Biodiversity and Conservation **13:** 493–500, 2004.

Herbivory and climatic warming: a Mediterranean outbreaking caterpillar attacks a relict, boreal pine species

JOSÉ A. HÓDAR* and REGINO ZAMORA
*Grupo de Ecología Terrestre, Departamento de Biología Animal y Ecología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain; *Author for correspondence (e-mail: jhodar@ugr.es; fax: +34-958-243238)*

Received 9 August 2002; accepted in revised form 29 January 2003

Key words: Climatic warming, Herbivory, Mediterranean mountains, Outbreaks, Plant–insect interactions, Range limits

Abstract. Climate change can harm many species by disrupting existing interactions or by favouring new ones. This study analyses the foreseeable consequences of climatic warming in the distribution and dynamics of a Mediterranean pest that causes severe defoliation, the pine processionary caterpillar *Thaumetopoea pityocampa*, and the effects upon the relict Andalusian Scots pine *Pinus sylvestris nevadensis* in the Sierra Nevada mountains (southeastern Spain). We correlated a set of regional data of infestation by *T. pityocampa* upon Scots pine, from a broad ecological gradient, with climatic data for the period 1991–2001, characterized by alternating warm and cold winters. Defoliation intensity shows a significant association with previous warm winters, implying that climatic warming will intensify the interaction between the pest and the Scots pine. The homogeneous structure of the afforested pine woodlands favours the outbreak capacity of the newcomer, promoting this new interaction between a Mediterranean caterpillar pest and a boreal tree at its southern distribution limit.

Introduction

Climatic change can have a major effect on many species, both directly by altering the impact of environmental conditions as well as indirectly by changing their phenology and geographical ranges (Possingham 1993; Parmesan et al. 1999; Peñuelas and Filella 2001; Thomas et al. 2001). Several studies have investigated the effects of global change on interactions between plants and outbreaks of insect herbivores (Landsberg and Stafford Smith 1992; Ayres 1993; Williams and Liebhold 1995; Neuvonen et al. 1999; Volney and Fleming 2000), predicting a growing outbreak capacity among defoliating insects. The change in distribution area of the interacting species will disrupt the established interactions, since they will begin to overlap with other species with which previous interactions have been limited or null (Bezemer and Jones 1998; Harrington et al. 1999; Whittaker 2001; Bale et al. 2002), altering the structure and functioning of communities (Peñuelas et al. 2002). However, evidence of such effects is mostly limited to temperate and cold ecosystems of northern latitudes, and to a few species (Parmesan et al. 1999; Bale et al. 2002; Peñuelas et al. 2002).

Altitudinal gradients in mountains may mimic, on a narrower spatial and temporal scale, changes taking place in latitudinal gradients while maintaining a similar habitat and photoperiod (see e.g. Whittaker and Tribe 1996; Fielding et al. 1999), thus providing a good framework to analyse these processes and predict the biological consequences of global change. If the interactive species differ in their speed of altitudinal migration, the interaction may be disrupted.

In this study, we analyse the foreseeable consequences of climatic change in the distribution and dynamics of a Mediterranean defoliating caterpillar, *Thaumetopoea pityocampa* (Denis and Schiff.), and the impact upon the relict populations of Andalusian Scots pine *Pinus sylvestris* (L.) *nevadensis* Christ in Sierra Nevada (southern Spain). Several factors suggest that this framework is a good case in point. First, the Mediterranean basin is one of the areas where the effects of climate change will be the most pronounced, with a registered steady increase in temperatures during the last century (Esteban-Parra et al. 1995; Piñol et al. 1998; Rodó and Comín 2001). Within this general warming trend, the fluctuations from very warm to very cold years in the 1990s (Junta de Andalucía 2001) provide the opportunity to anticipate and experiment with the conditions that will predominate in the future.

Second, *T. pityocampa* is a pest in most Mediterranean pine woodlands, feeding on several *Pinus* species, from sea level to ca. 1500 m in altitude. The larva develops during winter, and its population dynamics depend heavily on winter temperatures, while the moth emerges, mates and oviposits during summer (see Demolin 1969; Huchon and Demolin 1971; Breuer et al. 1989; Halperin 1990; Masutti and Battisti 1990; Hódar et al. 2002 for more details on the biology of the species).

Third, several species of the genus *Pinus* show altitudinal replacement in Mediterranean mountains (Ceballos and Ruiz de la Torre 2001). In the Sierra Nevada, the usual zone of attack by the pine processionary caterpillar is covered by Black pine (*P. nigra*), while the upper climatic belt presents the Andalusian Scots pine (Figure 1). This endemic variety of the widely distributed Scots pine is restricted to two isolated populations of $<5\ km^2$ each (Catalán 1991). Due to the altitude at which it grows, Scots pine is not among the usual hosts of *T. pityocampa* in nature (Torrent 1958; Demolin 1969; Huchon and Demolin 1971), although the caterpillar develops quite well when fed Scots pine needles in laboratory tests (Hódar et al. 2002).

Material and methods

Field work has been performed in eastern Andalusia (southeastern Spain), in the Protected Area of Sierra Nevada. During the years 1997–1999, a severe plague of *T. pityocampa* heavily defoliated most pine woodlands in this area (Hódar et al. 2002, 2003). The incidence of *T. pityocampa* was analysed, at a regional scale, with the infestation data from the Andalusian Environmental Council (Consejería de Medio Ambiente). A total of 22 pine stands, from 25 to 316 ha each in size, were monitored during the period 1991–2001, i.e. a total surface of 3526 ha of pine forest was surveyed. Every winter, trained rangers evaluated the degree of infestation in the

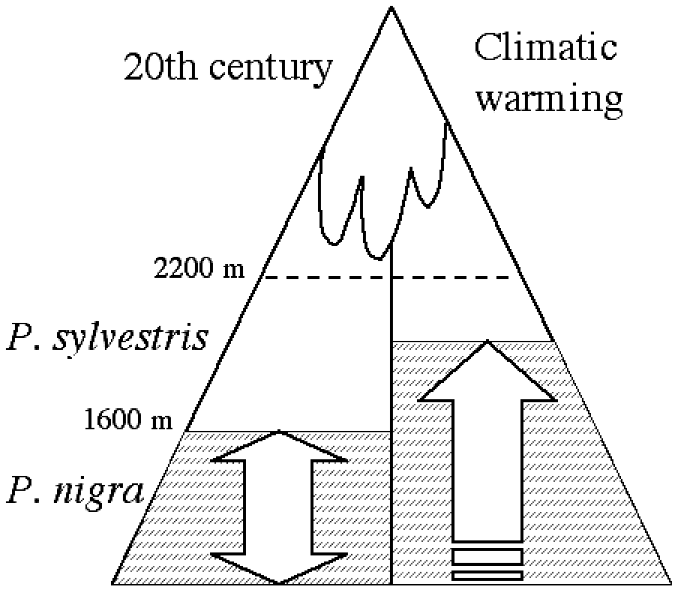

Figure 1. Schematic diagram of the *Pinus* spp. distribution in the mid-high mountain of Sierra Nevada (southeastern Spain), and the altitudinal range at which *T. pityocampa* lives. Until now (20th century, left), *P. sylvestris* was out of the activity range of *T. pityocampa* (double arrow), which lived mainly upon *P. nigra* at lower altitudes, below 1600 m (the old interaction area, stripped). In the current and future scenario (climatic warming, right), optimal climatic belts for all species will move upwards, but the speed of this movement will be quicker for insects (arrow upwards) than for plants. The interaction area of *T. pityocampa* with *Pinus* spp. will move uphill (emerging interaction area, stripped), but in the upper part the host plant will be *P. sylvestris* instead of *P. nigra*, then establishing a new plant–insect interaction.

marked pine stands, according to six categories: 0% defoliation = no infestation, 10% = scattered nests, scant defoliation, 25% = defoliation and nests visible at the stand borders, 50% = strong defoliation and numerous nests at the stand borders, some defoliation at the centre, 75% = very heavy defoliation both at the borders and the centre of stands, and 100% = massive defoliation, almost no foliage remaining. Pine stands were distributed in a region of ≈200 km^2, ranging between 1300 and 2200 m a.s.l., covering different landscape units (from natural forest to afforested woodlands), and different types of soil (from calcareous to siliceous). Scots pine, both autochtonous and afforested, is the main species in all the stands, although there is some mixture with other pine species (*P. nigra*, *P. pinaster*) at lower altitudes and, more rarely, with broadleaf tree species.

Climatic data were provided by a meteorological station situated at the Huenes valley (37°05′ N, 3°28′ W, 1680 m a.s.l.), all pine stands being within an 8-km radius from the meteorological station. Climatic data were available for the period 1991–2001, except for the year 1995, which was completely lacking – data for this year were estimated by correlating from a nearby station (15 km away; $R^2 = 0.93$). Average minimum winter temperature (November–February) was estimated for every stand as a function of its mean altitude, by using the altitudinal correction proposed by Roldán et al. (1996) for Sierra Nevada. For a better fit with the biological cycle of the plague, we considered year as the period October–September – that is, year 1999 refers to October 1998–September 1999, and winter 1999 refers to November 1998–February 1999.

Results and discussion

The period 1992–2001 fluctuated sharply in defoliation intensity, with averages from nearly 0 to 50% (Figure 2), although stands with massive defoliations were common during the years of outbreak. Winters 1998–2000 showed generally strong defoliation, but far weaker in the period 1995–1997 as well as 2001. The similarities between the intensity of defoliation and the temperature profile imply a climatic basis for the population dynamics of *T. pityocampa*, but also suggest a delayed response to the climatic conditions (Figure 2; see Hódar et al. 2001). In effect, the regression between defoliation and temperature in the same winter was not significant ($F_{1,8} = 0.002$, $P > 0.96$, $R^2 = 0.016$), while using temperature for the previous winter was ($F_{1,8} = 6.129$, $P = 0.038$, $R^2 = 0.434$), indicating a direct link between the climate experienced by *T. pityocampa* and the defoliation incidence the following winter. The basis for this 1-year delay is the life cycle of *T. pityocampa*: the mild winter promotes the survival of larvae that pupate and emerge as adults the next summer. This large number of adults mate and oviposit during summer, and produce the cohort of larvae that will cause defoliation the next winter. This agrees with the well established fact that winter temperature strongly determines the larval survival of *T. pityocampa* (Demolin 1969; Huchon and Demolin 1971; Breuer et al. 1989; Halperin 1990).

Since the rising temperatures found in the Iberian Peninsula during the past

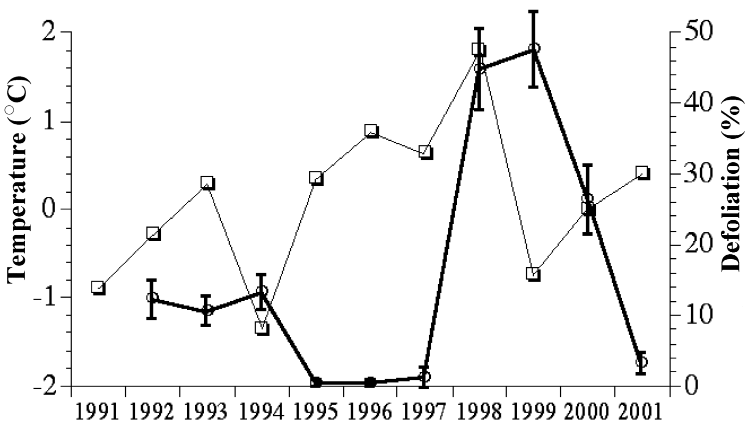

Figure 2. Mean minimum winter temperature (thin line with squares) at the Jardín Botánico de La Cortijuela (Sierra Nevada), and mean (solid line with open dots ±1 SE) percentage of defoliation for the 22 pine stands considered in this study, during the period October 1990–September 2001.

century result mainly from warmer winter temperatures (Esteban-Parra et al. 1995), it can be assumed that new climatic conditions will enable *T. pityocampa* outbreaks at altitudes higher than the present limits, thus coinciding with the distribution of the Scots pine populations. In agreement with this hypothesis, during the winters of 1997 and 1998 (the warmest of the 20th century; Junta de Andalucía 1998; see also Figure 2), the upper limit of massive defoliations by *T. pityocampa* was recorded at unusual altitudes in the *P. sylvestris* populations (2000–2100 m a.s.l.; personal observation). Among the stands analysed, 70.4% of the stands situated >1700 m a.s.l. showed 25% or higher defoliation during the winters 1998–2000, after the 'warming pulse' of 1996–1998 (see Figure 2), with some stands approaching 100%. By contrast, during the previous years (1992–1997) defoliation averaged 5% in these higher stands, and a scant 8% of them reached 25% defoliation. This also agrees with recent records in other parts of Spain, such as the Pyrenees, where *T. pityocampa* was found at 2000 m on *P. uncinata* (R. Montoya, personal communication), but sharply disagrees with older findings on this processionary in the mid-20th century. Huchon and Demolin (1971) fixed 1600 m as the maximum altitude at which the species lives in southern France, while Torrent (1958) noted that, in central Spain, it attacks Scots pine only in the lower (1300 m) part of the pine's distribution area.

The natural regeneration of Andalusian Scots pine in Mediterranean mountains is seriously limited by low seed production, high seed predation, and poor seedling survival due to summer drought (Castro et al. 1999; Castro 2000). Once juveniles are established, the high herbivory pressure by wild and domestic ungulates limits tree growth, especially in the treeline areas, where herbivory upon pines is stronger (Hódar et al. 1998; Gómez et al. 2001; Zamora et al. 2001). By contrast, adults are relatively immune to these problems. However, if winter warming increases the frequency and intensity of the episodic and massive defoliation by *T. pityocampa*, adult pines will deplete their reserves, causing: (1) a reduced seed production (Hódar et al. 2003), further collapsing the regeneration cycle, and (2) a limited response capacity against other negative factors, such as drought or adverse weather. This will hasten mortality in the, until now, long-lived adults (Hódar et al. 2001, 2003).

Warmer winter temperatures are currently triggering an uphill displacement of pests limited by low temperature (Ayres 1993; Neuvonen et al. 1999; Bale et al. 2002). This promotes a new interaction between a non-specialist Mediterranean caterpillar pest, *T. pityocampa*, with a boreal, suitable host occupying the Mediterranean high-mountain, the Scots pine. However, the outcome of this plant–herbivore emerging interaction is mediated by the structure of the habitat where the interaction takes place (Masutti and Battisti 1990; Watt 1992; Hill et al. 1999, 2001). Several authors have shown stable caterpillar populations in diversified habitats with mixed plant species and outbreaks when the habitats are extensive, homogeneous woodlands, or regular plantations (Tammaru et al. 1995; Floater and Zalucki 2000). In Mediterranean mountains, the remnant natural pine woodlands are small fragments of low-density forest, usually mixed (e.g. with *Quercus* spp.; Mesón and Montoya 1993). A forest structure with suitable hosts in a density low enough and scattered among different, unsuitable tree species hosts would dilute the effect of the population explosion. In contrast, the massive pine plantations in Mediterranean mountains during the last century (Junta de Andalucía 1990; Masutti and Battisti 1990) created a new scenario prone to pest spread. A homogeneous, extensive stand of planted pines, characterized by monospecific, even-aged stands, high density, regular spacing, and low variability among individuals, created a habitat in which *T. pityocampa* moths easily find suitable hosts. Therefore, the potential negative consequences of this new, emerging interaction are the synergic result of climatic warming, which favours uphill displacements, and humanized, homogeneous Scots pine woodlands, which represent a 'culture medium' promoting the outbreaking capacity of the newcomer. Clearly, an ecologically healthy way to mitigate *T. pityocampa* outbreaks in its new high-mountain woodland habitat is to manage these homogeneous stands, drastically reducing pine density in afforested woodlands, increasing species diversity in both autochthonous and afforested pine stands, encouraging the spread of non-*Pinus* species (e.g. *Acer*, *Quercus* or *Taxus*) and, consequently, increasing the diversity and spatial heterogeneity of the pine woodlands to resemble the original forests in the Mediterranean mountains.

Acknowledgements

We thank the Consejería de Medio Ambiente, Junta de Andalucía, and the Direction of the National Park, for permission to work in the Sierra Nevada. José M. Irurita provided the data of the defoliation in the pine stands, and Joaquín and Angel kindly provided the climatic data. D. Ramón Montoya offered unpublished data on *T. pityocampa* dynamics in the Pyrenees. José M. Gómez, Seppo Neuvonen and several anonymous referees gave helpful suggestions that improved the manuscript. Julie Bowen and David Nesbitt looked over the English version of the manuscript. This study was supported by projects AGF99-0618 and FEDER 1FD97-0743-CO3-02.

References

Ayres M.P. 1993. Plant defence, herbivory, and climate change. In: Kareiva P.M., Kingsolver J.G. and Huey R.M. (eds), Biotic Interactions and Global Change. Sinauer Associates, Sunderland, Massachusetts, pp. 75–94.

Bale J.S., Masters G.J., Hodkinson I.D., Awmack C., Bezemer T.M., Brown V.K. et al. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology 8: 1–16.

Bezemer T.M. and Jones T.H. 1998. Plant–insect herbivore interactions in elevated atmospheric CO_2: quantitative analyses and guild effects. Oikos 82: 212–222.

Breuer M., Devkota B., Douma-Petridou E., Koutsaftikis A. and Schmidt G.H. 1989. Studies on the exposition and temperature of nests of *Thaumetopoea pityocampa* (Den. and Schiff.) (Lep. Thaumetopoeidae) in Greece. Journal of Applied Entomology 107: 370–375.

Castro J. 2000. Dinámica de la regeneración de los pinares autóctonos de Pino silvestre (*Pinus sylvestris*

L. var. *nevadensis* Christ) de Sierra Nevada y Sierra de Baza, Ph.D. Thesis, University of Granada, Granada, Spain, 185 pp.

Castro J., Gómez J.M., García D., Zamora R. and Hódar J.A. 1999. Seed predation and dispersal in relict Scots pine forests from south Spain. Plant Ecology 145: 115–123.

Catalán G. 1991. Las regiones de procedencia de *Pinus sylvestris* L. y *Pinus nigra* Arn. subsp. *salzmannii* (Dunal) Franco en España. ICONA, Madrid, Spain.

Ceballos L. and Ruiz de la Torre J. 2001. Árboles y arbustos de la España peninsular. Mundi-Prensa, Madrid, Spain.

Demolin G. 1969. Bioecología de la procesionaria del pino *Thaumetopoea pityocampa* Schiff. Incidencia de los factores climáticos. Boletín del Servicio de Plagas Forestales 12: 9–24.

Esteban-Parra M.J., Rodrigo F.S. and Castro-Díez Y. 1995. Temperature trends and change points in the northern Spanish plateau during the last 100 years. International Journal of Climatology 15: 1031–1042.

Fielding C.A., Whittaker J.B., Butterfield J.E.L. and Coulson J.C. 1999. Predicting responses to climate change: the effect of altitude and latitude on the phenology of the spittlebug *Neophilaenus lineatus*. Functional Ecology 13: 65–73.

Floater G.J. and Zalucki M.P. 2000. Habitat structure and egg distribution in the processionary caterpillar *Ochrogaster lunifer*: lessons for conservation and pest management. Journal of Applied Ecology 37: 87–99.

Gómez J.M., Hódar J.A., Zamora R., Castro J. and García D. 2001. Ungulate damage by Scots pines in Mediterranean environments: effects of association with shrubs. Canadian Journal of Botany 79: 739–746.

Halperin J. 1990. Life history of *Thaumetopoea* spp. (Lep. Thaumetopoeidae) in Israel. Journal of Applied Entomology 110: 1–6.

Harrington R., Woiwod I. and Sparks T. 1999. Climate change and trophic interactions. Trends in Ecology and Evolution 14: 146–150.

Hill J.K., Collingham Y.C., Thomas C.D., Blakeley D.S., Fox R., Moss D. et al. 2001. Impacts of landscape structure on butterfly range expansion. Ecology Letters 4: 313–321.

Hill J.K., Thomas C.D. and Huntley B. 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margins. Proceedings of the Royal Society of London B 266: 1197–1206.

Hódar J.A., Castro J., Gómez J.M., García D. and Zamora R. 1998. Effects of herbivory on growth and survival of seedlings and saplings of *Pinus sylvestris nevadensis* in SE Spain. In: Papanastasis V.P. and Peter D. (eds), Ecological Basis of Livestock Grazing in Mediterranean Ecosystems. Official Publications of the European Communities, Luxembourg, pp. 264–267.

Hódar J.A., Castro J. and Zamora R. 2003. Pine processionary caterpillar *Thaumetopoea pityocampa* as a new threat for relict Mediterranean Scots pine forests under climatic warming. Biological Conservation 110: 123–129.

Hódar J.A., Zamora R. and Castro J. 2002. Host utilisation by moth and larval survival of pine processionary caterpillar *Thaumetopoea pityocampa* in relation to food quality in three *Pinus* species. Ecological Entomology 27: 292–301.

Hódar J.A., Zamora R., Castro J. and Baraza E. 2001. The effect of an outbreak of pine processionary caterpillar in the autochthonous woodlands of Sierra Nevada (SE Spain): suggestions for the plague control. In: Radoglou K. (ed.), Forest Research: A Challenge for an Integrated European Approach Vol. 1. NAGREF, Forest Research Institute, Thessaloniki, Greece, pp. 327–332.

Huchon H. and Demolin D. 1971. La bioécologie de la procesionnaire du pin. Dispersion potentielle – dispersion actuelle. Phytoma 225: 11–20.

Junta de Andalucía 1990. Plan Forestal Andaluz, Documento de Síntesis. Consejería de Agricultura y Pesca, IARA, Agencia de Medio Ambiente. Junta de Andalucía, Seville, Spain.

Junta de Andalucía 1998. Medio Ambiente en Andalucía. Informe 1997. Consejería de Medio Ambiente, Junta de Andalucía, http://www.cma.junta-andalucia.es/ima1997/ima1997.html.

Junta de Andalucía 2001. Medio Ambiente en Andalucía. Informe 2000. Consejería de Medio Ambiente, Junta de Andalucía, http://www.cma.junta-andalucia.es/ima2000/ima2000.html.

Landsberg J. and Stafford Smith M. 1992. A functional scheme for predicting the outbreak potential of herbivorous insects under global atmospheric change. Australian Journal of Botany 40: 565–577.
Masutti L. and Battisti A. 1990. *Thaumetopoea pityocampa* (Den. and Schiff.) in Italy. Bionomics and perspectives of integrated control. Journal of Applied Entomology 110: 229–234.
Mesón M. and Montoya M. 1993. Selvicultura mediterránea. Mundi-Prensa, Madrid, Spain.
Neuvonen S., Niemelä P. and Virtanen T. 1999. Climatic change and insect outbreaks in boreal forests: the role of winter temperatures. Ecological Bulletin 47: 63–67.
Parmesan C., Ryrholm N., Stefanescu C., Hill J.K., Thomas C.D., Descimon H. et al. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399: 579–583.
Peñuelas J. and Filella I. 2001. Responses to a warming world. Science 294: 793–794.
Peñuelas J., Filella I. and Comas P. 2002. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. Global Change Biology 8: 531–544.
Piñol J., Terradas J. and Lloret F. 1998. Climate warming, wildfire hazard, and wildfire occurrence in coastal eastern Spain. Climatic Change 38: 345–357.
Possingham H.A. 1993. Impact of elevated CO_2 on biodiversity: mechanistic population-dynamic perspective. Australian Journal of Botany 41: 11–21.
Rodó X. and Comín F. 2001. Fluctuaciones del clima mediterráneos: conexiones globales y consecuencias regionales. In: Zamora R. and Pugnaire F.I. (eds), Ecosistemas mediterráneos: análisis funcional. Textos universitarios no. 32, CSIC-AEET, Madrid, Spain, pp. 1–35.
Roldán C., Montávez J.P., Rodríguez A. and Jiménez J.I. 1996. Contribución al estudio del régimen térmico en la zona esquiable de Sierra Nevada. In: Chacón J. and Rosúa J.L. (eds), Sierra Nevada: conservación y desarrollo sostenible. Vol. 1. Universidad de Granada, Granada, Spain, pp. 55–70.
Tammaru T., Kaitaniemi P. and Ruohomäki K. 1995. Oviposition choices of *Epirrita autumnata* (Lepidoptera: Geometridae) in relation to its eruptive population dynamics. Oikos 74: 296–304.
Thomas C.D., Bodsworth E.J., Wilson R.J., Simmons A.D., Davies Z.G., Musche M. et al. 2001. Ecological and evolutionary processes at expanding range margins. Nature 411: 577–581.
Torrent J.A. 1958. Tratamientos de la procesionaria del pino (*Thaumetopoea pityocampa* Schiff.). Boletín del Servicio de Plagas Forestales 2: 65–80.
Volney W.J.A. and Fleming R.A. 2000. Climate change and impact of boreal forest insects. Agricultural Ecosystems and Environment 82: 283–294.
Watt A.D. 1992. Insect pest population dynamics: effects of tree species diversity. In: Cannell M.G.R., Malcolm D.C. and Robertson P.A. (eds), The Ecology of Mixed-Species Stands of Trees. Blackwell, Oxford, UK, pp. 267–275.
Whittaker J.B. 2001. Insects and plants in a changing atmosphere. Journal of Ecology 89: 507–518.
Whittaker J.B. and Tribe N.P. 1996. An altitudinal transect as an indicator of responses of a spittlebug (Auchenorrhyncha: Cercopidae) to climate change. European Journal of Entomology 93: 319–324.
Williams D.W. and Liebhold A.M. 1995. Forest defoliators and climate change: potential changes in spatial distribution of outbreaks of Western spruce budworm (Lepidoptera: Tortricidae) and Gypsy moth (Lepidoptera: Lymantriidae). Environmental Entomology 24: 1–9.
Zamora R., Gómez J.M., Hódar J.A., Castro J. and García D. 2001. The effect of browsing by ungulates on Scots pine growth in a Mediterranean environment: consequences for forest regeneration. Forest Ecology and Management 144: 33–42.