguilar *et al.*, 2005), negative (Prasse & Bornkamm, 2000; Serpe *et al.*, 2006; Deines *et al.*, 2007) or no effect (Pando-Moreno *et al.*, 2014) of these crusts on the germination process. Some authors attributed these contradictory findings to the investigated species (Kaltenecker, Wicklow-Howard & Pellant, 1999; Eldridge & Simpson, 2002), seed size (Li *et al.*, 2005; Serpe *et al.*, 2006; Langhans, Storm & Schwabe, 2009; Burmeier *et al.*, 2010), morphological characteristics of the crust (Li *et al.*, 2005) and crust age (Langhans, Storm & Schwabe, 2009). But, it is worth noting that most of these studies have considered both the plant and crust communities as a whole, without taking into consideration the species involved (Escudero *et al.*, 2007).

Little is known about the effects of biological soil crusts on plant establishment in southern regions of the Mediterranean. In a recent study (Ghiloufi, Büdel & Chaieb, 2017), it has been shown that mixed crusts enhanced the seed germination of *Stipa tenacissima* L., a Mediterranean tussock grass species widely distributed in *S. tenacissima* steppes of North Africa and Spain, and coexist with biological soil crusts. However, it has been reported that moss-dominated, lichen-dominated and mixed crusts differ in their chemical and structural characteristics and thus may have a different effect on seed germination (Zamfir, 2000; Belnap, 2006).

Soil lichens represent an important constituent of biological soil crusts in arid and semi-arid environments, and usually represent a later stage on its development (Belnap & Lange, 2001). In this study, we investigated the differential effects of two dominating lichen species (the crustose *Diploschistes diacapsis* (Ach.) Lumbsch and the squamulose *Fulgensia bracteata* (Hoffm.) Räsenen) in Mediterranean arid ecosystem on the germination, shoot emergence, root penetration and seed viability of *S. tenacissima* under laboratory conditions.

## Materials and methods

### *Study area and investigated species*

In Mediterranean *S. tenacissima* steppe from Southern Tunisia (34°42′35.21″N 10°31′47.61″E), soils were dominated by lichens. Their coverage is about 45% of the soil surface. Soils are alkaline sandy loam, with friable caliches at 10-25 cm depth and gypsum outcrops (Jeddi & Chaieb, 2009).

The tussock grass *S. tenacissima* and the lichen species *D. diacapsis* and *F. bracteata* are dominant components of the vegetation and biological soil crusts, respectively, in the study area. *D. diacapsis* is a terricolous crustose, verrucosely areolate, 1- to 3-mm-thick lichen with urceolate apothecia and white pruina (Lumbsch, 1988). *F. bracteata* is characterized by the presence of a false cortical layer, unicellular or one-septate spores and by attachment to the substratum with a felt of hyphae (Poelt, 1965). The thallus is not continuous but rather consists of widely scattered to densely crowded areoles or squamules (Westberg & Kärnefelt, 1998).

### *Sampling and growth chamber experiments*

We collected three soil treatments at a depth of ≈3 cm: bare soil, soil covered by *D. diacapsis* and soil covered by *F. bracteata*. Samples of bare soil, used as controls, were autoclaved to remove any effect of biological elements on the surface (Deines *et al.*, 2007).

Before sampling, soil crusts were previously sprayed with distilled water to avoid lichen breaking and to facilitate their extraction. Contiguous pieces of the top layer of lichen type and the soil layer underneath the tested lichens were collected, placed in Petri dishes and taken to the laboratory. There were no pretreatments for either the seeds of *S. tenacissima* or the lichen samples.

For each treatment, five replicates of 20 seeds were used. Dishes were placed in a growth chamber at the optimum temperature for the germination of *S. tenacissima* of 20°C (Krichen, Ben Mariem & Chaieb, 2014), with a photoperiod of 12 h. Soils were watered regularly with distilled water once a day.

Germination was recorded when the seed radicle emerged and was visible (Jurado & Westoby, 1992; Welbaum *et al.*, 1998). At the end of trials maintained for 30 days, we measured the following variables: seed germination (%), shoot emergence (%), root penetration (%) and seed viability (%). Germination percentages were expressed as the ratio of the number of germinated seeds on the total number of seeds. Per cent shoot emergence represents the proportion of seedlings that develop coleoptiles over the number of seeds that germinated. For rooting evaluation, we let the samples dry for a week and recorded the number of seedlings whose roots penetrated the soil surface (Mendoza-Aguilar, Cortina & Pando-Moreno, 2014). Per cent root penetration (%) is reported as the proportion of seedlings that entered the soil or crust over the number of seeds that germinated.

Ungerminated seeds in each treatment were tested for viability following the method of Hartmann & Kester (1983) by incubating half of the seeds for 12 h in solutions containing 0.1% tetrazolium chloride. The development of red colour throughout the embryo was taken as an indication that the seeds were viable (Deines *et al.*, 2007).

### *Statistical analyses*

Data were analysed using SPSS version 17. We used analysis of variance (ANOVA) and Tukey test to determine significant differences between lichen microsites compared to control treatment ($P \leq 0.05$).

## Results

Our results showed a delayed time of germination of *S. tenacissima* seeds particularly when sown on soils covered by the crustose lichen *D. diacapsis* (Fig. 1). In fact, the first seed sown on soil covered by the crustose lichen *D. diacapsis* germinated after 22 days; however, the first seed sown on soil covered by the squamulose lichen *F. bracteata* germinated after 2 weeks. 16 days took the first seed to germinate on bare soil.

The lowest values of mean germination percentages were recorded on soil surfaces covered by the crustose *D. diacapsis* (9%) followed by the squamulose *F. bracteata* (14%), while the highest value was measured on bare soil (18%) (Fig. 2). Compared to control seeds, significant differences were shown for seeds placed on *D. diacapsis* ($P = 0.008$) but not for those sown on *F. bracteata* ($P = 0.242$).

Shoot emergence values ranged from 20% to 56% (Fig. 3). No significant difference was found between bare soil and soil covered by *F. bracteata* ($P = 0.123$). However, *D. diacapsis* produced a significant reduction in shooting ($P = 0.030$).

Root penetration percentages (Fig. 4) showed that root penetration of germinating seeds on the bare soil was higher than those on the lichen crusts. Rooting of germinating seeds sown on *F. bracteata* was three times higher than those sown on *D. diacapsis*. The proportion of germinated seeds that rooted was weakly affected by *F. bracteata* ($P = 0.278$) but negatively significantly affected by *D. diacapsis* ($P = 0.004$).

Seed viability percentages (Fig. 5) ranged between 85% and 90%, and there were no significant differences between seedbed surfaces.

Overall, ANOVA results showed clearly significant differences in the measured parameters, excepting of seed viability, between the tested lichens.

## Discussion

Our findings showed that the tested lichens reduced the germination process of *Stipa tenacissima* compared to bare soil. However, significant differences compared to control treatment have been only shown for *D. diacapsis*. Generally, previous studies showed that lichens inhibited the germination of some grass species compared to bare soil (Deines *et al.*, 2007; Escudero *et al.*, 2007; Serpe *et al.*, 2008). It is worth noting that the seed germination disability of *S. tenacissima* (Rejeb, 1980; Krichen, Ben Mariem & Chaieb, 2014) and the delay imbibition and hydration caused by the presence of chaff (Dhief, Aschi-Smiti & Neffati, 2014) may verify both the delayed time of germination and the low germination percentages recorded at the different microsites.

While mixed crusts made up of lichens and cyanobacteria improved the germination of *S. tenacissima* compared to bare soil surface (Ghiloufi, Büdel & Chaieb, 2017), lichen crusts evaluated in this study showed no effect

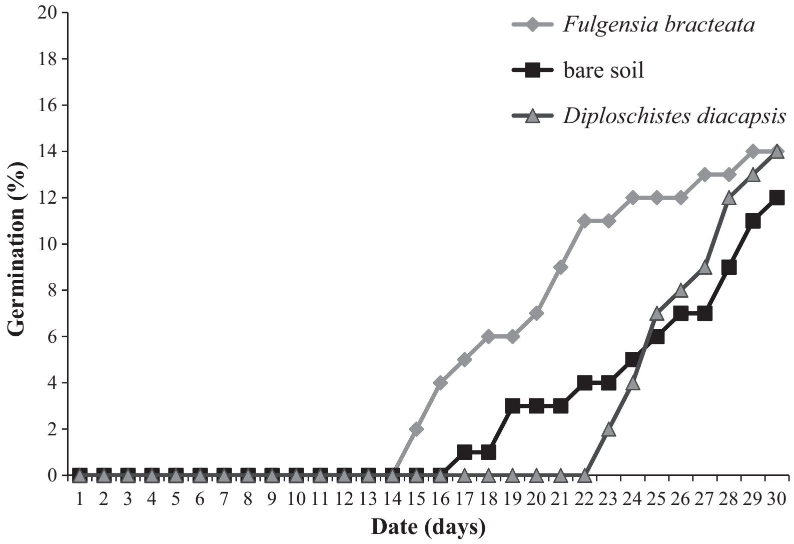

**Fig 1** Germination curves of *Stipa tenacissima* seeds sown on different soil types

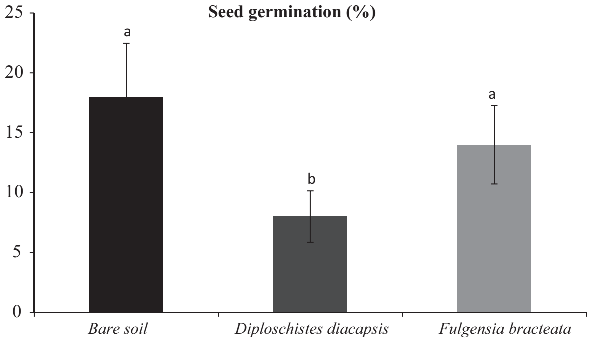

**Fig 2** Seed germination (mean ± CI) of *Stipa tenacissima* seeds sown on bare soil and soils covered by the investigated lichen species. Different letters denote significant differences ($P \leq 0.05$)

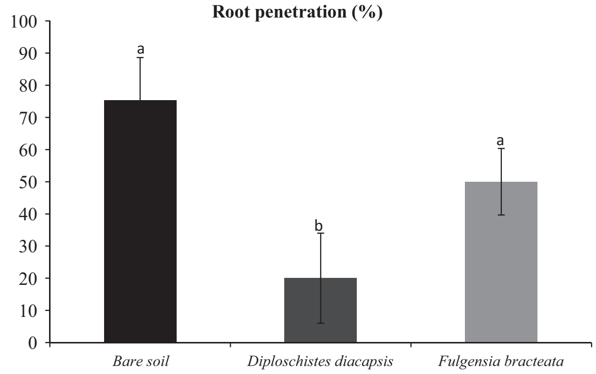

**Fig 4** Per cent root penetration (mean ± CI) of the germinated seeds. Different letters denote significant differences ($P \leq 0.05$)

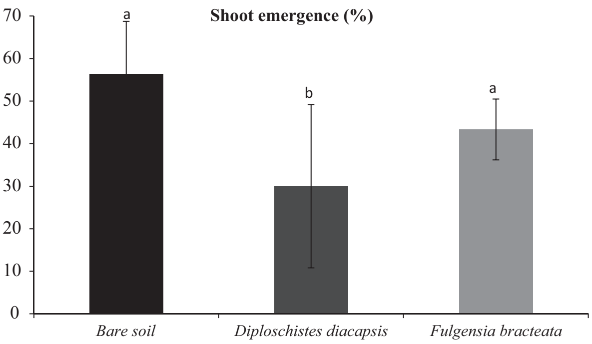

**Fig 3** Shoot emergence (mean ± CI) of germinated seeds on the different soil microsites. Different letters denote significant differences ($P \leq 0.05$)

(*F. bracteata*) or inhibiting effect (*D. diacapsis*) on the germination of *S. tenacissima*. These findings highlighted that mixed crusts and lichen crusts have a different effect on the seed germination of *S. tenacissima*. Indeed, our results showed a significant decrease in seedling and shoot emergence on soil surface covered by *D. diacapsis*, compared to bare soil. Concostrina-Zubiri *et al.* (2013) highlighted that *D. diacapsis* acidified the soil, which may affect seed germination. Some studies reported that soil acidification reduced seed germination and seedling (Ryan, Miyamoto & Stroehlein, 1975; Turner, Lau & Young, 1988). Ryan, Miyamoto & Stroehlein (1975) highlighted that seedling should be delayed until the acid has completely reacted with soil bases. Adding to that, the

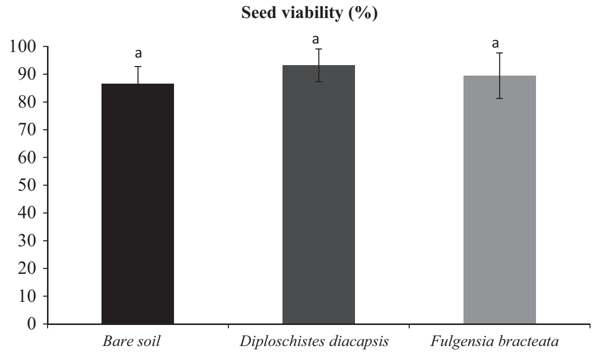

**Fig 5** Seed viability percentage (mean ± CI) on the different microsites. Different letters denote significant differences ($P \leq 0.05$)

lichen of the genus *Diploschistes* might seal the soil, thus reducing water availability during the germination period of some vascular plants (Otsus & Zoel, 2004; Morgan, 2006).

The highest root penetration percentage was recorded on bare soil surfaces compared to lichen crusts. The same result was reported by some previous studies (Deines *et al.*, 2007; Mendoza-Aguilar, Cortina & Pando-Moreno, 2014). By the way, we showed that rooting was highly and significantly reduced for seeds sown on *D. diacapsis* compared to those sown on *F. bracteata*. Regarding the differential effects of the tested lichens on seed viability, our results revealed no significant differences between treatments, which corroborated to the findings of Deines *et al.* (2007).

The current study showed that two distinct lichen species had significantly different effects on the germination, shoot emergence and root penetration of a Mediterranean tussock grass species. *D. diacapsis* produced a significant reduction in these parameters compared to *F. bracteata*. Our findings are in agreement with those of Escudero *et al.* (2007) which showed that crustose versus squamulose lichens (*D. diacapsis* and *Squamarina lentigera*) have species effects on the seedling emergence of three native plant species. This may be attributed to differences in the morphological and physiological characteristics of the lichens. For example, the thick and continuous thallus of *Diploschistes* is suggested to be very resistant to penetrating roots (Escudero *et al.*, 2007). Indeed, it has been reported that crustose lichens tend to absorb lesser amounts of water (Blum, 1973; Belnap, 2006). Thus, the low soil moisture maintained by *D. diacapsis* perhaps may decrease the germination of the studied plant species. However, the thallus of *F. bracteata* is not continuous consisting of areoles or squamules, which may ameliorate seeds entrapment and accumulation of water and nutrients. In this context, it has been reported that the lichen–substratum interface appears to play an important role in the hydric strategy of these lichens which in turn affects the penetration of water into the soil (Souza-Egipsy, Ascaso & Sancho, 2002).

Furthermore, because of the presence of species-specific lichen exudates, lichens could have some inhibitory or enhancing effects on seed emergence and seedling growth (West, 1990). For example, *D. diacapsis* secrete organic acids such as diploschistesic acid, lecanoric acid (both major compounds) and orsellinic acid (minor compound) that may explain the lowest seed emergence values recorded on soils covered by this crustose lichen.

The negative effects of the crustose lichen *D. diacapsis* on seed germination, shoot emergence and root penetration compared to the squamulose lichen *F. bracteata* demonstrated that *D. diacapsis* and crustose lichens generally can act as natural barrier to the establishment of *S. tenacissima* and may be for other grass plant species. Deines *et al.* (2007) reported that the negative effects of crustose lichens on seedling establishment would tend to decrease vegetation cover and contribute to the development of a patchy vegetation distribution in arid environments. Generally, it has been suggested that the differential effects of biological soil crusts can determine the local distribution of plant species (Sedia & Ehrenfeld, 2003; Kirpatrick, Barnes & Ossowski, 2006).

A better understanding of the effect of biological soil crusts at the species level on the germination process of vascular plants can improve arid land restoration efforts where numerous key plant species are menaced by degradation.

## Conclusion

Our research showed differential effects of two lichen types (crustose versus squamulose) on the establishment of *S. tenacissima*, key species in Mediterranean ecosystems. Differences observed between seedbed surface types may be attributed to a combination of physical and chemical factors.

It is worth noting that some limitations should be acknowledged in our experimental approach. On the one hand, under laboratory conditions wet conditions in the soil surface may occasionally occur (De Luís *et al.*, 2001) compared to field conditions. On the other hand, Petri dishes prevent diffusion or leaching of chemicals in contrast to the soil surface in the field (Escudero *et al.*, 2007). Thus, future studies under field conditions are needed to verify the findings observed in our experiment. Adding to that, it is particularly important to understand anatomical and chemical features of the upper cortex and characteristics of the thallus, which can help to explain the differential effects of lichen species on the germination process.

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