New insights on the understanding of forest fires impact in the Canary Islands pine forest

*Javier Méndez, *Gustavo Morales, *Celia García-Domínguez,
*Silvia Fernández, **Lea de Nascimento, *Rüdiger Otto,
***José María Fernández-Palacios

Abstract. Pine forest in the Canary Islands is mainly dominated by *Pinus canariensis*, the only species in this genus endemic in oceanic islands. This forest is the most affected by fires in the Archipelago, however adults of *P. canariensis* are highly adapted to fire. Keyprocesses in ecosystem maintenance such as long term post-fire regeneration dynamic and ecosystem recovery have not been deeply studied. The IEBG had developed in recent years several researches about dynamic of Canarian pine forest under fire regimens in Tenerife, La Palma and Gran Canaria. Despite adaptations to fire, sexual regeneration of *P. canariensis* not dependent on fire and appears to be adapted rather to phenomena involving the disappearance of adults, such as high winds or colonization of new habitats. Fires also change understory conditions allowing a progressive inflow of herbaceous species that were not part of the ecosystem before the fire. In less than 10 years, these species are displaced by ecosystem mature vegetation. The invertebrate fauna dependent on the Canarian pine mulch is also affected by fires, wich reduces it richness, abundance and composition. However, and because to the overall ecosystem is adapted to this type of disturbance, these effects are mitigated also in less than 10 years.

Key words: ????

^{*} PhD, Island Ecology and Biogeography Group, Instituto Universitario de Enfermedades Tropicales y Salud Pública de Canarias (IUETSPC), Universidad de La Laguna (ULL);

^{**} Postgraduate, Island Ecology and Biogeography Group, Instituto Universitario de Enfermedades Tropicales y Salud Pública de Canarias (IUETSPC), Universidad de La Laguna (ULL);

^{***} Professor, Island Ecology and Biogeography Group, Instituto Universitario de Enfermedades Tropicales y Salud Pública de Canarias (IUETSPC), Universidad de La Laguna (ULL); E-mail: jmendezh@ull.es

Introduction

The endemic Canarian pine (*Pinus canariensis*) is the only native pine of the Canary Islands. This species can reach 30 m high, with a maximum of more than 50m, and can live for more than 800 years (GÉNOVA and SANTANA, 2006). Genetic studies have shown the close relationship existing between the Canarian pine with current Mediterranean pines (*P. brutia, P. halepensis, P. heldreichii, P. pinaster* and *P. pinea*) and the Himalayan *P. roxburghii* (LISTON *et al.,* 1999; WANG *et al.,* 1999; GERNANDT *et al.,* 2005). Within the Mediterranean pine group, Canary pine is the species with more adaptations to resist fires, combining strategies that ensure both population resilience and individual survival. Some of the most remarkable adaptations to fire of Canarian pine are the sprouting ability after fire, unique among European pines, and the presence of serotine cones (CLIMENT *et al.,* 2004).

The species natural distribution is restricted to the highest Canary Island (Tenerife, La Palma, Gran Canaria, El Hierro and La Gomera) (DEL ARCO et al., 1997). However, a P. canariensis like fossil appeared throughout the Tethys basin during Miocene, from Iberia to Turkey, and the oldest fossil in the Canary is 13 m (KASAPLIGIL, 1976; MILLAR, 1993; GARCÍA-TALAVERA et al., 1995; MORLA et al., 2002). It is not clear why this high tolerant paleo-endemism disappeared from the Mediterranean basin. It was traditionally assumed that P. canariensis disappeared from its ancient distribution during the Plio-Pleistocene period due to its low tolerance to freezing temperatures (SAKAI, 1971). However, the latest fossils of P. canariensis from the Plio-Pleistocene boundary appears in areas where temperatures probably did not fall below - 5°C (Greece or Turkey), which could be tolerated by P. canariensis (KOVAR-EDER, 1987; BOYD, 2009). Although P. canariensis could have survived in these regions, its regeneration mechanisms would have been a disadvantage compared to obligate seeders pine species, which have a much higher seed production, faster growing rate and lower light requirements, in the same way that today P. halepensis invades areas occupied by pine trees with a more limited seed production and higher light requirements (GANATSAS and THANASIS, 2010).

Prehistoric human influence in the pine forest in the Archipelago is poorly unknown and only recently fossil micro-charcoal analyses revealed increased forest fire regimen since human arrived around 1000 BC in Tenerife (DE NASCIMENTO et al., 2009). After Europeans arrival during XV century, an intensive logging began, modifying deeply insular ecosystems (PARSONS, 1981). Reforestation and

conservation polities have been accomplished since the second half of the past century, reestablishing most of the potential area and connectivity of this ecosystem (ARÉVALO *et al.*, 2010). Considering that the Mediterranean pine forest is one of most flammable ecosystem in the region and the best adapted to forest fires, post-fire regeneration and ecosystem dynamics of *Pinus canariensis* had been poorly studied compared with other Mediterranean fire resistant pines such as *P. halepensis*, *P. brutia* or *P. pinaster*. This paper summarizes the recent studies by the Island Ecology and Biogeography Group of La Laguna University in natural and reforested stands in Tenerife, La Palma and Gran Canaria (Canary Islands). We first addressed relevant aspects of forest dynamics of *Pinus canariensis* unknown until now: natural and long-term post-fire regeneration dynamics, the understory and the arthropods fauna. An overall view from the dynamic process of Canarian pine will provide useful information for forest management in the Canary Islands.

Pinus canariensis post-fire regeneration

Sexual regeneration in Canarian pine have been studied addressing the effects of fires at short and medium-term, due to the high frequency of fires occurring in the pine forest (HÖLLERMANN, 2000; ARÉVALO et al., 2001). Presence of serotine cones in P. canariensis has lead to consider spatial and temporal pattern of seed rain mainly from a fire-related point of view (CLIMENT et al., 2004). However, MÉNDEZ (2010) and OTTO et al. (2012) found seed release throughout the year but increasing dramatically in summer, probably due to high temperatures. Consequently, seeds will be available for germination throughout the year (Fig. 1). These released seeds show low germination rates in comparison with controlled conditions, 2-18% of available seeds output versus 20-80% in laboratory (ESCU-DERO et al., 2002; GARCÍA-DOMÍNGUEZ, 2011). Many environmental factors affect this field germination rate, mainly rainfall and adults density, and germination shows a unimodal curve in response to time elapsed after fire (Fig. 2). Although we have not yet performed an experiment to confirm it, we hypothesize that early after fire, surviving adult pines invests mainly in the recovery of photosynthetic and woody tissues to the detriment of reproductive structures. Consequently, the seeds released will have reduced viability and low germination (KEELEY and ZE-DLER, 1998). Viability is recovering gradually until 13 years after, where competition among adults for light or space would begin to be, resulting in lowering of seed production and germination. Some studies show how soil nutrients, i.e. phosphorous, increase gradually after fire (DURÁN *et al.*, 2008) coinciding with the increase of pine germination.

Mortality of seedlings is particularly intense during the first months of life, although the probability to survive depends on the season of germination (MÉN-DEZ, 2010). Seedlings could live at least for five years if they overcome this initial phase (Fig. 3), maintaining its seedling stage without promotion to advanced ontogenetic phases. During this time, seedlings invest in developing the root system that will provide more water to the plant allowing its survival during drought events (CLIMENT *et al.*, 2011). This growth delay is known as "Oskar syndrome", considered as the ability of seedlings to survive under the forest canopy until its opening creates the appropriate conditions for a faster growing (HIBBS and FISCHER, 1979; SILVERTOWN, 1982). The succession and coexistence of different age cohorts, together with the constant provision of seeds ensures a permanent seedling bank throughout the year, which enables the response of the community to different perturbations.

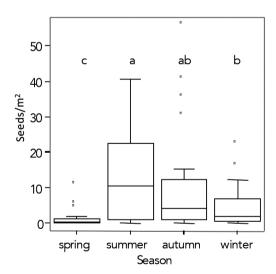


Figure 1 - Boxplot of seasonal distribution of Pinus canariensis seed rain (seed/m²). Letters shows significant differences using permutational analysis of variance (PERMANOVA) with p<0.05. Boxes shows quartiles 1 to 3, the center lines represent the median and intervals indicate the range of 95% of cases. Circles shows outliers values; asterisks shows extreme values.

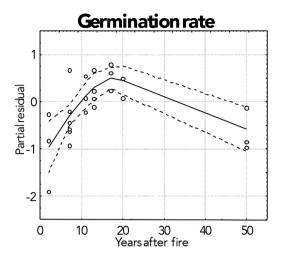


Figure 2 - Pattern of germination rate of P. canariensis with time elapsed after fire. Curves were obtained from the generalized additive model (GAM). Dashed lines indicate 95% confidence intervals (MENDEZ et al., in preparation).

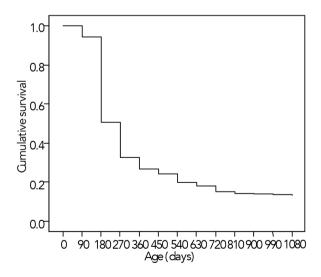


Figure 3 - Average Kaplan-Meier survival curve of Pinus canariensis seedlings in natural stands of La Palma Island (Canary Island) (MÉNDEZ, 2010). Curve shows instantaneous survival probability.

Post-fire recovery of the Canarian pine forest

Within a single fire event, intensity varies greatly on a landscape scale, due to topography, fuel accumulation, or microclimatic conditions, determining the extent of changes on vegetation and soils (TAKAOKA and SASA, 1996; MILLER and URBAN, 2000). The result is a mosaic of patches with different abiotic and biotic characteristics (TURNER *et al.*, 1994).

Low-intensity fires can increase the amount and availability of soil nutrients, as well as reduce competition among understory species, enhancing an increase of productivity. However, these fires rarely cause significant damages on adult pines. In turn, high-intensity fires may decrease nutrient content in the ecosystem, erode soils and drastically reduce biomass from both the understory and the canopy. This is the case for most of Mediterranean pine forests, where burned trees die and regeneration depends exclusively on seeds stored on serotine cones (TAPIAS *et al.*, 2001). Recovery in these ecosystems takes several decades.

Due to thick bark and sprouting ability, fires very rarely kill adult Canarian pine trees, even after high-intensity fires. Thus, the most significant effect of fire on Canarian pine tree is the removal of needles resulting in a temporary opening of the canopy, changing the understory light conditions during the short period lasting the canopy recovery. Regardless of fire intensity, understory vegetation might be severely damaged. Nutrient availabilities, also varies after fire in Canarian pine forests (DURÁN *et al.*, 2008; RODRÍGUEZ *et al.*, 2009). All these modifications in the understory affect species richness and composition (DUCEY *et al.*, 1996; ARÉVALO *et al.*, 2001; KUENZI *et al.*, 2008; SABO *et al.*, 2009).

Two to four years after fire, species richness begins to increase (Fig. 4). The first species to appear are mainly annual shade-intolerant plants absent in the understory composition before the fire (*Vicia* sp., *Tolpis* sp.). The number of woody species increases rapidly only a-few months after the fire (ARÉVALO et al., 2001; MORALES, 2010; GARCÍA-DOMÍNGUEZ, 2011). This fast recovery of understory species can be explained by different types of fire adaptations present in many native woody species, as the resprouting ability in *Erica arborea* or a fire-induced germination in *Adenocarpus* spp. or *Cistus* spp. (HÖLLERMANN, 2000). Ten years after fire, the canopy is completely recovered and woody species cover most of the understory replacing herbaceous species (MORALES, 2010).

Fires have been considered responsible for favouring exotic species in forests (CRAWFORD *et al.*, 2001; FLOYD *et al.*, 2006). However, we have not found a relationship between the number of exotic species and fires in Canarian pine for-

est (GARCÍA-DOMÍNGUEZ and FERNÁNDEZ-PALACIOS, 2009). Only exotic annual species increase soon after fire (Fig. 4), but they disappear when the canopy is restored to the original conditions (MORALES, 2010).

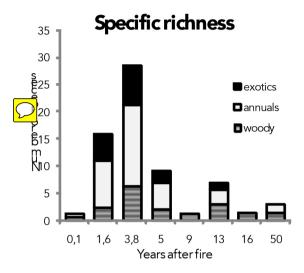


Figure 4 - Species richness of understory species (woody and herbaceous native species, and herbaceous exotic species) with time elapsed after fire (MORALES, 2010).

Diversity recovery of leaf-litter arthropods after a fire

Wildfires can significantly affect animal communities of leaf-litter layers, both directly by the death of those species unable to escape the fire or indirectly by changing their habitat conditions. The disappearance of critical organisms, such as, necrophagous, pollinators or decomposers, may significantly delay forest recovery (BOER, 1989). MORALES (2010) found that re-colonization process following fire can be divided in three stages (Fig. 5). The first stage, 2-3 years following fire is characterized by a low abundance and α -richness (number of species per surface area), mainly due to the direct fire effects. Conversely, β -richness, a measure of the species turnover, is high as shown in other studies (APIGIAN *et al.*, 2006; FERREN-BERG *et al.*, 2006). Increase in β -richness may be explained by a higher spatial heterogeneity due to fire, which allow the coexistence of characteristic species of the mature un-burned zone with pioneer species in the affected areas (KNAPP *et al.*, 2005).

This stage coincides with the first stages of the secondary succession, when the species richness of the understory is growing, which may also favour the increase in arthropods β -richness (FERRENBERG *et al.*, 2006).

After a fire, the first groups appearing are those able to avoid the fire by fleeing or by burying in the soil and avoiding high temperatures. Hymenoptera and Arachnida are the first groups in appear, together with introduced species, as in other forest areas (ANDERSEN and YEN, 1985; SULLIVAN *et al.*, 2003; RODRIGO and RETANA, 2006). In this case, there were two introduced species of isopods, which may act as opportunist species taking advantage on the first months after fire. In forest areas, Coleoptera use to appear during the first stages of colonization, however in Canarian pine forest this group only appear the first year after fire (EHN-STRÖM *et al.*, 1995; GANZ *et al.*, 2003; MCHUGH *et al.*, 2003; SULLIVAN *et al.*, 2003; FERRENBERG *et al.*, 2006). This may be result of most of the species of the group being xylophagous. In other ecosystems several death trees remain after fire, but in the Canarian pine forest most of the trees survive and most of the death wood is consumed by fire, so there is not available wood until the fall of death branches, which use to be related to strong winds or storms (SULLIVAN *et al.*, 2003).

During the second stage there is an increase in α -richness and abundance, although the community remain variable, since a species turnover can still be observed. The magnitude of the species turnover is lower than in the previous stage, approaching to the mature community values. It is in this moment, 5 years after fire, when pine forest start to be more stable regarding to environmental variables, having a canopy cover, net primary productivity, leaf-litter, organic matter decomposition, and understory species richness and composition similar to preburnt conditions, providing shelter and food to the invertebrate community of the leaf-litter layer.

In the third stage, after seven years following fire, the arthropods community is dominated by typical pine forest species, with seasonal changes in species abundance and α -richness that do not result in changes at the order level. β -richness remains stable, indicating that leaf-litter arthropods community has reached a high degree of maturity. Some groups (Julida, Pulmonata, Coleoptera and Araneae) remain stable at this point, probably because they have species that exploit broad niches, supporting both local and seasonal variations.

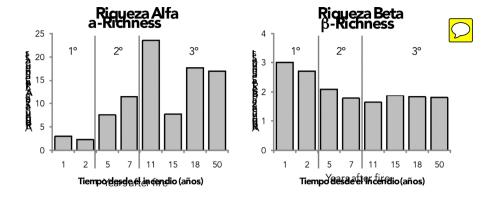


Figure 5 - Mean annual Alfa and Beta richness of litter invertebrates in a fire chronosequence in La Palma Island, Canary Island, (MORALES 2010).

Conclusions

We can conclude that sexual regeneration of *Pinus*, *canariensis* is not affected by fires unless these are intense enough to open the canopy completely, which is something unusual in the Canarian pine forests. Sexual regeneration in this species seems to be more adapted to events entailing the removal of adult trees, such as strong winds or volcanic eruptions. Its ability to colonize recent soils (i.e. lava flows) explains the invasive potential of *P. canariensis*, simultaneously being part of pioneer and mature communities. For the first time the long-term wildfire effects on leaf-litter arthropods of the Canarian pine forest were studied, finding that fire affects species richness, abundance and composition of the invertebrates of the leaf-litter layer. However, since this ecosystem is extremely well fire-adapted effects on invertebrates are mitigated in relatively short time. We ignore if, in the event of increasing fire frequency caused by humans, the Canarian pine will be adapted enough to resist recurrent perturbations.

References

ANDERSEN, A. N., YEN, A. L., 1985. Immediate effects of fire on ants in the semi-arid mallee region of northwestern Victoria. *Australian Journal of Ecology* **10**: 25-30.

APIGIAN, K.O., DAHLSTEN, D.L. STEPHENS, S.L., 2006. Fire and fire surrogate treatment effects on leaf litter arthropods in a western Sierra Nevada mixed-conifer forest. *Forest Ecology and Management* 221: 110-122.

- ARÉVALO, J.R., FERNÁNDEZ-PALACIOS, J.M., JIMÉNEZ, M.J., GIL, P., 2001. The effect of fire intensity on the understory composition of two *Pinus canariensis* reforested stands in Tenerife (Canary Islands). *Forest Ecology and Management* **148**: 21-29.
- ARÉVALO, J.R., NARANJO, A, FERNÁNDEZ-PALACIOS, J.M., FERNÁNDEZ-LUGO, S., 2010. Ecology and management of natural and reforested Canary Island pine stands. In: WALLACE, E.R. (Ed.). *Woodlands: Ecology, Management and Conservation*. Nova Science Publishers, Inc, pp 137-159.
- BOER, C., 1989. Effects of the forest fire 1982-83 in East Kalimantan on wildlife. FR Report No. 7. Samardinda, Indonesia, Deutsche Forstservice GmbH.
- BOYD, A., 2009. Relict conifers from the mid-Pleistocene of Rhodes, Greece. *Historical Biology* **21**: 1-15.
- CLIMENT, J., TAPIAS, R., PARDOS, J., GIL, L., 2004. Fire adaptations in the Canary Islands pine (*Pinus canariensis*). *Plant Ecology* **171**: 185-196.
- CLIMENT, J., SAN-MARTÍN, R., CHAMBEL, M.R., MUTKE, S., 2011. Ontogenetic differentiation between Mediterranean and Eurasian pines (sect. *Pinus*) at the seedling stage. *Trees* **25**: 175-186.
- CRAWFORD, J.A., WAHREN, C.H.A., KYLE, S., MOIR, W.H., 2001. Responses of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. *Journal of Vegetation Science* 12: 261-8.
- DE NASCIMENTO, L., WILLIS, K.J., FERNÁNDEZ-PALACIOS, J.M., CRIADO, C., WHITTAKER, R.J., 2009. The long-term ecology of the lost forests of La Laguna, Tenerife (Canary Islands). *Journal of Biogeography* **36**: 499-514.
- DEL ARCO, M.M., ATIENZA, E., ATOCHE, P., DEL ARCO, M.C., MARTÍN, M., 1997. Dataciones absolutas en la prehistoria de Tenerife. In: ATOCHE, P., MILLARES, A., LOBO, M. (Eds.). *Homenaje a Celso Martín de Guzmán (1946-1994)*. Universidad de Las Palmas de Gran Canaria, Las Palmas, pp. 65-77.
- DUCEY, M.J., MOSER, W.K., ASHTON, P.M.S., 1996. Effect of fire intensity on understory composition and diversity in a Kalmia-dominated oak forest, New England, USA. *Vegetation* **123**: 81-90.
- DURÁN, J., RODRÍGUEZ, A., FERNÁNDEZ-PALACIOS, J.M., GALLARDO, A., 2008. Changes in soil N and P availability in a *Pinus canariensis* fire chronosequence. *Forest Ecology and Management* **256**: 384–387
- EHNSTRÖM, B., LANGSTRÖM, B., HELLQVIST, C., 1995. Insects in burned forests—forest protection and faunal conservation (preliminary results). *Entomologica Fennica* **6**: 109-117.
- ESCUDERO, A., PÉREZ-GARCÍA F. LUZURIAGA, A.L., 2002. Effects of light, temperature and population variability on the germination of seven Spanish pines. *Seed Science Research* 12: 261-271.
- FERRENBERG, S.M., SCHWILK, D.W., KNAPP, E.E., GROTH, E., KEELEY, J.E., 2006. Fire decreases arthropod abundance but increases diversity: early and late season prescribed fire effects in a Sierra Nevada mixed-conifer forest. *Fire Ecology* 2: 79-102.

- FLOYD, M.L., HANNA, D., ROMME, W.H., CREWS, T.E., 2006. Predicting and mitigating weed invasions to restore natural post-fire succession in Mesa Verde National Park, Colorado, USA. *International Journal of Wildland Fire* **15**: 247-59.
- GANATSAS, P. THANASIS, G., 2010. Pinus halepensis invasion in Pinus pinea habitat in Strofylia forest (Site of NATURA 2000 network), southern Greece. *Journal for Nature Conservation* **18**: 106-117.
- GANZ, D. J., D. L. DAHLSTEN, SHEA, P. J., 2003. The post-burning response of bark beetles to prescribed burning treatments. In: OMI, P.N., JOYCE, L.A. (Eds.). *Fire, Fuel Treatments, and Ecological Restoration: Conference Proceedings: 16-18 April 2002: Fort Collins, Colorado.* Fort Collins, CO, USDA Forest Service, Rocky Mountain Research Station, Proceedings RMRS-P-29, pp 143-158.
- GARCÍA-DOMÍNGUEZ, C., 2011. Impacto del fuego en los procesos ecológicos relacionados con el mantenimiento de la diversidad en pinares repoblados de Pinus canariensis. Tesis doctoral, Universidad de La Laguna, La Laguna.
- GARCÍA-DOMÍNGUEZ, C., FERNÁNDEZ-PALACIOS, J.M., 2009. Effect of Fire Intensity on Non-Native Plant Species Community in a Canarian Pine Forest Three and Eleven Years After Fire. *The Open Forest Science Journal* 2: 70-77.
- GARCÍA-TALAVERA, F., SÁNCHEZ-PINTO, L., SOCORRO, S., 1995. Vegetales fósiles en el complejo traquítico-sienítico de Gran Canaria. *Revista de la Academia Canaria de Ciencias* 7: 77-91.
- GÉNOVA, M., SANTANA, C., 2006. Crecimiento y longevidad en el pino canario (*Pinus canariensis* Smith.). *Investigación Agraria: Sistemas y Recursos Forestales* **15**: 296-307.
- GERNANDT, D. S., LOPEZ, G. G., GARCIA, S. O., LISTON, A., 2005. Phylogeny and classification of *Pinus*. *Taxon* **54**: 29-42.
- HIBBS, D.E., FISCHER, B.C., 1979. Sexual and vegetative reproduction of striped mapple (*Acer pennsylvanicum* L.). *Bulletin of the Torrey Botanical Club* **106**: 222-227.
- HÖLLERMANN, P., 2000. The impact of fire in Canarian ecosystems 1983-1998. *Erdkunde* **54**: 70-75.
- KASAPLIGIL, B., 1976. A late-Tertiary conifer-hardwood forest from the vicinity of Güvem village, near Kizilkahamam, Ankara. *Bulletin of the Mineral Research and Exploration Institute of Turkey* 88: 25-33.
- KEELEY J.E., ZEDLER P.H., 1998. Evolution of life histories in *Pinus*. In: RICHARDSON, D.M. (Ed.). *Ecology and Biogeography of* Pinus. Cambridge University Press, Cambridge, pp. 219-251.
- KNAPP, E.E., KEELEY, J.E., BALLENGER, E.A., BRENNAN, T.J., 2005. Fuel reduction and coarse woody debris dynamics with early season and late season prescribed fires in a Sierra Nevada mixed conifer forest. *Forest Ecology and Management* **208**: 383-397.
- KOVAR-EDER, J., 1987. Pannonian (Upper Miocene) Vegetational Character and Climatic Inferences in the Central Paratethys Area. *Annalen des Naturhistorischen Museums in Wien* 88: 117-129.

- KUENZI, A.M., FULÉ, P.Z., SIEG, C.H., 2008. Effects of fire severity and pre-fire stand treatment on plant community recovery after a large wildfire. *Forest Ecology and Management* **255**: 855-65.
- LISTON, A., ROBINSON, W. A., PIÑERO, D., ALVAREZ-BUYLLA, E. R., 1999. Phylogenetics of *Pinus (Pinaceae)* based on nuclear ribosomal DNA internal transcribed spacer sequences. *Molecular Phylogenetics and Evolution* **11**: 95-109.
- MCHUGH, C.W., KOLB, T.E., WILSON, J.L., 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. *Environmental Entomology* **32**: 510-522.
- MÉNDEZ, J., 2010. Análisis del impacto del fuego en la regeneración sexual del pino canario a lo largo de una cronosecuencia de incendios en la isla de La Palma (Canarias). Tesis doctoral, Universidad de La Laguna, La Laguna.
- MILLAR, C.I., 1993. Impact of the Eocene on the evolution of *Pinus L. Annals of the Missouri Botanical Garden* **80**: 471-498.
- MILLER, C., URBAN, D.L., 2000. Connectivity of forest fuels and surface fire regimes. *Landscape Ecology* **15**: 145–154.
- MORALES, G., 2010. Análisis del impacto del fuego en la composición específica, estructura y función del pinar canario a lo largo de una cronosecuencia de incendios en la isla de La Palma (Canarias). Tesis doctoral, Universidad de La Laguna, La Laguna.
- MORLA, C., ALCALDE, C., BARRÓN, E., POSTIGO, J.M., 2002. Paleobiogeografía de *Pinus canariensis*: estróbilos y semillas fósiles del Plioceno ibérico (cuenca del Bajo Segura, Alicante, España). In: BELTRÁN, E., AROZENA, M.A., DORTA, P.J., (Eds.). *La biogeografía: ciencia geográfica y ciencia biológica: actas del II Congreso Español de Biogeografía, La Gomera,* 2002, pp. 311-323.
- OTTO, R., GARCÍA-DEL-REY, E., MÉNDEZ, J., FERNÁNDEZ-PALACIOS, J.M., 2012. Effects of thinning on seed rain, regeneration and understory vegetation in a *Pinus canariensis* plantation (Tenerife, Canary Islands). *Forest Ecology and Management* **280**: 71-81.
- PARSONS, J.J., 1981. Human Influences on the Pine and Laurel Forests of the Canary Islands. *Geographical Review* **71**: 253-271.
- RODRIGO, A., RETANA, J., 2006. Post-fire recovery of ant communities in Submediterranean *Pinus nigra* forests. *Ecography* **29**: 231-239.
- RODRÍGUEZ, A., DURÁN, J., FERNÁNDEZ-PALACIOS, J.M., GALLARDO, A., 2009. Wildfire changes the spatial pattern of soil nutrient availability in *Pinus canariensis* forests. *Annals of Forest Science* **66**: article 210. DOI: 10.1051/forest/2008092.
- SABO, K.E., CAROLYN, H.S., HART, S.C., BAILEY, J.D., 2009. The role of disturbance severity and canopy closure on standing crop of understory plant species in ponderosa pine stands in northern Arizona, USA. *Forest Ecology and Management* **257**: 1656-1662.
- SAKAI, A., 1971. Freezing resistance of relicts from Arcto-Tertiary flora. *New Phytologist* **70**: 1199–1205.
- SILVERTOWN, J.W., 1982. Introduction to Plant Population Ecology. Longman, London, 209 pp.

- SULLIVAN, B.T., FETTIG, C.J., OTROSINA, W.J., DALUSKY, M.J., BERISFORD, C.W., 2003. Association between severity of prescribed burns and subsequent activity of coniferinfesting beetles in stands of longleaf pine. *Forest Ecology and Management* **185**: 327-340.
- TAKAOKA, S., SASA, K., 1996. Landform effects on fire behaviour and post-fire regeneration in the mixed forests of northern Japan. *Ecolological Research* **11**: 339-349.
- TAPIAS, R., GIL, L., FUENTES-UTRILLA, P., PARDOS, J.A., 2001. Canopy seed bank in Mediterranean pines of southeastern Spain: a comparison between *Pinus halepensis* Mill., *P. pinaster* Ait., *P. nigra* Arn. and *P. pinnea* L. *Journal of Ecology* **89**: 629-638.
- TURNER, M.G., HARGROVE, W.W., GARDNER, R.H., ROMME, W.H., 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *Journal of Vegetation Science* 5: 731–742.
- WANG, X. R., TSUMURA, Y., YOSHIMARU, H., NAGASAKA, K., SZMIDT, A. E., 1999. Phylogenetic relationships of Eurasian pines (*Pinus*, *Pinaceae*) based on chloroplast *rbc*L, *mat*K, *rp*120-*rps*18 spacer, and *trn*V intron sequences. *American Journal of Botany* **86**: 1742-1753.

Entregue para publicação em falta Aceite para publicação em falta