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ECOSYSTEMS

Previous Land Use Alters the Effect of Climate Change and Facilitation on Expanding Woodlands of Spanish Juniper

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ABSTRACT

In Mediterranean–continental regions, changes in land use are leading to the expansion of valuable habitats like endemic *Juniperus thurifera* woodlands, but the impact of reduced rainfall, due to climate change, on this expansion remains uncertain. We assessed the early performance of *J. thurifera* in different global change scenarios with and without facilitation. Saplings were transplanted in three ecosystems types with different previous land use (woodlands, former agricultural fields, and former livestock pastures), microhabitats (open vs. understory of adult trees) and were subjected to two watering regimens. We characterized the abiotic environment and measured survival, growth and two ecophysiological parameters. Former livestock pastures were the least favorable ecosystem, where the nursing effect was greatest. Former agricultural fields had the highest survival, but were more sensitive than woodlands to water scarcity. Reduced rainfall decreased photochemical efficiency, particularly in the least favorable scenarios, but did not affect survival. Water use efficiency enhanced growth under the canopy, but not in the open, whereas photochemical efficiency enhanced growth and survival more in the open. Facilitation was critical for effective recruitment in the harshest scenarios: former livestock pastures and reduced rainfall. Comparison with previous studies suggests that establishment depends on infrequent wet episodes. In Mediterranean ecosystems, changes in land use and climate change are leading to woodland expansion due to the modulating effect of facilitation of the oncoming adverse drier conditions. Nevertheless, the positive effect of facilitation and the negative impact of aridity on tree recruitment are strongly influenced by previous land-use history.

Key words: climate change; facilitation; global change; *Juniperus thurifera*; land-use change; Mediterranean–continental; photochemical efficiency (F_v/F_m); structural equation modelling (SEM); water use efficiency (WUE).

INTRODUCTION

Global change drivers exert dramatic pressures on ecosystems and interactions among them frequently generate non-additive effects that cannot

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be predicted based on single-factor studies (Sala and others 2000; Matesanz and others 2009). Assessing the effect of simultaneous global change drivers is particularly demanding in ecosystems subjected to intense human exploitation for millennia, like those in the Mediterranean region. There, ecosystems have suffered intense transformation from woodlands into croplands and pastures, leading to massive losses of forest habitat (Valladares 2004). Nevertheless, this trend has been reversed in mountainous and continental areas of the north-western Mediterranean region since the second half of the twentieth century. This is due to the abandonment of traditional practices and population exodus (Bonet 2004; Chauchard and others 2007). This land-use change profoundly impacts ecosystem structure and functioning and can affect biodiversity conservation (Van Auken 2000; Archer and others 2001; Breshears 2006; Maestre and others 2009a; Hatna and Bakker 2011). But it also increases habitat availability and connectivity for remaining genuine forest species (Schroter and others 2005).

This land-use change, woodland expansion into abandoned croplands and pastures, usually occurs spontaneously (Jessup and others 2003; Van Auken 2009). In contrast, in water-limited environments, woodland expansion can be severely constrained (Weltzin and McPherson 1999; Bonet 2004; Dickie and others 2007). This is the case in the Mediterranean region, where successful tree recruitment is primarily limited by water availability (Villar-Salvador and others 2004; Sánchez-Gómez and others 2006), a limitation that will be exacerbated under oncoming climatic conditions (Christensen and others 2007). Plant performance is affected by not only changing trends in temperature and rainfall but also increased climatic variability and frequency and severity of extreme climatic events, associated with climate change (Peñuelas and others 2007; Giorgi and Lionello 2008; Sillmann and Roeckner 2008). In fact, wetter than usual episodes can have a disproportionate importance for tree recruitment in water-limited environments (Weltzin and McPherson 2000; League and Veblen 2006; Matias and others 2011).

As a consequence, predictions of the final outcome of the interaction between land use and climate change are not easily foreseeable and should account for factors limiting successful woodland expansion into abandoned fields. In the Mediterranean region, other biotic and abiotic constrains besides water availability limit successful recruitment like: herbivory, dispersal ability, light-excess, extreme temperatures, and nutrient supply (Martinez-Ferri and others 2003; Sánchez-Gómez and others 2006; Sardans and Peñuelas 2007; Matesanz and others 2009). These constraints can be buffered under the canopy of nurse plants (Siemann and Rogers 2003; Gomez-Aparicio and others 2005; Pausas and others 2006). We expect nurse plants to facilitate tree establishment during woodland expansion in Mediterranean regions. Furthermore, we hypothesize that tree establishment will be more nurse dependent under a drier climate change scenario (Bertness and Callaway 1994; Maestre and others 2009b). We also expect facilitation to be more important in abandoned fields than in mature woodlands, where soils have more nutrients (Jessup and others 2003; Dickie and others 2007) and water-stress tends to be lower, due to a higher percentage of shaded area with lower evaporative demand (Breshears and others 1997; Matias and others 2011). In abandoned fields, facilitation would be provided by adult individuals, remnants from previous land uses, historically used to separate properties (Manning and others 2006). Later, facilitation would be provided by first established juvenile trees in a nested regeneration process in which new individuals may accelerate regeneration of the woodland as a whole. Therefore, we expect woodland expansion to be constrained by more stressful oncoming climate conditions, which can be mitigated by the facilitative effect of conspecific adults.

Endemic Spanish juniper (*Juniperus thurifera* L.) woodlands offer an exceptionally good model to evaluate how woodland expansion into abandoned fields operates under a climate change scenario. In many scarcely populated areas in central Spain, abandoned agricultural fields and livestock pastures are being colonized by expanding *J. thurifera* woodlands that dominate the surrounding areas (Blanco and others 2005). Under rapidly changing environmental conditions, the prospects for these valuable endemic woodlands remain uncertain (Olano and others 2008).

Here, we performed a field experiment to assess the effects of land use and climate change—two global change drivers acting simultaneously in continental Mediterranean regions. We also tested for the importance of facilitation on early plant performance, by considering microhabitat heterogeneity related to conspecific tree canopies, due to its potential influence on plant response to environmental changes. We evaluated the performance of *J. thurifera* saplings transplanted into three ecosystem types differing in previous land use (mature woodlands, abandoned agricultural fields, and livestock pastures). In each ecosystem type, we chose two microhabitats and we applied two different watering regimes mimicking different climatic scenarios. We tested the following hypotheses: (i) the early performance of *J. thurifera* varies depending upon previous land use, with mature woodlands being the most suitable ecosystem type for establishment; (ii) the early performance of *J. thurifera* is improved under the canopy of nurse trees, and (iii) with facilitation being more important under stressful conditions such as water scarcity and reduced fertility.

METHODS

Natural History and Study Sites

Juniperus thurifera L. (Cupressaceae) is a dioecious tree species with a relict Tertiary distribution confined to the western Mediterranean Basin. It is usually the dominant species in low-density woodlands in infertile, shallow, rocky soils (calcareous but occasionally also in acidic soils), at a variety of altitudes (300–3200 m a.s.l) in climates that range from arid to sub-humid Mediterranean–continental types (Gauquelin and others 1999).

The study was conducted at the Alto Tajo Natural Park and its surroundings, in Central Spain. In the study sites, the parental rocks are Cretaceous and Jurassic limestone. The climate is continental Mediterranean with hot and dry summers and cold and cloudless winters. Mean (±SE) annual rainfall is 499.7 ± 14.4 mm and mean annual temperature is 10.2 ± 0.1°C, (Molina de Aragón: 40°50′40″ N, 1°53′07″ W, 1063 m a.s.l., 1951–2009 period, data provided by the Spanish Bureau of Meteorology). The study landscape consisted of a complex matrix of different areas subjected to intense human use in the past (agricultural, free-ranging livestock, and timber-extraction), with some remnants of partially degraded woodlands. Currently, this human use has largely ceased, due to socio-economic changes and rural exodus occurring since the end of the Spanish Civil War (1936–1939) and later accelerated in the 1960s. Land-abandonment has lead to the expansion of juniper woodlands into former agricultural fields and livestock pastures and to increased tree density in remnant mature woodlands (Figure 1; Gimeno and others 2011).

Experimental Design and Plant Material

We selected three ecosystem types differing in previous land use (Table 1): mature juniper woodlands and expanding woodlands located in abandoned livestock pastures and former agricultural fields. Ecosystem types were established after a detailed survey of aerial photographs of the study area taken on different dates (1957, 1985, and 2006) and on-foot surveys of the region (Figure 1). We distinguished abandoned agricultural fields from livestock pastures by differences in grass cover, landscape morphology (former agricultural terraces were still detectable), and soil rockiness (former livestock pastures had rockier soils). Among these ecosystem types we selected seven study sites where *J. thurifera* was the dominant species: three mature woodlands [Cerro de Ablanque (ABW), Alto de Ribarredonda (RRW), and Río Salado (RSW)], two former livestock pastures [Huertahernando (HHL) and Ribarredonda (RRL)], and two former agricultural fields [Ablanque (ABA) and La Riba (LRA)].

At each study site, we selected two types of microhabitats: open interspaces with no trees within a radius of 4 m (open treatment) and under the canopy of adult (height >2 m) *J. thurifera* trees (canopy treatment). At each study site we established a minimum of 8 and 10, open and canopy plots, respectively. Within each study site, plots were located 5 m away from each other. In February 2008, we transplanted five saplings of *J. thurifera* at each open plot and 3–5 saplings at each canopy plot (due to space limitations) located in the northern part of the canopy at 2/3 of the canopy radius from the trunk. Plants were planted at 50–75 cm from each other, in manually dug holes of 30-cm depth × 30-cm diameter. The number of plots varied among study sites due to differences in microtopography and sizes of available nurse trees (see Table 1 for the number of plots of each type and numbers of transplanted saplings at each study site). We selected a similar number of male and female trees as nurses, because it has been shown that the gender of the nurse tree can influence the performance of the facilitated individuals underneath them (Verdú and others 2004; Montesinos and others 2007). Because gender did not show any effect on any of the response variables we discard this predictor in further analyses (data not shown). Overall, we transplanted 642 *J. thurifera* saplings in 165 plots. Each plot was in one study site and belonged to one type of microhabitat and one ecosystem.

Transplanted *J. thurifera* saplings were 3–4 years old and were obtained from Viveros El Fleix (Buñol, Valencia, Spain). Plants were grown in an open-air nursery (39°25′4.9″ N, 0°47′29.1″ W, 365 m a.s.l.) exposed to a mean annual temperature of 13°C and mean annual total rainfall of 536 mm. Seeds were sown in a mixture of peat (60%) and coconut rind (40%) in forestry trays

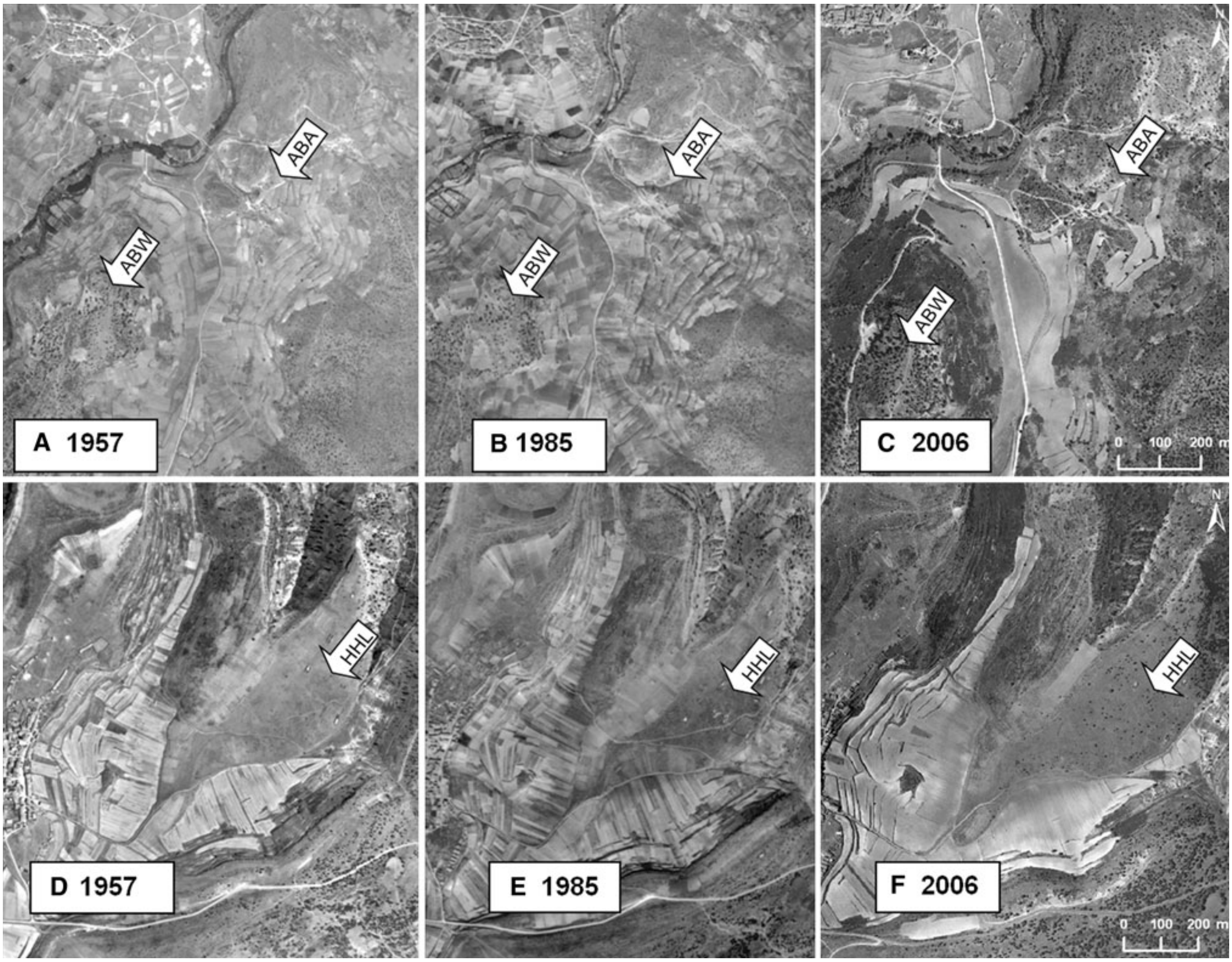

Figure 1. Aerial photographs of 1957, 1985, and 2006 showing the temporal evolution of one of the study sites located at each ecosystem type: woodland (ABW), former agricultural field (ABA), and former livestock pasture (HHL). Site codes as in Table 1. *Data source* For 1957 (**A**, **D**) Centro Cartográfico y Fotográfico del Ejército del Aire (CECAF). For 1985 (**B**, **E**) Departamento de Fotografía Aérea del Centro Nacional de Información Geográfica (CNIG). For 2006 (**D**–**F**) Instituto Geográfico Nacional (IGN) and Autonomous Community of Castilla La Mancha.

and were treated with Alagamix (LIDA Química, Almussafes, Valencia, Spain).

To mimic predicted rainfall conditions, we applied a watering treatment in spring 2009. The treatment had two levels: mesic (watered plants) and dry (non-watered plants). The watering treatment was performed during May and June 2009. Because the year was exceptionally dry, the non-watered (dry treatment) plants received ambient rainfall, equivalent to future drier scenarios (due to the opportunity given by a very dry spring), and the watered plants (mesic treatment) received ambient rainfall plus the added water, equivalent to a typical year with an average rainfall (similar to Matesanz and others 2009). Our watering treatment was conducted in these months for two reasons. First, the projections of the most likely future climate scenarios for the Mediterranean indicate significant reductions in mean annual rainfall, primarily decreasing precipitation during spring and summer (Christensen and others 2007). Actually, 2009 was warmer and drier than a usual year in the study area, particularly during the spring and summer (2009 was one of the three warmest years since 1965, Appendix 2 in Supplementary material). Second, these months coincide with the main peak of radial growth of this species (Camarero and others 2010), which is sensitive to spring precipitation (Bertaudiere and others 1999). The watering treatment was performed only in former agricultural fields and woodlands, due to the low survival rate observed in former livestock pastures during 2008. At each study site we randomly assigned each plot to one watering treatment.

Table 1. Characteristics of the Seven Study Sites at the Three Different Ecosystem Types, Including Mean (SE, $n = 10$) Percentages of Surface Covers

Ecosystem	Woodland			Former agricultural fields		Former livestock pastures	
Site	**Cerro de Ablanque**	**Alto de Ribarredonda**	**Río Salado**	**Ablanque**	**La Riba**	**Huertahernando**	**Ribarredonda**
Code	ABW	RRW	RSW	ABA	LRA	HHL	RRL
Latitude (N)	40°53′32″	40°52′10″	40°50′32″	40°53′40″	40°55′04″	40°49′24″	40°52′23″
Longitude (W)	2°13′34″	2°17′47″	2°18′1″	2°13′6″	2°17′30″	2°16′40″	2°17′53″
Elevation (m a.s.l.)	1110	1030	975	1050	1010	1140	1020
Slope (%)	8	11	12	10	8	6	14
Aspect	SW	E	N	W	W	S	NW
%Bare soil	6.3 (3.3)	11.2 (2.8)	11.7 (2.7)	12.5 (3.6)	12.5 (3.7)	4.5 (1.4)	9.8 (2.6)
%Rock	35 (5.3)^{A}	26.5 (4.2)^{A}	19 (4.6)^{A}	2.5 (1.5)^{B}	13 (5.7)^{B}	57 (7.2)^{C}	27 (5)^{C}
%Moss and lichen	32 (5)^{A,a}	15.3 (4.7)^{A,b}	15.1 (3.9)^{A,b}	4.5 (1.2)^{B}	4 (1.5)^{B}	9.5 (3.5)^{B}	9.7 (1.7)^{B}
%Woody	6.7 (3.1)^{A,a}	15 (4.8)^{A,ab}	32.5 (6)^{A,b}	17 (11.4)^{AB}	8 (3.3)^{AB}	0.5 (0.5)^{B}	9 (4.3)^{B}
%Herbaceous	15 (2.5)^{A}	24 (5.9)^{A}	13.7 (3.1)^{A}	60 (10.9)^{B}	50.5 (6.1)^{B}	25.5 (4.4)^{A}	36.7 (7.2)^{A}
%Litter	5 (1.2)	8 (2.7)	8 (0.8)	4 (1.2)^{a}	12 (2)^{b}	4.5 (1.2)	8.8 (2.1)
No. SH[1] plots	18	17	10	15	16	13	14
No. SU[2] plots	10	10	10	8	8	8	8
No. SH[1] Plants	51	53	50	40	40	42	48
No. SU[2] Plants	50	51	49	42	44	40	42

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[1] *Under the canopy of adult trees.*

[2] *In open spaces without trees.*

Significant differences ($P < 0.05$) are indicated with capital letters (among ecosystem types) and lower-case letters (among sites within ecosystem types).

Irrigation consisted of adding 1–1.5 L of water per plant at each irrigation event (see Appendix 1, Table A1 in Supplementary material for a detailed description of the irrigation experiment). Water addition was reduced 25% in canopy plots to simulate canopy rainfall interception (Breshears and others 1997; Valladares and others 2008). Because our approach was dependent on current weather conditions we checked daily for rainfall events and consequently adjusted our watering treatments. Ambient rainfall was monitored with a HOBO® weather station close to the study sites (40°49′08″ N, 2°12′47″ W, 1200 m a.s.l.) with a rain gauge (RGA-M0XX). Readings were recorded every 30 min with a data logger (HOBO® H21-001; all components from HOBO® Onset Computer Corporation, Bourne, MA, USA). Water was carefully added with a watering can to avoid runoff and to maximize absorption by the soil. A 50 × 50 cm (0.25 m^2) rigid frame was placed around each plant so that the entire surface was watered; each application was equivalent to 4–6 mm rainfall events. Irrigation was carried out at 3- to 5-day intervals.

Abiotic Characterization of the Experimental Treatments

Percentages of surface covered by bare soil, rock, lichen, moss, litter, woody and herbaceous species were estimated visually on ten randomly selected 0.25 m^2 in open interspaces without trees within a 4-m radius, at each of the seven study sites.

Light availability was estimated at each plot with hemispherical photographs (Rich 1990; Valladares and Guzman 2006). Photographs were taken at 40-cm height (similar to that of the plants) with a digital camera (CoolPix 995, Nikon, Tokyo, Japan), set horizontally on a tripod, coupled to a fish-eye lens, of 180° field of view (FCE8, Nikon). Photographs were taken either on cloudy days or before/after sunrise/sunset to ensure homogenous sky illumination and good contrast between the canopy and the sky. Photographs were processed with Hemiview v. 2.1 software (Delta-T Devices Ltd, Burwell, UK). We estimated the proportion of direct [direct site factor (DSF)], indirect [or diffuse, indirect site factor (ISF)], and total [global site factor (GSF)] radiation reaching each plot, relative to a location with no sky obstruction. Mean annual daily photosynthetically active radiation (in mol PAR m^{-2} day^{-1}) at each microsite was calculated by multiplying GSF by measured mean annual daily PAR (Appendix 2 in Supplementary material; Valladares and Guzman 2006).

In June 2009, we collected three soil sub-samples, between 5- and 15-cm depth, of approximately 200 g from each plot with a spade (avoiding major rocks); these were thoroughly mixed, air-dried, and sieved (2-mm grain) for further soil nutrient analyses. To measure total nitrogen and phosphorus content soil samples were first digested according to the Kjedhal method and then measured with an automatic wet chemistry analyzer (Skalar 4000 SAN System, Segmented Flow Analyzer; Skalar, Breda, The Netherlands). Soil content of organic carbon (C_{org}) was estimated from the content of soil organic matter, determined by combustion in a muffle furnace (Walkley and Black 1934). Na, K, Ca, and Mg were first extracted with ammonium acetate at pH 7 and then determined spectrophotometrically. These analyses were performed with an elemental analyzer (PLASMA ICP Optima 4300 DV, Perkin-Elmer, Waltham, Massachusetts, US) at the service of general analyses of the Institute of Agricultural Sciences (ICA-CSIC, Madrid, Spain).

Ecophysiological and Morphological Measurements

Predawn maximum photochemical efficiency of photosystem II (F_v/F_m) was measured at four different dates (beginning and end of the spring and summer and mid-summer, in two consecutive years (2008–2009). F_v/F_m is the ratio of variable (F_v) to maximum (F_m) fluorescence: $F_v/F_m = (F_m - F_o)/F_m$, where F_o is the minimum fluorescence. F_v/F_m is an estimator of plant physiological status. Values below the optimum (around 0.8 according to Maxwell and Johnson 2000) indicate photoinhibitory damage in response to high/low temperatures, light-excess and/or water-stress (Valladares and Pearcy 1997; Maxwell and Johnson 2000). F_v/F_m was measured with a FMS-2 fluorometer (Hansatech, UK) in 20–25 plants per combination of ecosystem type, study site, and microhabitat. At each campaign, measured plants were randomly selected within each treatment combination. All measurements were completed in 2–3 consecutive days per campaign in the seven study sites.

At the end of the watering experiment (end of June 2009), we randomly selected a mean of 16 plants (maximum: 28, minimum: 10, sample size varied upon survival) per treatment combination (ecosystem type, study site, microhabitat, and watering treatment). We collected, dried, and ground some current-year scaly leaves from the upper and most exposed part of each selected plant, to analyze their carbon isotope composition ($\delta^{13}C$). $\delta^{13}C$ is an index of intrinsic water use efficiency (WUE) integrated over the time of plant organ growth (Dawson and others 2002). Determination of $\delta\,^{13}$C was performed on 0.5–1 mg subsamples of dried and ground materials by combusting at 1020°C in a Carlo Erba EA1500 NC elemental analyzer on-line with a Finnigan Delta Plus XL mass spectrometer. Stable isotope abundance (^{13}C/^{12}C) was expressed in standard notation relative to V-PDB [Vienna international standard series supplied by the IAEA vs. the classical calcite standard from Pee Dee Belemnite (PDB)] according to: $\delta^{13}C = [(R_{\text{sample}}/R_{\text{standard}}) - 1] * 1000$, where R is the molar abundance ratio of the two C isotopes [$R = (^{13}C/^{12}C)$], of the sample and standards, respectively. All samples for isotope composition were analyzed twice and on different days, with two standards every ten samples. These analyses were performed at the Instituto Andaluz de Ciencias de la Tierra stable isotope mass spectrometry facility (Granada, Spain). Based on numerous measurements of inorganic and organic international reference standards, the analytical precision of the system was about $\pm 0.1‰$ (1σ).

Survival censuses were performed every 15 days for the first 9 months and monthly for the following 15 months. Additionally, survival was monitored in June and September 2010 to estimate survival after the third summer. We labelled as dead those individuals presenting no photosynthetically active leaves and exhibiting loss of flexibility in the branches. These estimates seem to be valid because plants presumed to be dead did not resprout or produce any new tissue in the succeeding year. Maximum plant height was measured three times in all plants: right after being transplanted (H1), at the beginning (H2) and at the end (H3) of the spring 2009 (when the watering experiment was performed). Three growth estimates were calculated: growth during 2008 (H2–H1), growth during the spring 2009 (H3–H2), and total growth (H3–H1).

Data Analyses

Differences in abiotic characteristics (light availability and soil nutrient concentrations), F_v/F_m, and WUE among ecosystem types and study sites and between microhabitats were analyzed with linear models (LMs) with the following factors: ecosystem type, study site (nested within ecosystem type), microhabitat, and the interaction between woodland type and microhabitat. Normality was checked prior to analyses and when necessary variables were log-transformed, type III sum of squares was used. To test for differences in growth we performed a similar model, but controlled for the effect of plant size by including plant height at the start of the experiment as a covariate. A similar LM with an additional factor (watering) was used to test the effect of the watering treatment (data only from 2009) and its interactions with microhabitat and ecosystem type on: F_v/F_m, WUE and growth. Significant differences between levels of each factor were analyzed with post hoc Tukey's honest significant differences (HSD) test. A single LM was performed for F_v/F_m measured at each date because these measurements were independent (a randomly chosen sub set of plants from each treatment combination was measured at each campaign) and because we were not interested in differences among dates but among treatment combinations within dates.

Survival curves of each treatment combination (ecosystem type and microhabitat) were estimated with the Kaplan–Meier product limit method. Differences among the shape of the survival curves of different treatment combinations were assessed with a χ^2-multiple comparison test. Log-rank tests were used afterwards to test for significant differences in survival between treatment combinations for all pair-wise comparisons (Pyke and Thompson 1986). The same procedure was followed to test for differences among study sites in survival curves. Given the low mortality rate observed after the watering treatment (1.1 ± 0.32 plants dead per treatment combination 1 year after the watering treatment, mean ± SE, $n = 20$) we did not analyze the effect of the watering treatment on the survival function. Cumulative survival at the end of the experiment was analyzed with generalized LMs (GLM). We adjusted a binomial distribution and used the logit-link as a link function. We modelled survival including the following predictors: microhabitat, ecosystem type, and study site (nested within ecosystem type). Analyses were performed with Statistica 6.0 (StatSoft, Tulsa, OK, US).

We used structural equation modelling (SEM) to test the direct and indirect influence of ecosystem type and abiotic factors on measured ecophysiological and morphological traits. We constructed an aprioristic model in which the causal relationships between our variables were explicitly included (Shipley 2000; Iriondo and others 2003). We built independent models for each microhabitat because we hypothesized the causal relationships among variables may profoundly change between them. We limited the number of predictors included in the model as much as possible, without violating the proposed rule of thumb of $n = 10$ per observed variable in the model (Tanaka 1987). We included ecosystem type in our model by transforming it to an ordinal variable accounting for the underlying previous domestic herbivory pressure as the most important historic process related to the past land use of each ecosystem (former livestock pastures, 0; woodlands, 1; and former agricultural fields, 2). We selected two variables to characterize the abiotic environment at small spatial scales: light, as the mean annual daily PAR, and a measure of soil fertility estimated from a principal components analysis with all the measured soil variables (PCA; see Appendix 5 in Supplementary material); two ecophysiological variables: WUE and first year midsummer F_v/F_m; and two morphological variables: total growth in height and final survival. For these models, we considered plot as our experimental unit. PAR, soil fertility, and survival were measured at the plot level, whereas each plot was given a single value of WUE, F_v/F_m, and growth by averaging all measurements within each plot. Our model considered a complete set of hypotheses based on the literature and on our own experience in the field. Thus, we hypothesized that growth and survival would be influenced by the abiotic conditions (PAR and soil fertility; Aerts and Chapin 2000; Sánchez-Gómez and others 2006) and also by the ecophysiological status (WUE and F_v/F_m), which in turn would also be influenced by the abiotic conditions (Valladares and others 1997; Aranda and others 2007). Furthermore, successive processes along ontogeny might influence each other; hence, growth would influence survival (Aragon and others 2010; Matias 2010). Ecosystem type would not only directly influence all morphological and physiological variables monitored but also indirectly by affecting measured abiotic variables. Additionally, we included in the model the correlation between abiotic variables simply because we do not expect this correlation to be null (Figure 5A). All variables were assessed for normality prior to analysis and when necessary they were log-transformed (growth) to meet multinormality which is a pre-requisite in SEM. The maximum likelihood algorithm was used to estimate the path coefficients (Shipley 2000). The model fit was tested with a goodness-of-fit χ^2. Non-significant χ^2 indicate that the pattern of covariance predicted by the hypothesis does not differ from the observed covariances, thus the model can be considered congruent with the observed data. The results of the χ^2 need to be interpreted with caution because it is prone to Type I errors. Therefore, we provide two supplementary measures of fit: the Bentler–Bonett's normed fit index (NFI) and the Bentler's comparative fit index (CFI). NFI and CFI range between 0 and 1 and values greater than 0.9 indicate a good fit of the model to the data (Iriondo and others 2003). Analyses were conducted in AMOS 5.0 (Arbuckle 1994).

RESULTS

Differences in Abiotic Characteristics Among Treatments

We found significant differences among study sites and ecosystem types (Table 1) in the percentage of soil covered by rock, mosses and lichens, and woody species (among sites: $F = 6.2$, 4.0, 3.2, $P < 0.01$, among ecosystems: $F = 23.5$, 16.0, 3.2, $P < 0.01$, respectively). Ecosystem types also differed in herbaceous species cover ($F = 21.0$, $P < 0.001$; Table 1).

In all study sites and ecosystem types, light availability (DSF, ISF, and mean annual daily PAR) was greater ($F = 2225.6$, 3011.9, and 3103.4, for DSF, ISF, and PAR respectively, $P < 0.001$) in the open than under the canopy of adult trees (2). The seven sites did not differ in light availability ($F = 1.0$, 0.4, and 0.8, respectively, $P > 0.4$). Ecosystem type had no significant direct effect on light availability ($F = 0.2$, 0.3, and 0.3, respectively, $P > 0.7$), but we found a significant interaction between ecosystem type and microhabitat ($F = 11.0$, 7.8, and 11.3, respectively, $P < 0.001$): the difference between open and canopy was greatest in former livestock pastures (Table 2).

Heterogeneity was the norm for most soil nutrient concentrations (Na, K, Mg, Ca, N, P, and C_{org}) among sites and ecosystems, except for the ratio of C_{org} to N (Appendix 2 in Supplementary material). Concentrations of K, Ca, N, P, C_{org} were higher, lower for Na and Mg, in woodlands than in former agricultural fields, whereas former livestock pastures showed similar concentrations to those of woodlands of most nutrients. Study sites differed in several nutrient concentrations. Finally, concentrations of all nutrients were significantly higher under the canopy of adult trees than in open interspaces in woodlands and former livestock pastures (except P in the latter). In former agricultural fields, only concentrations of Ca, N, and C_{org} were significantly higher under the canopy than in the open (Appendix 2 in Supplementary material).

Physiological and Morphological Measurements

Photochemical efficiency (F_v/F_m) varied significantly between microhabitats in every campaign

Table 2. Mean (SE) Percentages of Direct and Indirect Radiation, and Mean Annual Daily Photosynthetically Active Radiation (in mol PAR m^{-2} day^{-1}) Estimated for Each Ecosystem Type and Microhabitat

Ecosystem type	Microhabitat	
	Canopy	Open
Woodlands		
DSF	22 (1.4)†	88.9 (1.3)‡
ISF	32.9 (1.3)†	90.5 (0.8)‡
PAR	7.6 (0.44)†	28.7 (0.4)‡
Former agricultural fields		
DSF	19.9 (1.7)†	92.9 (1.3)‡
ISF	31 (2.2)†	94.6 (0.6)‡
PAR	6.9 (0.55)†	30 (0.38)‡
Former livestock pastures		
DSF	15.5 (1.3)†	97.2 (0.9)‡
ISF	27.1 (1.5)†	97.4 (0.4)‡
PAR	5.6 (0.42)†	31.4 (0.27)‡

n is the number of plots for each combination of habitat type and microhabitat indicated in Table 1.

DSF = direct site factor; ISF = indirect site factor.

†,‡*Significant differences ($P < 0.05$) between microhabitats.*

(Table 3) but was always higher in plants under the canopy than in plants in the open (Figure 2). Similarly, we found significant differences among ecosystem types on $F_{\mathrm{v}}/F_{\mathrm{m}}$ (except mid-summer in 2008, Table 3; Figure 2A). In 2008, differences among ecosystems varied along time, with plants in former livestock pastures showing the lowest $F_{\mathrm{v}}/F_{\mathrm{m}}$ values at the end of the summer (Figure 2A). In 2009, plants in mature woodlands had the highest $F_{\mathrm{v}}/F_{\mathrm{m}}$ values on all dates, followed by former livestock pastures in the spring and by former agricultural fields in the summer (Figure 2B). We also found a significant interaction between ecosystem type and microhabitat in four measuring campaigns (Table 3). Differences between microhabitats were greatest in former livestock pastures and lowest in woodlands (Figure 2B). Watering increased $F_{\mathrm{v}}/F_{\mathrm{m}}$ and differences between watered and non-watered plants were greater in former agricultural fields than in woodlands (Table 3; Figure 2C). We found that the triple interaction (watering × ecosystem type × microhabitat) had a significant effect on not only $F_{\mathrm{v}}/F_{\mathrm{m}}$ measured right after the treatment (at the end of the spring) but also $F_{\mathrm{v}}/F_{\mathrm{m}}$ in mid-summer (Table 3). Finally, study sites differed in $F_{\mathrm{v}}/F_{\mathrm{m}}$ in all measuring campaigns, except in June 2009 (Table 3).

We found significant differences between microhabitats (Table 3) in water use efficiency (WUE, estimated by C-isotope composition: δ^{13}C). Plants under the canopy of adult trees had more negative values of δ^{13}C than those in the open (Figure 3), indicating a higher C-isotope discrimination rate (Figure 3), that is, lower WUE. The effect of the microhabitat on δ^{13}C was maintained across ecosystem types (Figure 3) and ecosystems did not differ in δ^{13}C (Table 3). The watering treatment did not have any significant direct or indirect effect on δ^{13}C (Table 3).

There were significant differences among treatment combinations of ecosystem and microhabitat on survival curves ($\chi^2 = 128.8$, $P < 0.001$; Figure 4). Plants died faster in the open than under the canopy, in all habitat types (Figure 4). Log-rank tests showed that there were specific differences among treatment combinations (Figure 4). We also found significant differences among study sites in the survival curves ($\chi^2 = 88.3$, $P < 0.001$). According to the results of the GLM, final survival differed among ecosystem types ($\chi^2 = 816.0$, $P < 0.001$), between microhabitats ($\chi^2 = 761.1$, $P < 0.001$) and among study sites ($\chi^2 = 737.1$, $P < 0.001$). Final survival was maximal in former agricultural fields (78 ± 3%, mean ± SE estimated survival), intermediate in mature woodlands (58 ± 3%) and lowest in former livestock pastures (37 ± 4%). Final survival was significantly higher under the canopy (70 ± 3%) than in the open (44 ± 3%).

We found differences in growth among habitats, during 2008: plant growth in height was greatest in woodland and lowest in former livestock pastures ($F = 0.85$, $P = 0.039$). There were no significant differences among ecosystem types in growth during the spring of 2009 (data not shown). The watering treatment had a significant effect on total plant growth (Table 3). Interestingly, we found a significant interaction: ecosystem × microhabitat × watering: growth did not differ between watered and non-watered plants in the open in woodlands (Table 3, Appendix 4 in Supplementary material).

Structural Equation Models

Models had NFI and CFI greater than 0.9 (Figure 5) for the two microhabitats and non-significant χ^2 ($P > 0.05$), indicating that they provide an excellent fit. These results showed that the proposed model suited the observed data in the two microhabitats, although some of the hypothesized relationships varied between microhabitats. The best fitted variable (with the highest squared multiple correlation estimate) was survival in both microhabitats (0.42 under the canopy and 0.58 in the

Table 3. Results of the Analyses (F and P) of the Effects of the Different Study Sites and Experimental Treatments on Maximum Photochemical Efficiency (F_v/F_m) for Different Dates, Water Use Efficiency (WUE) and Growth

Variable	Study site	EC	MH	EC × MH	W	EC × W	MH × W	EC × MH × W
F_v/F_m, May 15, 2008								
F	6.03	9.02	141.90	1.97				
P	<**0.001**	<**0.001**	<**0.001**	0.141				
F_v/F_m, July 1, 2008								
F	8.35	3.86	30.02	1.74				
P	<**0.001**	**0.022**	<**0.001**	0.178				
F_v/F_m, August 9, 2008								
F	17.04	2.08	45.41	0.42				
P	<**0.001**	0.128	<**0.001**	0.658				
F_v/F_m, September 10, 2008								
F	25.78	15.40	34.74	4.53				
P	<**0.001**	<**0.001**	<**0.001**	**0.012**				
F_v/F_m, May 5, 2009								
F	9.73	13.75	85.58	3.62	0.20	4.58	6.03	10.86
P	<**0.001**	<**0.001**	<**0.001**	**0.028**	0.657	**0.034**	**0.015**	**0.001**
F_v/F_m, June 23, 2009								
F	2.10	30.61	73.22	5.09	16.67	19.07	2.16	8.80
P	0.084	<**0.001**	<**0.001**	**0.007**	<**0.001**	<**0.001**	0.143	**0.003**
F_v/F_m, August 25, 2009								
F	15.86	44.71	32.16	18.47	0.14	1.33	1.53	17.61
P	<**0.001**	<**0.001**	<**0.001**	<**0.001**	0.713	0.251	0.218	<**0.001**
F_v/F_m, October 5, 2009								
F	7.04	9.64	10.33	0.50	0.39	1.54	0.05	0.48
P	<**0.001**	<**0.001**	**0.002**	0.607	0.535	0.216	0.832	0.489
WUE								
F	3.44	1.57	57.25	0.21	0.71	1.31	0.07	0.02
P	**0.012**	0.213	<**0.001**	0.815	0.400	0.255	0.785	0.877
Total growth								
F	1.87	0.85	**2.16**	0.17	**7.16**	0.62	0.04	**4.76**
P	0.118	0.429	**0.143**	0.843	**0.008**	0.430	0.848	**0.023**

EC = ecosystem; MH = microhabitat; W = watering.
Significant effects ($P < 0.05$) are indicated in bold.

open). Ecosystem type had a significant effect on survival. Survival increased from former livestock pastures, to mature woodlands, to former agricultural fields. Ecosystem type had a significant effect on soil fertility: it was lowest in former agricultural fields (Figure 5B, C). The magnitude of the ecosystem effects was greatest in the open. Soil fertility only affected plant performance in the open: it had a weak, but significant, positive effect on survival, which was counterbalanced by the strong indirect effect of soil fertility on survival through F_v/F_m (Figure 5C). Light had similar effects on both microenvironments on ecophysiological variables: it had a positive effect on WUE and negative on F_v/F_m and these effects were greatest in the open. Light had a negative effect on plant survival, only under the canopy (Figure 5B). As expected, F_v/F_m had a positive effect on growth and survival in both microhabitats; in contrast WUE only enhanced growth under the canopy (Figure 5B). Finally, in the open, we found that the greater the growth, the lower the survival (Figure 5C).

Discussion

We expected climate to severely constrain sapling survival in abandoned fields, because the main limitation for successful establishment is survival to the first summer after emergence or transplant (Weltzin and McPherson 1999; Villar-Salvador and others 2004; Sánchez-Gómez and others 2006). Our results were not an exception, with mortality peaking after the first summer in all ecosystems. Still, we recorded high survival in comparison with Montesinos and others (2007) and other studies with different species in the Mediterranean region

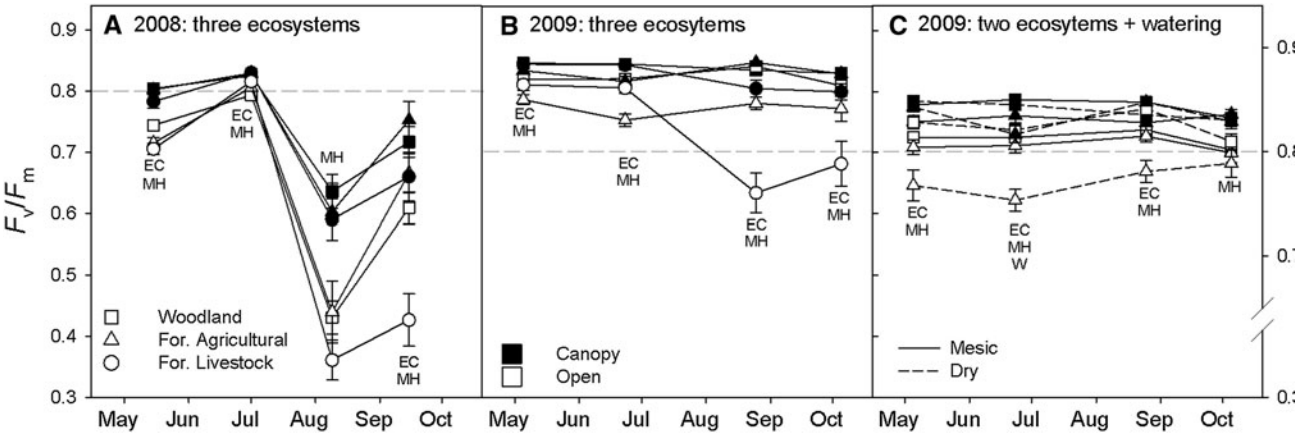

Figure 2. Maximum photochemical efficiency of photosystem II (F_v/F_m) during the measuring campaigns of 2008 (A) and 2009 (**B**, **C**) in different ecosystem types (woodlands, former livestock pastures, and agricultural fields), microhabitats (in the open and under the canopy), and under different watering levels (mesic and dry, **C**). *Symbols* represent the mean (±SE, *n* varied upon treatment combination) of all plants measured at each treatment combination. *Letters* indicate significant effects ($P < 0.05$) of the ecosystem type (EC), microhabitat (MH), and the watering treatment (W). *Dashed grey line* depicts the optimum value of F_v/F_m according to Maxwell and Johnson 2000.

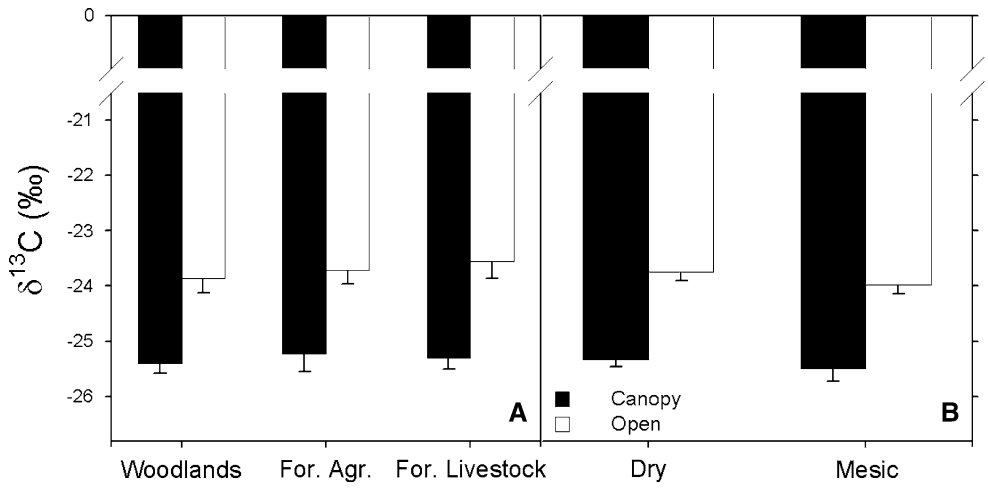

Figure 3. Carbon isotope composition ($\delta^{13}C$) in different microhabitats (in the open and under the canopy), ecosystem types (**A** woodlands, former agricultural fields, and livestock pastures, only non-watered plants) and watering treatments (**B**). *Bars* represent mean ± SE (*n* varied upon survival and treatment combination). Significant differences ($P < 0.05$) were found between microhabitats (Table 3).

(Maestre and others 2003; Gomez-Aparicio and others 2005; Rey-Benayas and others 2005; Cuesta and others 2010). Probably, this was a consequence of the wet months experienced right after transplant in 2008. This result reinforces the idea that in water-limited environments, infrequent wet episodes can be more relevant for recruitment than, for example, extreme droughts (Weltzin and McPherson 2000; Castro and others 2005; Matias and others 2011). We suggest that under a climatic scenario with increased aridity and climatic variability (Christensen and others 2007), *J. thurifera* establishment in abandoned fields might not be compromised, if these sporadic recruitment windows are maintained. Even more, according to the predictions of current climate models, these windows could become more frequent and intense due to increased second-order variability (Giorgi and Lionello 2008; Matias and others 2011).

We expected woodlands to be the best sites for sapling establishment (Matias and others 2011). However, final survival was highest in former agricultural fields followed by woodlands. Meanwhile, former livestock pastures had the lowest survival and photochemical efficiency (F_v/F_m). We argue that this is due mainly to microclimatic

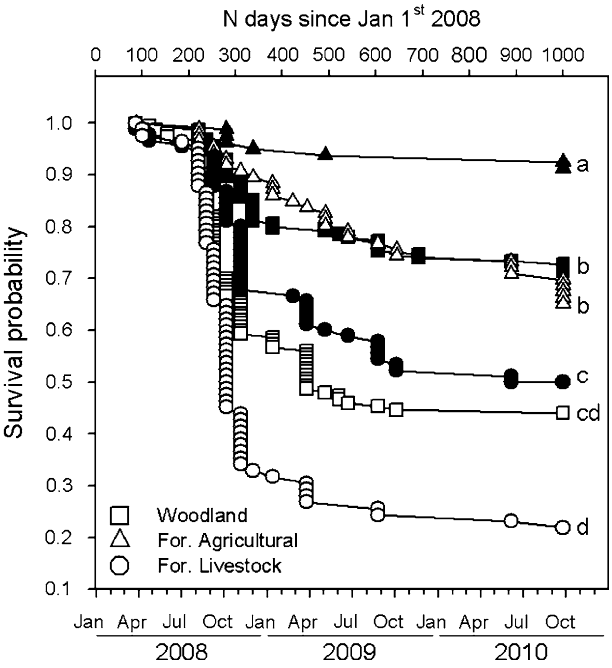

Figure 4. Survival probability functions for each treatment combination: ecosystem type (woodlands, former agricultural fields, and livestock pastures) and microhabitats (*open symbols* in the open and *closed symbols* under the canopy). *Different letters* indicate significant differences ($P < 0.05$) among treatment combinations.

differences among ecosystems, more than differences in soil nutrient content. This would explain the poor performance of saplings in former livestock pastures—despite having soils with similar nutrient content to woodlands. Former livestock pastures had the rockiest soils and therefore the lowest water retention. They had the open microhabitat with the maximum irradiance and thus higher evaporative demand. In contrast, the high survival in former agricultural fields can be attributed to higher soil water-retention capacity, due to lower rockiness and previous ploughing (Flinn and Marks 2007). Finally, we found that F_v/F_m, WUE, and growth of surviving plants in woodlands and former agricultural fields did not differ. This indicates that once plants had overcome the stressful first summer, former agricultural fields and woodlands were equally suitable for sapling survival and growth.

The effect of the watering treatment supported our premise that *J. thurifera* would be particularly sensitive to spring precipitation. Plants subjected to a watering regime mimicking the median of precipitation of the last 30 years grew more and had higher F_v/F_m than non-watered plants. In contrast, WUE did not increase in response to water scarcity (see Ogaya and Peñuelas 2008 for similar results), likely because newly formed leaves were produced using substrates synthesized during the previous year, not only during May and June. Survival after summer 2008 was highest in former agricultural fields, therefore, when we applied the watering treatment in 2009, we expected the watering effect to be greater in mature woodlands than in former agricultural fields, but we found the opposite. We propose two possible, non-excluding explanations for this result. First, it could be a carryover effect: greater water-stress in woodlands would have selected more resistant saplings the first summer, whereas in former agricultural fields more benign conditions would have imposed a less strict filter to plant survival (Lambers and others 2000). In the following dry spring, these less resistant saplings would be more affected by water-stress than those that survived in mature woodlands. Second, it could be due to higher competition for water with grasses in former agricultural fields. Grass cover has a negative effect on woody sapling establishment in abandoned fields, in water-limited environments (Rey-Benayas and others 2002; Dickie and others 2007). Higher grass cover in former agricultural fields might have imposed greater water-stress on non-watered saplings during the dry spring, whereas in the wet spring, abundant water supply would have diluted the competitive effect.

We found that *J. thurifera* saplings survived more and had higher F_v/F_m under the canopy of adult trees than in the open, evidencing facilitation, similar to other woody species (Weltzin and McPherson 1999; Gomez-Aparicio and others 2005; Kunstler and others 2007) including *J. thurifera* (Montesinos and others 2007). The sign of the nursing effect was the same in all ecosystems differing in previous land use. Yet, we found that the nursing effect was largest in the ecosystem that proved the least favorable—former livestock pastures—and on non-watered plants. Later in the ontogeny, the nurse effect could disappear or turn into competition (Escudero and others 2004; Soliveres and others 2010). Competition decreases *J. thurifera* growth (Gimeno and others 2011) and can decrease WUE (Linares and others 2009). Furthermore, shading negatively affected WUE in all ecosystem types, as in Aranda and others (2007) and Valladares and others (2008). Reduced WUE can be detrimental for water-stress tolerance (Ehleringer 1993), a key trait in drought-prone environments like the Mediterranean region. Therefore, being in the shade could compromise acclimation to water-stress.

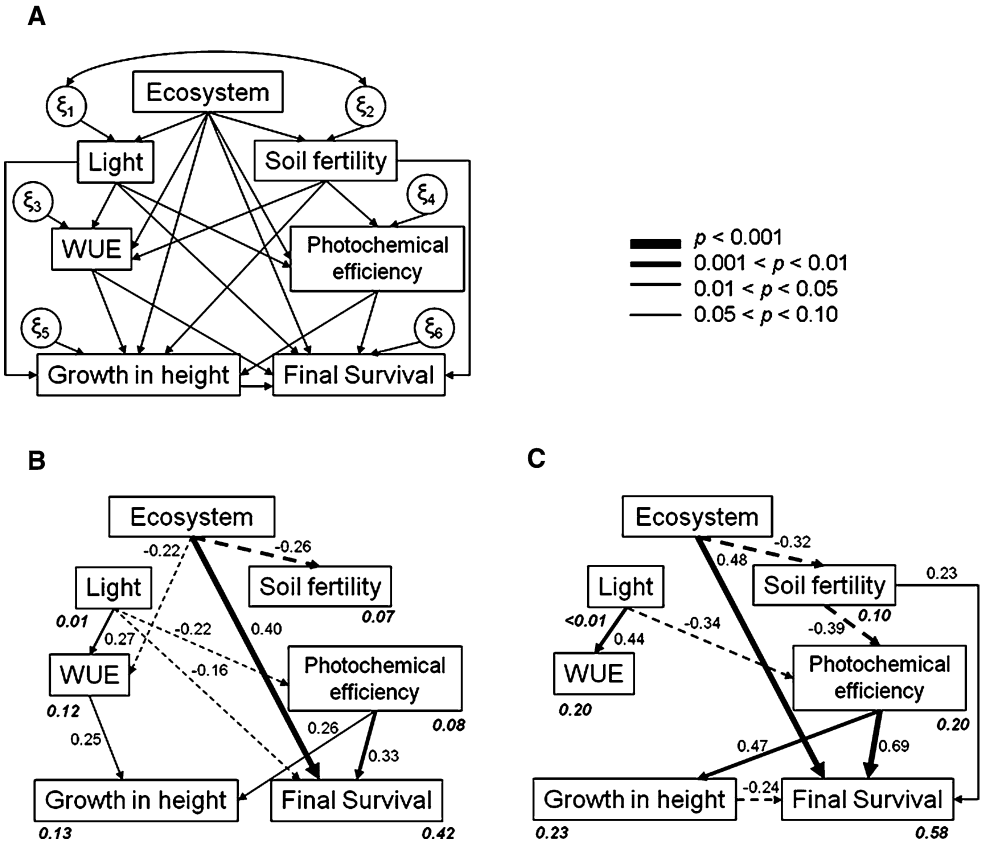

Figure 5. Path diagrams representing hypothesized causal relationships among ecosystem types, abiotic predictors, ecophysiological, and morphological variables. General path model (**A**) and results for different microhabitats: under the canopy (**B**) and in the open (**C**). *One-headed arrows* depict causal relationships, whereas *two-headed arrows* depict correlations. Positive effects are indicated by *solid lines* and negative effects by *dashed lines*, with standardized estimated regression weights indicated. Squared multiple correlation estimates are indicated for each endogenous variable (***numbers*** in *bold* and *italic*). *Arrow* widths are proportional to *P* values. Paths with coefficients non-significantly different from 0 ($P < 0.1$) are omitted. Sample size (N), normed fit index (NFI), comparative fit index (CFI), χ^2, and *P* values are given. **B** canopy: $N = 104$, NFI = 0.98, CFI = 1.00, $\chi^2_{\text{df}=1} = 1.1$, $P = 0.30$ and **C** open: $N = 61$, NFI = 1.00, CFI = 1.00, $\chi^2_{\text{df}=1} = 0.3$, $P = 0.61$.

According to our results, canopy more than soil effects benefited sapling performance (Gomez-Aparicio and others 2005). Shade reduced irradiance, temperature and evaporative stress, thus, alleviated heat and water-stress during the summer (Breshears and others 1997). Besides, nurses protected saplings against cold and frost (Castro and others 2004; Valladares and others 2008), which was responsible for a secondary mortality wave. Finally, nurses provided photoprotection (Rey-Benayas and others 2005), particularly important during the winter in Mediterranean–continental regions, where cold temperatures coexist with excess of irradiance (Martinez-Ferri and others 2003; Valladares and others 2008). We did not find any net positive effect of increased nutrient concentration under the canopy on plant performance. Instead SEM showed that higher nutrient concentration negatively affected F_v/F_m in the open. Increased nutrient concentrations cause either a positive (Shangguan and others 2000; Cruz and others 2003) or a null effect on F_v/F_m (Bungard and others 1997), thus, we argue that there must be an additional mechanism modulating this relationship, maybe competition with grasses.

CONCLUSIONS

Our results show that survival of *J. thurifera* saplings in abandoned fields is strongly dependent on previous land use. Former agricultural fields proved more suitable for sapling establishment than former livestock pastures. Nevertheless, long-term survival in former agricultural fields could be compromised under a climatic scenario with more frequent and severe periods of sustained rainfall scarcity. Comparison of our results with those from Montesinos and others (2007) suggests that early establishment is dependent on the occurrence of infrequent but crucial wet episodes during the spring. We found that nurse adult trees facilitated the establishment of conspecific saplings. However, conclusions on the importance of facilitation and on the impact of increased aridity on woody plant recruitment in Mediterranean regions must account for the previous history of each particular site. We expect *J. thurifera* woodlands to naturally expand into abandoned fields as a consequence of the current global change trends as this process is strongly dependent on the episodic occurrence of wetter than usual episodes.

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