

Acacia salicina, *Pinus halepensis* and *Eucalyptus occidentalis* improve soil surface conditions in arid southern Tunisia

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ABSTRACT

Despite low growth rates, plants in arid areas have a strong ability to modify soil surface properties affecting ecosystem processes and community dynamics. But our knowledge on species effects on soil properties in these areas comes largely from observational studies, increasing the risk of confounding factors and precluding estimations of rates of change. We evaluated changes in soil surface properties underneath *Acacia salicina*, *Pinus halepensis* and *Eucalyptus occidentalis* in a 10-year-old common garden experiment established on a degraded *Stipa tenacissima* steppe in southern Tunisia. The three species tested improved soil properties compared to those of open areas. *Acacia salicina* ranked first as soil modifier as the soil underneath this species showed higher total organic carbon, total nitrogen, available phosphorus, soil CO₂ efflux and infiltration rate, and lower soil hydrophobicity than soil in open areas. The richness of vascular plants was higher under *A. salicina* than under the other types of cover. This species showed higher ability to improve microsite conditions and foster succession. Short rotations of *A. salicina* could thus be employed for the restoration of degraded *S. tenacissima* steppes provided that other aspects of its ecology are controlled. *Pinus halepensis* represents a good alternative when native species are a priority, albeit facilitative ability is lower.

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1. Introduction

Plants have a strong capacity to modify soil properties, with strong implications for carbon sequestration (Lal, 2003; Vågen et al., 2005), evolutive dynamics (Valiente-Banuet et al., 2006) and ecosystem functioning (Whitford, 2002). In addition to the uptake of soil resources such as water and nutrients, plants may decrease the evaporative demand by shading, may translocate water, nutrients and soluble salts within the soil profile, may increase water infiltration rates, and may alter soil rooting volume by rock weathering and caliche precipitation. But species differ in their capacity to modify soil properties. The impact of a particular plant species depends on its abundance and growth rate (Jones et al., 1994), but also on specific traits such as the capacity to fix atmospheric nitrogen, produce litter with allelopathic effects, or deposit

soluble salts on the soil surface (Inderjit and Duke, 2003; Lesica and DeLuca, 2004; Spehn et al., 2002).

Despite low productivity, changes in soil properties in drylands can be very fast (Albaladejo et al., 1998; Hibbard et al., 2001). Climatic and soil conditions are commonly harsh, and unfavourable for plant growth as a result of high evaporative demand, limiting water, nitrogen and phosphorus availability, low soil organic matter content, low rooting volume, and high salinity (Safriel et al., 2005). In these areas, a small modification of microhabitat conditions may have strong effects on the performance of neighbouring plants (Maestre et al., 2003a; Moro et al., 1997; Pugnaire et al., 1996a). Furthermore, xerophytes are commonly small and isolated, compared to plants from temperate and tropical regions. Their shape and spatial distribution favour the concentration of litterfall, throughfall, stemflow, decaying fine roots and shade in a restricted area underneath the canopy, intensifying plant effects on microclimate and soil properties (Aerts et al., 2006a; Cortina and Maestre, 2005; Whitford et al., 1997). Finally, isolated plants act as obstacles for runoff and wind carrying organic matter, nutrients, sediments and seeds (Aerts et al., 2006b; Greene et al., 2001), which may accentuate the contrast between enriched areas underneath vegetation patches and depleted open areas.

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In drylands, soils underneath patches of woody vegetation commonly show an increase in the content of soil organic matter, total nitrogen and available phosphorus (Cortina and Maestre, 2005; Lemma et al., 2007). Although the increase is consistent across soil types, climatic conditions and patch properties, its magnitude is highly variable, ranging from virtually no effect, to more than three-fold increases in soil organic matter, total nitrogen and available phosphorus (Cortina and Maestre, 2005). However, most studies describing plant effects on soil properties are based on observations rather than experiments, and observational studies cannot establish cause–effect relationships (Binkley and Giardina, 1998). For example, soils under vegetated patches may have differed from those in open areas before plants were established (Harper et al., 1965; Maestre et al., 2003b), and thus differences in soil properties between vegetated patches and open areas could erroneously be attributed to the presence of the plant. Observational studies frequently lack information on plant age, and thus they cannot provide reliable information on temporal rates of change in soil properties. An alternative to observational studies are common garden experiments, where species are planted under common growing conditions. This experimental design has been successfully used to compare the performance of different species and genotypes (Lavergne and Molofsky, 2007; Mnif et al., 2005) and evaluate the effect of abiotic factors on plant performance and interspecific interactions (Agrawal et al., 2005). They have also been used to evaluate plant effects on soils in a wide range of biomes (Kaye et al., 2000; Menyailo et al., 2002; Reich et al., 2005). But their use in drylands has been scarce.

We evaluated the effect of three woody species (*Pinus halepensis* Mill., *Eucalyptus occidentalis* Endl. and *Acacia salicina* Lindl.) on soil surface properties in a *Stipa tenacissima* L. steppe, 10 years after the establishment of a mixed plantation in arid southern Tunisia. Our hypotheses were: (1) 10 years after planting the three species improve the fertility of the surface soil compared to the levels of unplanted areas; and (2) changes in microhabitat conditions facilitate the establishment of vascular plants.

2. Materials and methods

2.1. Study site

The study was conducted at an afforested *Stipa tenacissima* L. (Alfa, Esparto or Needlegrass) steppe close to El Gonna, 20 km West of Sfax (34° 42' 19"N, 10° 30' 53"E) in southern Tunisia (Fig. 1). The climate is Mediterranean lower arid with temperate winters (Emberger, 1954), and a mean annual precipitation of 196 mm. Temperatures range from an annual mean minimum of 2 °C to a mean maximum of 24 °C. Soils are alkaline sandy loam, with friable caliches at 10–25 cm depth and gypsum outcrops. Topography is hilly. The area was occupied by an overgrazed *Stipa tenacissima* L. steppe, showing sparse perennial plant cover with species such as *Thymelaea hirsuta* Endl., *Artemisia campestris* L., *Plantago albicans* L. and *Retama raetam* (Forssk.) Webb.

In 1995, a variety of tree species was planted by the Forest Service, the most widespread being *Acacia salicina*, *Pinus halepensis* and *Eucalyptus occidentalis*. The area was protected from grazing afterwards. Ten years after planting, average stem height was higher than 2 m, and most trees showed well developed isolated canopies. Intercanopy areas were dominated by herbaceous vegetation.

Pinus halepensis (Aleppo pine) is a widely distributed tree species throughout the Mediterranean basin, where it is one of the few native tree species that can thrive under semiarid and arid conditions (Maestre and Cortina, 2004; Quézel, 2000). *Eucalyptus*

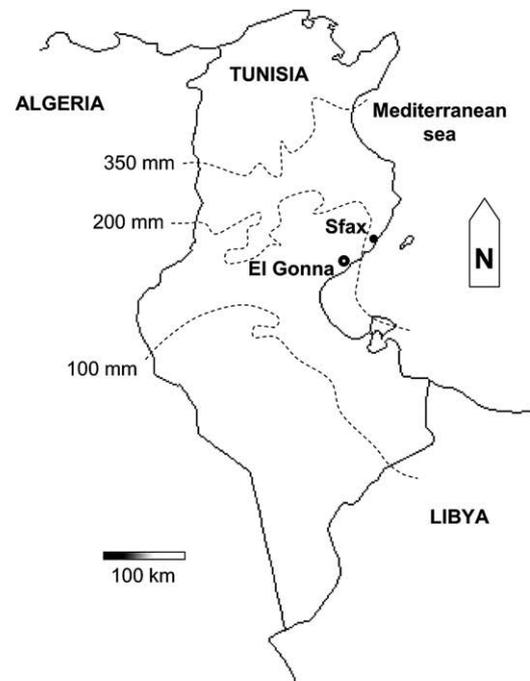


Fig. 1. Location of the experimental site in El Gonna (Agareb, Tunisia; top) and aerial image of the forested area captured from Google-Earth (bottom). Rainfall isohyets are shown as dotted lines on the map. To the left of the black dot signalling the experimental sites are dryland crops, mainly olive trees.

occidentalis Endl. (Swamp yate) and *Acacia salicina* (Willow wattle) are Australian tree species that have been extensively used for forestation in arid areas of the Mediterranean basin, as they provide high quality wood and fodder, and are highly resistant to drought and salinity (Lovenstein et al., 1991; NAS, 1980).

2.2. Soil sampling and analyses

In April 2006, we selected three 40 × 40 m blocks within the area planted with the three dominant tree species. The areas were separated by ca. 100 m from each other. In each block, we randomly located three trees of each species, and three areas where trees failed to establish (open areas hereafter). These areas may have experienced a similar degree of disturbance during planting operations as areas where trees were established, and thus they represent a better reference to evaluate the effect of trees on soil than areas that were not planted. When trees showed some evidence of anomalous growth or deformities, the closest healthy tree of the same species was selected. Soil samples were collected on June 2006 under the canopy of each tree species and on the open

areas from the upper 5 cm of soil, excluding litter and stones. They were air-dried and passed through a 2 mm sieve for chemical analyses. Oxidable soil organic matter was determined by using the Walkley-Black method (Nelson and Sommers, 1982). Data were transformed to organic carbon by using a transformed Van Bemmelen factor of 2 (Nelson and Sommers, 1982). An outlier datum was deleted before statistical analysis. Kjeldahl's method and Olsen's bicarbonate extraction (Olsen and Sommers, 1982) were used to analyse total nitrogen and extractable phosphate, respectively.

Soil CO₂ efflux was measured by using air-tight 250-mL polyethylene flasks containing 5 g of soil at field capacity and vials containing 10 mL of 0.1 M NaOH. The flasks were kept in darkness at 25 °C for 48 h. The CO₂ emitted was measured by quantifying the amount of NaOH remaining after the incubation (Emteryd, 1989). Soil respiration is expressed as micrograms of carbon per gram of soil per day. Relative respiration rate was estimated from the ratio between CO₂ efflux and soil organic carbon content.

Soil hydrophobicity was measured in the laboratory on undisturbed soil samples. We collected the soil samples by carefully inserting a Petri dish on the surface soil underneath the canopy of each tree and on open areas with the help of a knife. Once in the lab, the samples were air-dried. Then, we deposited one 0.05-mL drop of distilled water on the soil surface by using a micropipette, and measured the time before the drop was fully incorporated into the soil. This measurement was repeated three times per soil sample. We evaluated infiltration capacity in each sample using the method described by Zaady (1999). Before measurements, soil samples used in the previous analysis were moistened to saturation and allowed to settle for 24 h in the dark. We drilled five 1-mm diameter holes under the Petri dishes containing the surface soil sample moistened to saturation, and fixed them to plastic funnels. Then, we added 100 mL of distilled water by using a micro rainfall simulator located 20 cm above the surface soil, and measured the time until the first drop of water percolated, and the total amount of water collected after 5 min. We used these data to calculate infiltration rates.

2.3. Vascular plant community

We recorded all vascular plants present under the canopy of each tree species and on the empty planting holes in April 2006, and estimated species richness from these data. Early spring is an adequate period to characterise the composition of annual plants in this area (Floret, 1981). Plant traits and names are based on Cuénod and Pottier-Alapetite (1954), Pottier-Alapetite (1979) and Chaieb and Boukhris (1998).

2.4. Statistical analysis

We evaluated the effect of tree species and block on soil properties and species richness by using two-way analysis of variance with one fixed factor (species) and one random factor (block) with four and three levels, respectively. When ANOVA showed significant differences, we used Tukey's HSD test to perform pairwise comparisons. Percentages of soil organic matter and total Kjeldahl nitrogen were transformed by using the expression: $\arcsin(x)^{0.5}$ prior to statistical analyses. All variables fulfilled the assumptions of normality and homoscedasticity except when noted. Homoscedasticity could not be achieved for soil organic matter content. In this case, we used non-parametric multivariate analysis of variance with one fixed factor (species) and one random factor (block), with four and three levels, respectively, and soil organic matter data included in the matrix of dependent variables by using the PERMANOVA program

(Anderson, 2001, 2005). The overall species effect on soil properties was evaluated by using the same procedure and the complete data set. In all cases, the significance of the Euclidean dissimilarity measure and post-hoc comparisons was estimated from 9999 permutations.

Covariance between soil properties was evaluated by calculating Pearson's product moment correlation coefficient. Statistical tests on soil properties were conducted with the SPSS 12.0 for Windows package (SPSS Inc., Chicago, IL, USA).

The effect of tree species on vascular plant composition was analysed by using non-parametric multivariate analysis of variance with one fixed factor (species) and one random factor (block), with four and three levels, respectively, and the presence/absence data for each of the species included in the matrix of dependent variables by using the PERMANOVA program (Anderson, 2001, 2005). The significance of the Sorensen dissimilarity measure was estimated from 9999 permutations.

3. Results

3.1. Climatic conditions

In 2006, precipitation at the study site was 286 mm, 68% above the 10-year average (Fig. 2). The planting year 1996 was also very humid (460 mm). Humid years of this kind are common in the study area, where rainfall analysis of this decade (1995–2006) shows that 60% of all years have above-average annual precipitation values. Mean annual temperatures between 1995 and 2006 were relatively constant and ranged between 19.0 °C in 1995 and 20.2 °C in 2004.

3.2. Effects of tree species on soil properties

Total organic carbon ranged between 3.89 mg g⁻¹ and 7.43 mg g⁻¹ (Fig. 3). We found a significant effect of cover type on this variable (Table 1). Open areas showed lower soil organic carbon content than areas covered by *P. halepensis*, *A. salicina* and *E. occidentalis*, but differences between tree species were not statistically significant. By considering organic carbon content in open areas as the base level we were able to calculate the rate of change in this variable, i.e. net accumulation rate. Organic carbon incorporation under the three species studied ranged from 0.92 ± 0.21 mg C g⁻¹ year⁻¹ to 1.30 ± 0.21 mg C g⁻¹ year⁻¹ for *E. occidentalis* and *A. salicina*, respectively.

Mean values of total soil nitrogen ranged between 0.69 mg g⁻¹ and 1.21 mg g⁻¹ for *A. salicina* and open areas, respectively. The type of cover had a significant effect on soil nitrogen, *A. salicina*

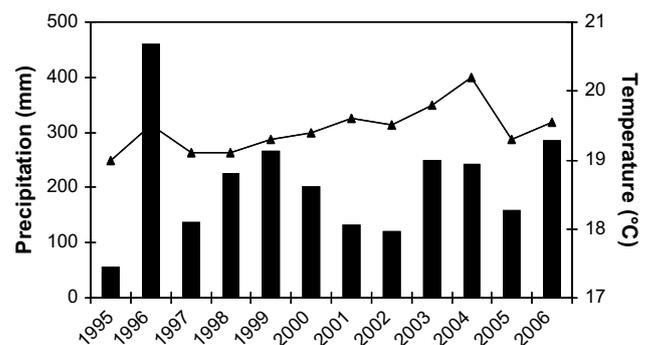


Fig. 2. Mean annual air temperature (line) and precipitation (bars) at the study site between 1995 and 2006.

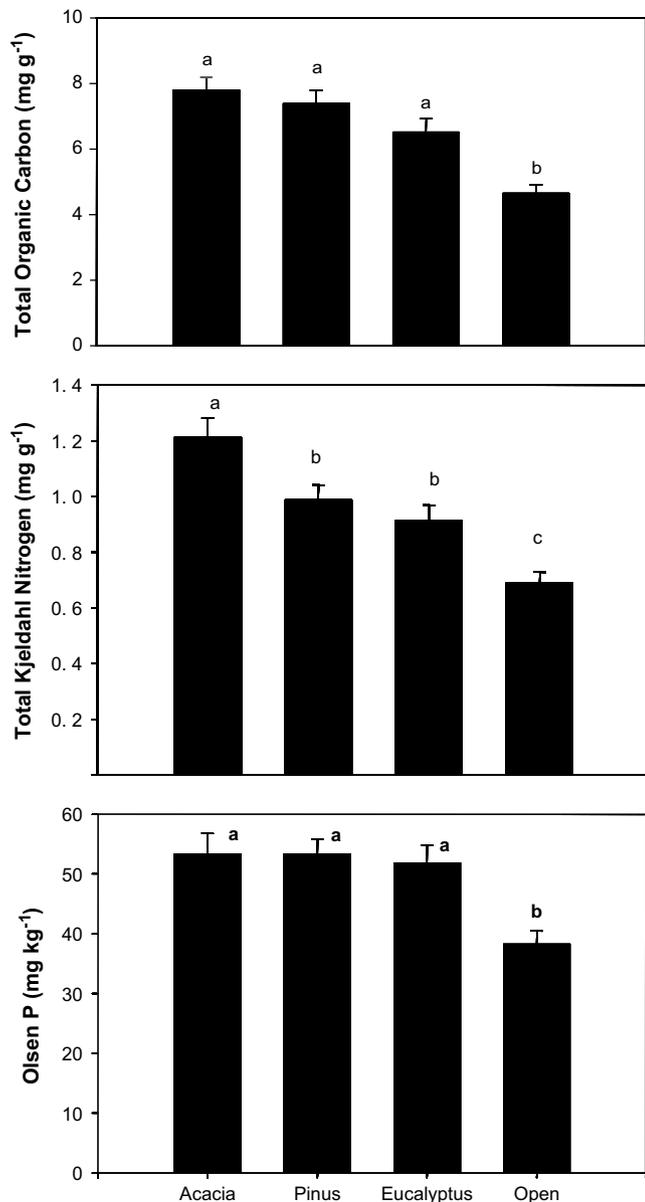


Fig. 3. Soil chemical properties under the canopy of three tree species and on open areas. Acacia, *Acacia salicina*; Pinus, *Pinus halepensis*; Eucalyptus, *Eucalyptus occidentalis*; Open, open areas. Different letters denote significant differences between cover types (Tukey's HSD test at $p < 0.05$).

showing higher values than *P. halepensis* and *E. occidentalis*, and these being higher than open areas. The net rate of N increase in the surface soil, as defined for organic carbon, ranged from $0.02 \pm 0.01 \text{ mg N g}^{-1} \text{ year}^{-1}$ to $0.05 \pm 0.01 \text{ mg N g}^{-1} \text{ year}^{-1}$ for *E. occidentalis* and *A. salicina*, respectively. Total nitrogen and soil organic carbon were positively correlated ($r = 0.806$, $p < 0.0001$, $N = 35$). The C:N ratio ranged between 5.8 and 7.3 for open areas and *P. halepensis*, respectively (Table 2). The C:N ratio under *P. halepensis* and *E. occidentalis* was higher than under *A. salicina* and open areas. Despite its relative uniformity, we found a significant effect of cover type on the C:N ratio.

Soil CO₂ efflux was affected by the type of cover (Fig. 4). *A. salicina* and *P. halepensis* showed the highest soil CO₂ efflux rates. Soil CO₂ efflux and soil organic matter were positively correlated ($r = 0.706$, $p < 0.0001$, $N = 35$). Relative respiration rate was

Table 1

Results of the non-parametric (total organic carbon, TOC) and parametric (total Kjeldahl nitrogen, TKN, and available P) analysis of variance to evaluate the effect of cover type and block and their interaction on soil properties.

	TOC	TKN	Olsen P
Cover	$F_{3,6} = 8.48$, $p = 0.010$	$F_{3,6} = 8.63$, $p = 0.014$	$F_{3,6} = 11.95$, $p = 0.006$
Block	$F_{2,24} = 0.05$, $p = 0.955$	$F_{2,6} = 0.38$, $p = 0.699$	$F_{2,6} = 4.13$, $p = 0.075$
Cover × block	$F_{6,24} = 1.31$, $p = 0.296$	$F_{6,24} = 2.27$, $p = 0.071$	$F_{6,24} = 0.57$, $p = 0.750$

remarkably uniform and showed no significant effect of cover. The three tree species showed similar values of available soil P, which were higher than the ones observed in open areas. Block or the interaction between species and block had no significant effect on any of the soil properties evaluated.

We found a significant effect of tree species on infiltration rate (Table 3). Soil under *A. salicina* showed the highest infiltration rate, but the time for the first drop to percolate was not significantly higher under this species than under *P. halepensis* and *E. occidentalis*. Infiltration rate was lower and infiltration time was higher in open areas than in vegetated areas. Kruskal–Wallis non-parametric test on infiltration rate showed similar results as parametric ANOVA ($H_3 = 21.830$, $p < 0.001$), suggesting that the effect found did not result from heteroscedasticity. Infiltration rate and time for the first drop to percolate were significantly correlated with soil organic matter ($r = 0.640$, $p < 0.0001$, $N = 35$, and $r = -0.742$, $p < 0.0001$, $N = 35$ respectively). *Acacia salicina* showed the lowest hydrophobicity under dry conditions, and significant differences with *E. occidentalis* and open areas, but not with *P. halepensis* (Table 3). Soil in open areas was significantly more hydrophobic than the soil under the canopy of any of the three species. Indeed, hydrophobicity was negatively correlated with soil organic matter ($r = -0.716$, $p < 0.0001$, $N = 35$).

The magnitude of the changes in physical soil properties under vegetated patches was higher than for chemical and biological properties. While the presence of trees increased soil chemical properties and CO₂ efflux by an average of ca. 50%, infiltration rate showed a three-fold increase, and infiltration time and hydrophobicity decreased by 78 and 93%, respectively. Neither block nor the interaction species × block had a significant effect on soil physical properties.

Species had a significant effect on the ensemble of soil properties (Table 4). Soil properties under *A. salicina* were different from under *P. halepensis* and *E. occidentalis*. The latter species did not significantly change soil properties compared to open areas.

Table 2

Carbon to nitrogen ratio and the ratio between CO₂ efflux and soil C content in surface soils under four cover types in a forested *Stipa tenacissima* steppe.

Cover type	C:N	Relative respiration rate (day ⁻¹ × 10 ⁶) ^a
<i>A. salicina</i>	$6.4 \pm 0.35a$	3.48 ± 0.09
<i>P. halepensis</i>	$7.3 \pm 0.43b$	3.38 ± 0.28
<i>E. occidentalis</i>	$6.9 \pm 0.32b$	3.15 ± 0.37
Open	$5.8 \pm 0.54a$	3.39 ± 0.54
Cover	$F_{3,6} = 3.09$, $p = 0.047$	$F_{3,6} = 0.269$, $p = 0.847$
Block	$F_{2,6} = 1.22$, $p = 0.315$	$F_{2,6} = 0.068$, $p = 0.035$
Cover × block	$F_{6,24} = 2.38$, $p = 0.062$	$F_{6,24} = 0.532$, $p = 0.779$

Data are means and standard errors of $N = 9$ trees per species. Results of two-way analyses of variance are shown for each variable. Different letters denote significant differences between cover types (Tukey's HSD test at $p < 0.05$).

^a ANOVA performed after log₁₀ transformation.

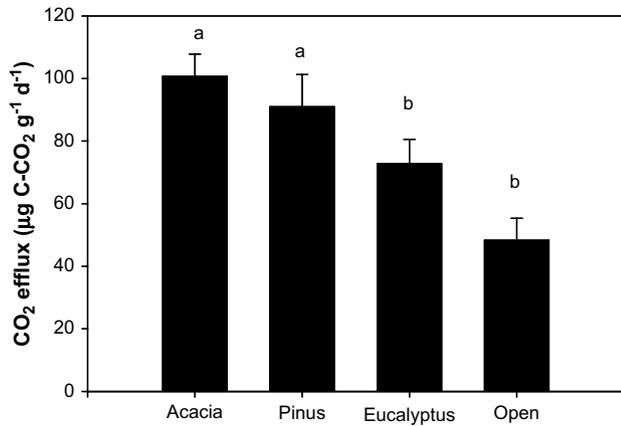


Fig. 4. Soil CO₂ efflux under four types of cover in a forested *Stipa tenacissima* steppe. Acacia, *Acacia salicina*; Pinus, *Pinus halepensis*; Eucalyptus, *Eucalyptus occidentalis*; Open, open areas. Different letters denote significant differences between cover types (Tukey's HSD test at $p < 0.05$).

3.3. Species richness and composition

The total number of species observed in the area was 43 (Appendix A). The number of vascular plants growing under the canopy of a particular tree species or on the corresponding open area ranged from 18 to 32 species. Species richness differed among the four types of cover type ($F_{3,6} = 8.65$, $p = 0.013$; $F_{2,6} = 3.99$, $p = 0.079$, and $F_{6,24} = 0.76$, $p = 0.605$, for species, block and species \times block, respectively; Fig. 5). *Acacia salicina* showed the highest number of vascular plant species (32), of which 19 were perennials. Species richness did not differ underneath *P. halepensis*, *E. occidentalis* and in open areas. Species composition, i.e. the presence/absence of vascular plants as analysed by multivariate non-parametric ANOVA, was affected by cover type ($F_{3,6} = 2.78$, $p = 0.0037$), and block ($F_{2,6} = 4.71$, $p = 0.0001$), but not by the interaction between both factors ($F_{6,24} = 0.96$, $p = 0.566$). Dissimilarity between open and vegetated areas was higher than dissimilarity between vegetated patches.

4. Discussion

4.1. Effect of tree species on chemical soil properties

Our results showed a significant effect of tree species on surface soil properties 10 years after planting and thus, they are in

Table 3

Physical properties of the soil under the canopy of three tree species and of open areas in arid central Tunisia.

Cover type	Infiltration rate (mL min ⁻¹) ^a	Infiltration time (s)	Hydrophobicity (s)
<i>A. salicina</i>	20.8 ± 2.7a	14.2 ± 2.6a	0.6 ± 0.2a
<i>P. halepensis</i>	12.3 ± 0.9b	18.4 ± 1.8a	1.2 ± 0.4a
<i>E. occidentalis</i>	10.6 ± 3.0b	30.0 ± 7.6a	3.6 ± 0.9b
Open	5.3 ± 0.4c	64.2 ± 9.8b	8.3 ± 0.9c
Cover	$F_{3,6} = 10.64$, $p = 0.008$	$F_{3,6} = 9.50$, $p = 0.011$	$F_{3,6} = 38.39$, $p < 0.001$
Block	$F_{2,6} = 1.25$, $p = 0.352$	$F_{2,6} = 1.09$, $p = 0.394$	$F_{2,6} = 1.64$, $p = 0.270$
Cover \times block	$F_{6,24} = 1.62$, $p = 0.185$	$F_{6,24} = 1.97$, $p = 0.110$	$F_{6,24} = 0.72$, $p = 0.634$

Means of $N = 9$ replicated measurements and standard errors are shown. Results of two-way analyses of variance are shown for each variable. Different letters denote significant differences between soil surface types (Tukey's HSD test at $p < 0.05$).

^a Homoscedasticity could not be achieved for this variable (Levene's test; $p < 0.05$).

Table 4

Results of the multivariate non-parametric analysis of variance to evaluate the effect of cover type on soil physico-chemical properties.

Factor	F	d.f.	p
Species	10.13	3,6	0.0011
Block	2.07	2,24	0.1222
Species \times block	1.13	6,24	0.3675

agreement with studies showing increases in soil organic matter underneath vegetated patches in drylands (Cortina and Maestre, 2005). In their review, Cortina and Maestre (2005) found that most studies showed that soil organic matter under vegetated patches was 50–100% higher than in nearby open areas, and thus similar to the differences found in the current study (62–91% increases in soil organic matter for *E. occidentalis* and *A. salicina*, respectively). These fast changes in soil properties were probably favoured by the low levels of fertility found in the study area compared to other drylands. We may note, however, that we only analysed soil from the surface 5 cm which is commonly more sensitive to changes in plant cover than deeper soil horizons (Abule et al., 2005).

Total soil nitrogen and available P followed the same pattern, supporting other studies showing a high degree of covariation between soil organic matter and nutrient content (Whitford et al., 1987). But in contrast to the pattern shown by soil organic matter, *A. salicina* increased soil nitrogen content above the levels found under *P. halepensis* and *E. occidentalis*. *A. salicina* is an active N-fixing species (Ferrari and Wall, 2004; Franco and Faria, 1997), and suggests that fixed N is quickly incorporated into the soil, probably increasing soil N availability.

Increases in phosphorus availability under vegetated patches have been observed elsewhere (Franco-Pizaña et al., 1996; Whitford et al., 1997) and may be a consequence of various processes, including animal fragmentation of particulate organic matter and soil aggregates (Graham et al., 2004) and higher root phosphatase activity (Chen et al., 2003). According to our result, the increase in P availability was close to 40% and did not depend on the tree species. Both open areas and vegetated patches showed relatively high P availability compared to other carbonated soils (Henkin et al., 1994; Olsen and Sommers, 1982).

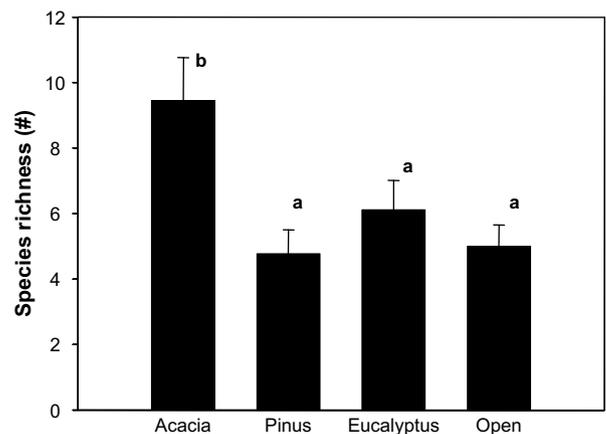


Fig. 5. Richness of vascular plant species underneath *A. salicina* (Acacia), *P. halepensis* (Pinus), *E. occidentalis* (Eucalyptus) and in open areas (Open). Bars are means and standard errors of $N = 9$ trees per species. Different letters denote significant differences between cover types (Tukey's HSD test at $p < 0.05$).

Despite substantial changes in soil organic matter content, total nitrogen content, and soil respiration rates, indicators of soil organic matter quality such as the C:N ratio and relative respiration rate were weakly affected by cover type. Gradual homogenisation of probably heterogeneous aboveground and belowground litter inputs may result from (1) the ‘filtering’ action of the decomposer community and (2) limited incorporation of fresh organic residues by soil fauna. Several studies have shown that initially heterogeneous fresh litter may converge towards relatively homogeneous decomposing organic matter in a given soil (Melillo et al., 1989; Berg and Cortina, 1995), in a process that has been termed “decay filter”. On the other hand, the relatively low C:N ratio found under all types of cover suggests that soil organic matter in the surface soil was well humified, and thus fresh litter incorporation into the mineral soil by burrowing animals was low. This is in agreement with the morphological integrity shown by the litter layer underneath the three species studied (mostly composed of L or Oi horizons), and suggests that isopods found in the area (J. Cortina, personal observation) may have had a small effect on litter incorporation so far, as observed elsewhere (Hattenschwiler et al., 2005).

4.2. Effect of tree species on physical soil properties

Besides improving chemical soil properties, trees also improved physical soil condition when compared with open areas. Indeed, they showed higher infiltration rates and lower infiltration times than those on the open areas. These results are in agreement with those shown by Maestre et al. (2002) in a semiarid *S. tenacissima* steppe from Spain, who found a clear microsite effect, with higher infiltration rate and less time required by first drop to percolate in vegetated patches than in open areas. The higher infiltration rates and the lower infiltration times under trees were probably related to the organic matter content in soils which affects aggregate development and creates more macro-pores (Mapa, 1995) and to the fungal hyphae which maintain continuous pores (Whitford, 2002).

Contrary to other studies (Harper and Gilkes, 1994), soil hydrophobicity in the studied plantations was negatively correlated with soil organic matter. Furthermore, soil on the open areas was more hydrophobic than under tree species. This is somewhat surprising, as the genera *Acacia*, *Pinus* and *Eucalyptus* have been related to high water repellency in soils (Jaramillo, 2004, and references therein). This variable is often linked to the presence of hydrophobic substances directly derived from plant residues (Doerr et al., 2000). In our case the lack of a positive relationship between soil organic matter and hydrophobicity may be explained by the low degree of incorporation of fresh organic matter in the mineral soil (Buczko et al., 2005; Doerr et al., 2000).

4.3. Comparing the ability of tree species to modify soil properties

In our study, tree species differed in their effects on soil properties, *Acacia salicina* having the strongest effects. *Acacia salicina* is a leguminous shrub or small tree introduced to many regions as a multipurpose species (Le Houérou, 1986; Rehman et al., 1999), and successfully establishes on degraded areas (Grigg and Mulligan, 1999). The beneficial effects of *A. salicina* on soil fertility were probably enhanced by its capacity to fix atmospheric N as observed in other *Acacia* species in Tunisia (Nasr and Sghaier, 1999), and accumulate high amounts of N-rich litter (Garay et al., 2004), although the decomposition rate may be relatively low (Witkowski, 1991). Legumes have a strong potential to increase TOC and N content (Binkley, 2005; Paul et al., 2002).

The rate of change in TOC found in the present study (0.09–0.13% year⁻¹) was substantially high. For example, Paul et al. (2002) found that C content in the soil surface of 0–10-year-old plantations decreased by an average of 0.47% year⁻¹. The proportional C to N increase was also higher in *A. salicina* in the present study than in average forest plantations with legumes (45 vs. 15.5, respectively; Binkley, 2005). We may note, however, that in both reviews TOC and N dynamics included the effects of soil preparation.

P. halepensis followed *A. salicina* as a soil modifier. Its positive effect on soil properties is however emphasised by the fact that *P. halepensis* was the only native species evaluated. Other studies have shown increases in soil fertility under *P. halepensis* compared to open areas (Bautista, 1999; Maestre et al., 2003a), although its capacity to improve soil fertility may be lower than the capacity shown by evergreen sclerophyllous shrubs (Goberna et al., 2007; Maestre and Cortina, 2004). The capacity of this species to positively affect community composition and ecosystem function in semiarid lands is controversial (Maestre and Cortina, 2004). This is in agreement with the lack of difference in the richness of vascular plants under *P. halepensis* compared to empty planting holes found in the current study.

Of the three species assessed, *E. occidentalis* showed the lowest capacity to improve soil conditions compared to open areas. Numerous studies have described the effect of *Eucalyptus* sp. on soil properties, particularly in temperate and tropical regions (d’Annunzio et al., 2008; Mendham et al., 2002; Poore and Fries, 1985). Reductions in soil organic matter after forestation have been observed, especially during the first 10–15 years (Turner and Lambert, 2000), which is in agreement with general patterns of SOM accumulation after forestation (Paul et al., 2002). In our study, reductions in native SOM after soil preparation were not accounted for, as we compared empty with vegetated planting holes, and the reduction, if any, was common for both microsites. Thus inability of *E. occidentalis* to modify soil properties in the short-term was probably responsible for the weak effect of this species.

4.4. Effect of tree species on vascular species richness

Vascular species richness in our study differed significantly between the four types of soil surface. In addition, floristic composition was significantly different under tree canopies than in open areas. Patches of woody vegetation can modify plant community composition and dynamics in drylands by trapping seeds and creating suitable microhabitats (Aerts et al., 2006b; Bochet et al., 1999; Cortina and Maestre, 2005). *Acacia salicina* showed the highest number of vascular plant species, which is in agreement with the observed improvement in chemical and physical soil properties and previous studies on the effects of *Acacia* sp. on floristic composition (Aerts et al., 2006c; Munzbergova and Ward, 2002). We may note, however, that El Gonna has been protected from grazing since the area was forested. The impact of the studied species on soil properties and, especially, on accompanying vascular plants would be lower if the area was grazed.

5. Conclusion

Introducing woody species as a restoration tool can be a crucial step to combat desertification and degradation in *S. tenacissima* steppes (Cortina et al., in press). However, their use in restoration must be carefully evaluated considering their effect on microhabitat conditions and other aspects of their ecology, particularly the risk of using alien species (Ewel and Putz, 2004). Outside their original distribution area, both

A. salicina and *E. occidentalis* may trigger unwanted changes in community composition and ecosystem function (Macdonald and Wissel, 1992; Nel et al., 2004). But the introduction of *A. salicina* can be of interest for various reasons, including the production of fodder, fuelwood, furniture and tannins, and the positive effects on soil and vegetation found in our study. The risk of naturalisation of these species could be minimised by reducing rotation period and favouring management practices aimed at controlling its spread.

We have shown that the three species studied quickly modify soil surface properties, and thus they are suitable to create islands of resources in protected *S. tenacissima* steppes. Of the three species, *A. salicina* showed a higher ability to improve microsite conditions and foster succession. *Pinus halepensis* represents a good alternative when native species are a priority, albeit with a lower facilitative ability.

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Appendix A

A list of the plant species present at the experimental site. The family, life form and degree of lignification are shown for each species, as well as its presence (1) or absence (0) under each type of cover. H, hemicryptophyte; Ch, chamaephyte; G, geophyte; Nph, nanophanerophyte; Th, therophyte; Par, parasite; H, herbaceous; L, woody.

Species	Family	Life form	Lignification	<i>Pinus halepensis</i>	<i>Acacia salicina</i>	<i>Eucalyptus occidentalis</i>	Open
<i>Aegylops geniculata</i> Roth	Poaceae	Th	H	0	1	1	1
<i>Allium roseum</i> L.	Alliaceae	G	H	0	1	0	0
<i>Anagallis arvensis</i> L.	Primulaceae	Th	H	0	1	0	0
<i>Artemisia campestris</i> L.	Asteraceae	Ch	L	1	0	0	1
<i>Asteriscus pygmaeus</i>	Asteraceae	Th	H	0	1	0	1
<i>Astragalus armatus</i> Willd.	Fabaceae	Ch	L	0	1	0	0
<i>Astragalus caprinus</i> L.	Fabaceae	Th	L	1	1	1	1
<i>Atractylis serratuloides</i> Sieber ex Cass.	Asteraceae	Ch	L	0	1	1	0
<i>Bromus madritensis</i> L.	Poaceae	Th	H	0	1	0	0
<i>Cistanche phelypaea</i> (L.) p. Cout.	Orobanchaceae	Par	H	0	1	1	1
<i>Cuscuta epithimum</i> (L.) L.	Convolvulaceae	P	H	1	0	0	0
<i>Cutandia dichotoma</i> (Forssk.) Trab.	Poaceae	Th	H	0	1	1	0
<i>Cynodon dactylon</i> (L.) Pers.	Poaceae	H/G	H	1	1	1	1
<i>Deverra tortuosa</i> (Desf.) DC.	Apiaceae	Ch	L	0	1	1	1
<i>Digitaria nodosa</i> Parl.	Poaceae	H	H	1	0	1	0
<i>Dipcadi serotinum</i> (L.) Medik.	Liliaceae	G	H	1	0	1	1
<i>Diploxix harra</i> (Forssk.) Boiss.	Brassicaceae	Th	H	0	1	1	0
<i>Echiochilon fruticosum</i> Desf.	Boraginaceae	Ch	L	1	1	1	1
<i>Erodium glaucophyllum</i> (L.) L'Hér. in Aiton	Geraniaceae	G	H	0	0	1	0
<i>Erodium hirtum</i> Willd.	Geraniaceae	Th	H	0	1	0	1
<i>Eucaria pinnata</i> (Boiss.) Greuter & Burdet	Cruciferae	Th	H	0	1	0	0
<i>Euphorbia retusa</i> Forssk	Euphobiaceae	Th	H	0	1	1	1
<i>Helianthemum kahiricum</i> Delile	Cistaceae	Ch	L	1	0	0	0
<i>Helianthemum sessiliflorum</i> (Desf.) Pers.	Cistaceae	Ch	L	1	1	1	1
<i>Hippocrepis bicontorta</i> Loisel	Fabaceae	Th	H	1	1	1	1
<i>Hordeum marinum</i> Huds.	Poaceae	T	H	1	1	1	1
<i>Kixcia aegyptiaca</i> (L.) Nabelek	Scrophulariaceae	Th	L	1	1	1	0
<i>Koeleria pubescens</i> (Lamark) Beauv	Poaceae	Th	H	1	1	1	1
<i>Launea angustifolia</i> (desf.) Kuntze	Asteraceae	Th	H	0	1	1	0
<i>Launea residifolia</i> (L.) Kuntze	Asteraceae	H	H	0	1	0	0
<i>Lygeum spartum</i> Loeffl. ex L.	Poaceae	H	H	0	1	1	0
<i>Medicago minima</i> (L.) L.	Fabaceae	Th	H	1	0	0	0
<i>Plantago albicans</i> L.	Plantaginaceae	H	H	1	1	1	1
<i>Retama raetam</i> (Forssk.) Webb	Fabaceae	Nph	L	0	1	0	0
<i>Salvia aegyptiaca</i> L.	Labiatae	Ch	L	0	1	0	0
<i>Scabiosa rizanthal</i> Viv.	Dipsaceae	Th	L	1	1	1	0
<i>Senecio gallicus</i> L.	Asteraceae	Th	H	0	0	0	1
<i>Silene arenarioides</i> Desf.	Caryophyllaceae	H	H	0	0	1	0
<i>Stipa capensis</i> Thunb.	Poaceae	Th	H	1	0	0	0
<i>Stipa lagascae</i> R. et Sch	Poaceae	H	H	1	1	1	1
<i>Stipa tenacissima</i> L.	Poaceae	H	H	1	0	0	0
<i>Stipagrostis ciliata</i> (Desf.) De V	Poaceae	H	H	0	1	0	0
<i>Thymelaea hirsuta</i> (L.) Endl.	Thymelaeaceae	Ch	L	0	1	1	0

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