

Changes in land use and physiological transitions of a *Juniperus thurifera* forest: from decline to recovery

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Abstract: Forest decline is frequently associated with infection; however, infections habitually affect trees that have been previously debilitated by environmental stress. Nevertheless, the causes and physiology of noninfectious forest decline are not well known. Some *Juniperus thurifera* L. forests presented severe (noninfectious) declines, with defoliations over 50%. The goal of this study was to determine the causes and characterize the physiology of this noninfectious decline, and we hypothesized that it could be related to environmental stress from increasing interspecific competition resulting from land abandonment. We randomly assigned 60 trees to either a control group or one of two competition-release treatments, i.e., vegetation clearing or soil ploughing. We characterized the physiological state of the trees both before treatment application and 14 months after treatment application. The *J. thurifera* trees that were declining experienced significantly lower soil nutrient and water availability, which resulted in lower leaf nutrient concentrations, lower photosynthetic rates, higher water stress, and arrested growth and reproduction. We confirmed that competition release increased nutrient availability and acquisition, reduced water deficit, improved photosynthetic rates, and abruptly stopped defoliation. Competition plays an increasingly critical role in forest conservation, particularly with the reported increase in the number of species colonizing previously unfeasible habitats due to global change and the absence of traditional activities that used to buffer competition.

Key words: forest management, forest decline, global change, *Juniperus thurifera*, land abandonment.

Résumé : Le dépérissement des forêts est souvent associé à des agents biotiques; cependant, les agents biotiques infectent habituellement les arbres déjà affaiblis par un stress environnemental. Malgré tout, les causes et la physiologie des dépérissements qui ne sont pas associés à des agents biotiques sont peu connues. Certaines forêts de *Juniperus thurifera* L. ont subi des dépérissements sévères d'origine abiotique qui ont causé plus de 50 % de défoliation. Nous avons cherché à déterminer les causes et caractériser la physiologie de ce dépérissement d'origine abiotique et nous avons émis l'hypothèse qu'il pourrait être relié à un stress environnemental provoqué par l'augmentation de la compétition interspécifique à la suite de l'abandon des terres. Nous avons aléatoirement assigné 60 arbres à un groupe témoin ou à l'un ou l'autre des deux traitements visant à éliminer la compétition : le défrichage et le labourage. Nous avons caractérisé l'état physiologique des arbres avant et 14 mois après l'application des traitements. Les arbres qui dépérissaient ont souffert d'une disponibilité en eau et en nutriments du sol significativement réduite entraînant une plus faible concentration de nutriments dans les feuilles, un taux de photosynthèse plus bas, un stress hydrique plus prononcé ainsi que l'arrêt de la croissance et de la reproduction. Nous confirmons que l'élimination de la compétition a accru la disponibilité et l'acquisition des nutriments, réduit le déficit hydrique, amélioré le taux de photosynthèse et brusquement arrêté la défoliation. La compétition joue un rôle de plus en plus important dans la conservation de la forêt, particulièrement avec l'augmentation rapportée du nombre d'espèces qui colonisent des habitats jusque-là impraticables à cause du changement global et en l'absence d'activités traditionnelles qui avaient l'habitude de réguler la compétition. [Traduit par la Rédaction]

Mots-clés : aménagement forestier, dépérissement de la forêt, changement global, *Juniperus thurifera*, abandon des terres.

Introduction

Forest decline is frequently associated with infection (Franklin et al. 1987; McGraw et al. 1990); however, pathogens are normally the executioners, the newcomers to a list of pre-existing factors that have been wearying the trees during long stretches (Boddy and Rayner 1983; Jurskis 2005; Galiano et al. 2012). However, forest decline is usually preceded by some form of abiotic stress that subsequently intensifies the importance of competition, ultimately leading to higher vulnerability to infection and disease. Consequently, forest decline is usually related to chronic stress and often influenced by human management (Jurskis 2005). Numerous studies characterize different physiological aspects of tree

decline, but such studies most often focus on trees already affected by diseases or wounds (Boddy and Rayner 1983). As a result, the physiology of declining forests unaffected by plague or disease has been insufficiently studied.

Low-intensity arable systems in which farmers preserved trees for shelter, wood, food, and forage maintained pseudo-steppes, which were once common across Europe (Bignal and McCracken 2000; McNeely and Schroth 2006). The abandonment of low-intensity agriculture and the progressive reduction in traditional livestock herding across Europe (Rozas et al. 2008; DeSoto et al. 2010) is increasing the pressure exerted by competitor species on numerous forests (Walther 2003; Petit et al. 2005; Hampe 2011; Olano et al. 2012). Changes in land use, combined with an increase

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in temperatures or a reduction in precipitation as predicted due to global change (Intergovernmental Panel on Climate Change (IPCC) 2001; Petit et al. 2005; Schröter et al. 2005), are likely to synergistically increase environmental stress and are expected to change the forest structure and to reduce productivity (Gimeno et al. 2012). However, to date, these stressors have not been directly linked to specific cases of forest decline and severe defoliation.

Juniperus thurifera L. (Spanish juniper) trees occupied large areas of southern Europe, forming steppe-like forests during the Tertiary period. Nowadays, the species is relegated to disjunct populations in areas with poor soils, long and cold winters, and warm and dry summers (Terrab et al. 2008) in a compromise between high environmental stress (Montesinos et al. 2010) and interspecific competition (Costa Tenorio et al. 1997; Olano et al. 2012). These low-density forests have been traditionally used for seasonal, low-intensity cereal-crop farming and livestock herding (Costa Tenorio et al. 1997). Large areas of *J. thurifera* forests in Alpuente, Spain, presented severe degrees of defoliation with no signs of disease since at least 1998 (García Post et al. 2006; D. Montesinos, personal observation, April 2008). A preliminary study indicated that traditional farming could have had a positive impact on juniper forest conservation via increased nutrient availability and leaf production (García Post et al. 2006). This study aims to characterize the physiological mechanisms of juniper decline and to experimentally recreate the effects of traditional herding and farming by, respectively, removing vegetation (clearing) or simulating traditional ploughing techniques (ploughing) 10 m around the affected trees, while also studying a group of control trees. Particularly, we aimed to answer the following specific questions. (i) What are the physiological determinants of relictual forest decline? (ii) What are the physiological mechanisms involved in forest recovery after competition release? (iii) Is increased competition derived from land use changes responsible for defoliation and decline of these relict forests?

Materials and methods

Study species

Juniperus thurifera trees occur in disjunct populations scattered across the mountains of the western Mediterranean Basin (Gauquelin et al. 2002; Terrab et al. 2008). Juniper forests are classified as priority habitats for conservation by the European Union (Directive 92/43/EEC, EUNIS 9560, http://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm, accessed 13 April 2015) and form low-density pure stands or mixed open forests with *Quercus ilex* L., *Quercus faginea* Lam., *Pinus nigra* J.F. Arnold, *Pinus sylvestris* L., and *Pinus pinaster* Aiton. Trees are 5–10 m high (20 m in exceptional cases) and often live for centuries (Bertaudière et al. 1999). Cones take 22 months to develop and ripen and contain, on average, 3.5 (range, 1–7) seeds (Montesinos et al. 2010). Seedling recruitment is severely limited by drought and nutrient availability, which can be partially alleviated by sex-biased self-facilitation (Montesinos et al. 2007). *Juniperus thurifera* is a mast-seeding species (Montesinos et al. 2012a). Although anthropogenic pressure is a serious problem for *J. thurifera* forests in northern Africa (Bertaudière et al. 2001; Gauquelin et al. 2002), regeneration in Europe is usually nonproblematic and is mainly limited by abiotic environmental factors such as nutrient availability and water stress (Montesinos et al. 2007, 2012b). Global change has been found to be already limiting to tree-ring growth in the most xeric populations as a result of increasing aridity (DeSoto et al. 2012).

Study site

Study site is located at an elevation of 1165 m near the town of Alpuente, Valencia, Spain (approximately 39°57'25.48"N, 1°00'01.99"W). Climate is classified as cold, semi-arid Mediterranean. Mean annual precipitation is 472 mm, and mean annual temperature is

12 °C. Soils are calcareous on top of consolidated material, with calcium carbonate on all horizons and an organic horizon that is always less than 20 cm thick (Rubio Delgado et al. 1996). The area still presents some cereal crops intercalated with low-density *J. thurifera* forests, although frequent abandoned terraces and other farming structures prove that these crops were far more common in the past. *Juniperus thurifera* appears accompanied by *Quercus ilex* ssp. *ballota* (Desf.) Samp. and several pine species (*P. nigra*, *P. sylvestris*, *P. pinaster*, and *Pinus halepensis* Mill.) of uncertain origin, with an important presence of shrubs and herbs that is mainly composed of individuals of *Rosmarinus officinalis* L., *Juniperus oxycedrus* L., *Juniperus phoenicea* L., *Thymus vulgaris* L., *Lavandula latifolia* Medik., *Genista scorpius* (L.) DC., *Santolina chamaecyparissus* subsp. *squarrosa* (DC.) Nyman, and *Euphorbia nicaeensis* All.

Experimental design

Sixty trees were randomly selected across the population of Alpuente, where most individuals presented intense defoliation and a lack of reproduction. Trees were individually marked and assigned to one of three experimental groups of 20 individuals each: control, cleared, and ploughed. To facilitate the application of treatments at field sites, while including a representative number of individuals and environmental conditions within the study population, we grouped 10 individuals of each experimental group into two subareas that included 30 individuals each (10 for each treatment), were separated from each other by 200 m, and had areas of 0.5 and 0.9 ha. Control trees were left as they were. For cleared treatments, all herbaceous and shrubby vegetation was removed in a 10 m radius around each tree, and for the ploughed treatment, vegetation was removed and soil was ploughed to a depth of 50 cm to at least a 10 m radius from each tree. For both clearing and ploughing, removed vegetation was shredded into small pieces and left on site. Treatments were applied during July 2010. In addition to that initial treatment, ploughing was repeated two more times in April and November 2011. At the beginning of the experiment, we morphologically characterized the 60 marked trees, which had a mean diameter at breast height (1.5 m) of 0.596 ± 4.89 cm (mean \pm standard error (SE)) (coefficient of variation (CV) = 63%) and mean tree height of 3.933 ± 0.019 cm (CV = 35%). Mean tree biomass, as derived from height and crown diameter measurements (Zaoui et al. 2000), was 154.40 ± 31.06 kg (CV = 20%). Initial defoliation (see methodology below) was $55.68\% \pm 2.64\%$ (CV = 36%). We did not find significant differences in biomass (general linear model: $F_{[2,57]} = 0.43$; $p = 0.652$) or for initial defoliation ($F_{[1,2]} = 2.79$; $p = 0.070$) among individuals assigned to the three different experimental groups. After the application of the different treatments, we made a number of measurements on all marked trees, including measurements of soil chemistry, leaf chemistry, and changes in defoliation.

- Soil chemistry. In September 2011, we took three samples at different points below each individual with a cylinder that was 10 cm in diameter and 15 cm in depth. All three samples from below each individual were mixed together and analyzed by Agrolab Analítica S.L. (Navarra, Spain) to determine the relative concentration in essential nutrients, particularly organic matter (OM) by potentiometry, nitrogen (N) by the Kjeldahl method (Lang 1958), phosphorous (P) by the Olsen method (Olsen 1954) and colorimetry at 880 nm, and potassium (K) by spectrophotometry of atomic absorption.
- Leaf chemistry. In September 2011, we took the terminal tip (15 cm) at 1.5 m height of three different branches on three different random orientations from each individual. The three samples from each tree were combined and analyzed to determine its relative concentration on essential nutrients, particularly total N by the Kjeldahl method and P and K both by spectrophotometry of induced plasma (ICP-OES).

- Changes in defoliation. We estimated the defoliation before the initiation of the treatments (September 2009) and before a final defoliation (June 2011), based on the standardized methodology for the estimation of forest defoliation developed by the United Nations and the European Network for Forest Damages (ICP Forests 2010), on which the official European regulations are based (EC regulation 1696/87; <http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:31987R1696>, accessed 13 April 2015). The methodology is based on visual estimations of defoliation of a target tree in 5% steps compared with a reference tree representing the typical crown morphology and age of trees in the vicinity, to which a 0% defoliation value is attributed (see detailed methodology at <http://icp-forests.net/page/icp-forests-manual>, accessed 13 April 2015).

Branch photosynthetic rate (A , $\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was estimated with a portable photosynthetic system (LCi, ADC BioScientific Ltd., Herts, UK). Because leaves were tiny and scale-like, physiological measurements were taken from shoots, for which surface areas were estimated following allometric transformations previously developed for this same species (Montesinos et al. 2012b). Photosynthetic rates (A) were measured on one shoot per individual at breast height and random orientation at noon on three different clear days in July, August, and September of 2011. Water potential was estimated following the same procedure at noon on the same days with a Scholander chamber (SKPM 1400 series, Skye Instruments Ltd., Powys, UK).

Finally, reproductive efforts were estimated by counting the number of male or female cones (hereafter, flowers) and fleshy berries (hereafter, fruits) present on the final 20 cm of 10 branches randomly chosen around the crown of each of the 60 individuals during the 3 years of study (2009–2011). Flowering was estimated during January, and fruiting was estimated during October.

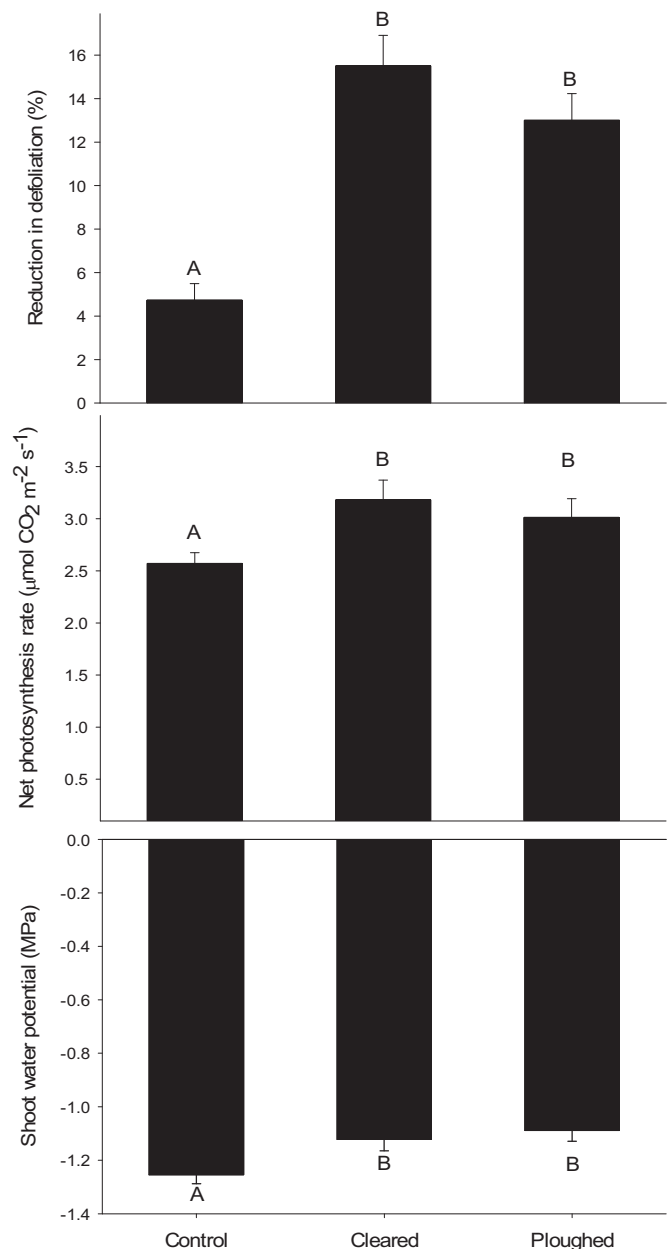
Statistical analyses

Statistical analyses were performed with IBM-SPSS 19 (Norusis 2002), and data were tested for homoscedasticity. Soil and leaf chemistry, as well as reduction in defoliation rates, were analyzed by a general linear model with treatment as a fixed factor and Tukey's b post-hoc tests. Differences in A , water potential (Ψ), flowering, and fruiting were assessed by linear mixed models, with those variables as dependent variables, shoot biomass as the covariable, treatment as a fixed factor, and time as a repeated measurement, by using a first-order autoregressive covariance structure.

Results

Consistently, for all variables, competition release by shrub clearing or ploughing similarly improved tree conditions. *Juniperus thurifera* trees presented an initial defoliation of 55% in the studied area; after 21 months, trees experiencing either of the two treatments had reduced defoliation to an average of only 40% ($F_{[1,2]} = 7.50$; $p = 0.001$), a total reduction of 27% in the defoliation rate (there were no differences between clearing and ploughing, $p = 0.828$; Fig. 1). Treatments improved tree water potential by 10% overall ($F_{[2,72]} = 4.45$; $p = 0.015$), with no difference between clearing and ploughing ($p = 0.472$; Fig. 1; Supplementary Fig. S1¹). Photosynthesis net rate improved similarly, with treated individuals having 20% higher photosynthetic rates than controls overall ($F_{[2,61]} = 3.72$; $p = 0.030$), with no differences between clearing and ploughing ($p = 0.832$; Fig. 1; Supplementary Fig. S1¹). Soil nutrient analysis also showed that both clearing and ploughing significantly increased nutrient availability in terms of OM (80% increment; $F_{[2,57]} = 8.79$; $p < 0.001$), N concentration (35% increment; $F_{[2,57]} = 7.52$; $p = 0.001$), P concentration (153% increment; $F_{[2,57]} =$

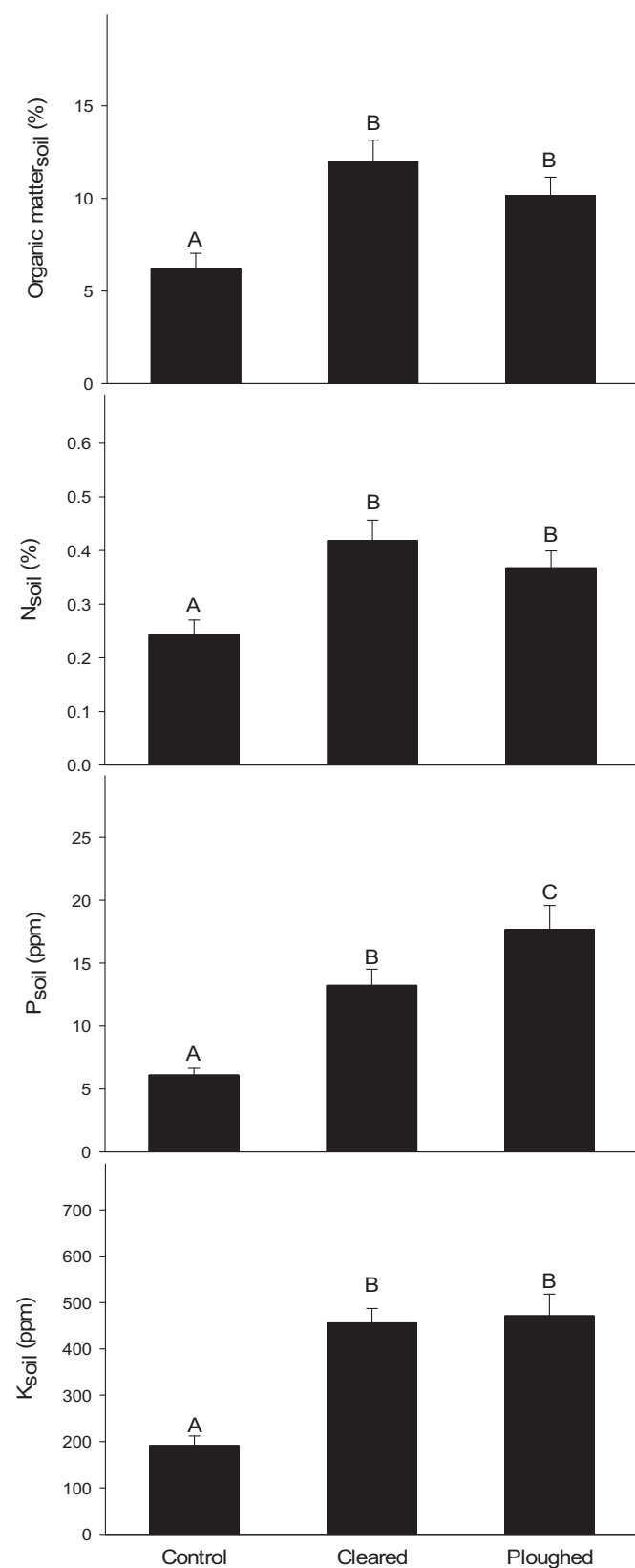
Fig. 1. Reduction in defoliation (%), net photosynthesis rate ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and shoot water potential (MPa) of trees from each of the three groups: control, cleared, and ploughed (mean \pm SE). Different letters indicate statistically significant differences among groups.



17.75; $p < 0.001$), and K concentration (243% increment; $F_{[2,57]} = 20.43$; $p < 0.001$). Post-hoc tests showed that clearing and ploughing presented similar values between them but were higher than controls ($p < 0.05$), except for P concentration, which was significantly higher in cleared soils than in controls (116% increment; $p < 0.05$) but significantly lower than in ploughed soils (190% increment compared with controls; $p < 0.05$; Fig. 2). Leaf chemical analyses closely mirrored soil chemical analyses, although reflecting different assimilation ratios for each nutrient. Treatments increased branch nutrient concentration for both N (35% higher concentration than controls; $F_{[2,57]} = 42.04$; $p < 0.001$) and P (20% increase; $F_{[2,57]} = 5.20$;

¹Supplementary Fig. S1 is available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2014-0468>.

Fig. 2. Nutrient (K, potassium; P, phosphorus; N, nitrogen) and organic matter (OM) concentrations on soil collected under trees from each of the three groups: control, cleared, and ploughed (mean \pm SE). Different letters indicate statistically significant differences among groups.



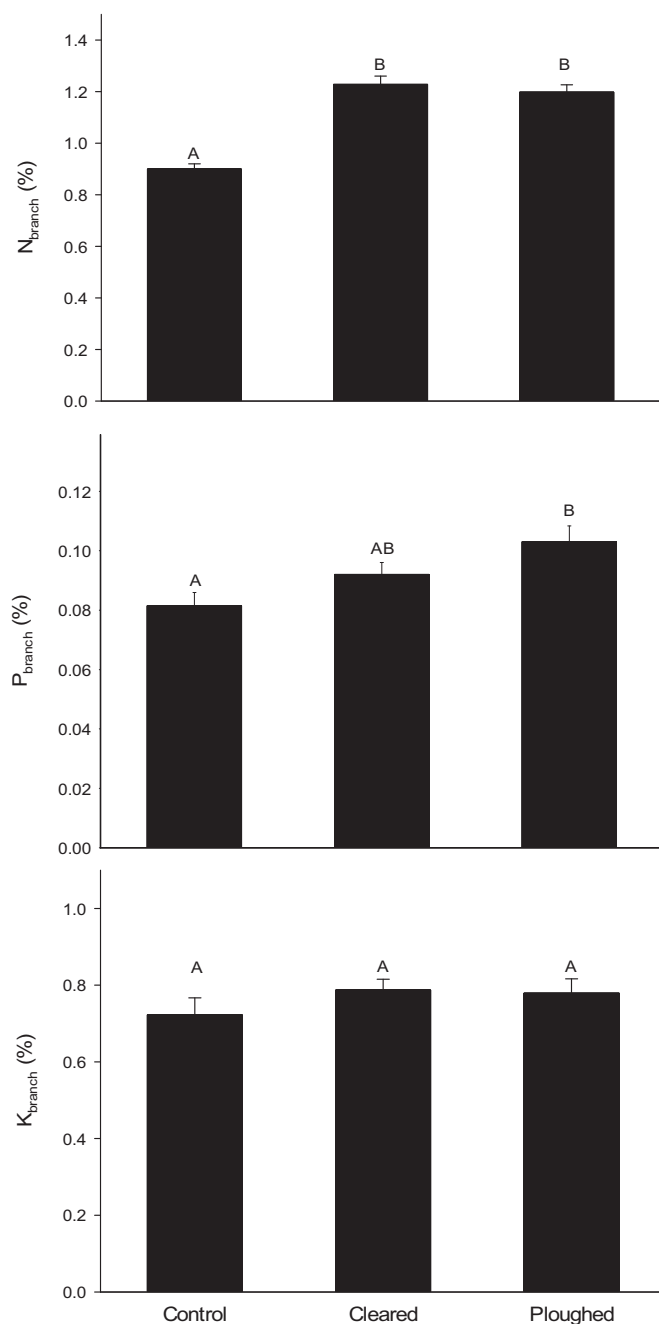
$p = 0.008$), although no differences among treatments were found for K ($F_{[2,57]} = 0.91$; $p = 0.409$). Post-hoc tests showed that both clearing and ploughing significantly increased N concentration over the concentration present on control individuals ($p < 0.05$). P concentration presented a similar pattern in soils, although for branch P, differences were not as important, finding statistically significant differences ($p < 0.05$) between control and ploughing (26% increase over controls), whereas the individuals on the cleared sites (13% increase over controls) presented intermediate values that were not significantly different from either of the other two groups (Fig. 3). Finally, no significant differences were found among treatments for flowering rates (8.02 ± 3.08 flowers per branch; $F_{[2,60]} = 0.90$; $p = 0.412$) or for fruiting rates (1.41 ± 0.69 fruits per branch; $F_{[2,57]} = 1.47$; $p = 0.238$).

Discussion

Experimental simulation of traditional land management resulted in the recovery of decaying *J. thurifera* trees. Physiological characterization of the transitions between decline and recovery showed that, compared with treated individuals, declining trees experienced significantly lower soil nutrient and water availability, which resulted in lower leaf nutrient concentrations, lower photosynthetic rates, higher water stress, and arrested reproduction and growth. Simulation of traditional farming consistently reversed all these processes, rapidly increasing nutrient availability, which directly translated into increased nutrient acquisition, reduced water deficit, improved photosynthetic rates, and dramatic reductions in defoliation (i.e., branch growth). After experimental release from competition, defoliation decreased from 55% to 40%, a clear indicator of the general improvement (27%) in the health condition of the treated individuals. This improvement could be related to the general increase in soil nutrient content, reflecting the addition of OM via shredded vegetation, the liberation and mobilization of soil nutrients due to degradation of the roots of former competitors, and the development of denser crowns (Prescott 2002; but see Munger et al. (2003)). This resulted in important increases in branch nutrient concentration and in improved physiological values overall. The physiology of defoliation on declining forests has been studied mainly as a consequence of either disease or herbivory (Franklin et al. 1987; McGraw et al. 1990), but water scarcity also plays a critical role on crown condition and forest decline, particularly in Mediterranean environments (Galiano et al. 2012). In our study, water potential of treated individuals improved by 10%, reflecting the escape from competition for water with shrubs. Consequently, with such a significant improvement in both water availability and nutrient concentration, treated individuals increased their photosynthetic rates by 20%, which explains why treated trees produced more branches and reduced defoliation so quickly, in line with previous studies of changes in tree-ring growth after forest clearings (Rozas et al. 2008) and with preliminary studies in *J. thurifera* (García Post et al. 2006). Reproduction is one of the first detectable traits of stress and decline (García et al. 1999; Hensen et al. 2005). The lack of improvement in reproduction in the short term was anticipated for *J. thurifera*, a masting species with cycles longer than 5 years, requiring long periods to reflect changes in the environment at the reproductive level (Montesinos et al. 2012a, 2012b).

Our study experimentally confirmed the importance of low-intensity traditional activities for the conservation of relict populations by releasing individuals from competition. Human activities are key to controlling the competitive displacement of many relict forests (Grabherr et al. 1994; Gottfried et al. 1999; Alward et al. 1999; Saxe et al. 2001; Walther 2003; Olano et al. 2012). Herding is one of those traditional activities, and *J. thurifera*, as most junipers, has a high tolerance to herbivory, as sheep and goats prefer other more palatable species if they are available; recent studies indicate that a generalized reduction in livestock

Fig. 3. Branch nutrient (K, potassium; P, phosphorus; N, nitrogen) concentrations (%) in trees from each of the three groups: control, cleared, and ploughed (mean \pm SE). Different letters indicate statistically significant differences among groups.



pressure in the Iberian Peninsula is causing a competitive displacement of these junipers by other species that used to be controlled by traditional herding (Montesinos et al. 2007; Rozas et al. 2008). Consequently, many pure *J. thurifera* forests are slowly transforming into mixed forests with a significant presence of *Q. ilex* and *P. sylvestris* due to competitive displacement (DeSoto et al. 2010; Olano et al. 2012). This pattern could be reinforced by climate change, which is expanding the distributions of potential competitor species (Grabherr et al. 1994; Gottfried et al. 1999; Alward et al. 1999; Walther 2003) and is already diminishing *J. thurifera* tree growth in the most xeric populations (DeSoto et al. 2012). Data from this study confirm this trend and suggest that

traditional farming and herding facilitated the conservation of *J. thurifera* forests in areas in which they could have been competitively displaced otherwise. It is necessary to remark, however, that an excessive anthropogenic pressure could also have a negative impact on *J. thurifera* forests (DeSoto et al. 2010; Gimeno et al. 2011), as appears to happen on the southern Moroccan populations (Bertaudière et al. 2001; Gauquelin et al. 2002).

Historically, the distribution of *J. thurifera* has been considered to be limited by competition with species with higher growth rates and faster life cycles (Ruiz de la Torre and Ceballos 1971; Loehle 1998), and in fact, it is able to colonize recently abandoned lands due to lowered competition in these areas (Gimeno et al. 2011). It has been suggested that long-living species could buffer the effects of changes in climate (Bennet et al. 1991). However, our data indicate that competition can result in rapid declines, which could become irreversible after only a few decades as a consequence of halts on reproduction and regeneration (Montesinos et al. 2009) in a species known to be highly sensitive to microhabitat conditions for recruitment (Montesinos et al. 2007; Gimeno et al. 2012). The widely distributed *J. communis* is known to be similarly sensitive to competition and water limitation, particularly at the extremes of their latitudinal distribution, where their populations occur scattered in relict mountain areas (García et al. 2000; Verdú et al. 2004; García and Zamora 2003). Such species would potentially benefit from maintaining traditional farming and herding or from alternative competition-release treatments in those populations limited by climate or competition (Hampe 2011).

Robust models studying the dynamics of several Iberian forest species, including *J. thurifera*, predict that global change will strongly increase the impact of competition in the following years and recommend competition alleviation to manage vulnerable species (Gómez-Aparicio et al. 2011). Other models also indicate that competition release could have a significant positive impact on the conservation of European forests vulnerable to climate change induced drought (Guillemot et al. 2014). Our data contribute to the experimental validation of those models, confirming that selective interventions by bush cleaning are effective management techniques, particularly in the face of changes in complex physiological interactions as a result of global change.

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