Effects of drought and heat on forest insect populations in relation to the 2003 drought in western Europe

Gaelle Rouault, Jean-Noël Candau, François Lieutier, Louis-Michel Nageleisen, Jean Claude Martin, Nathalie Warzée

To cite this version:

Gaelle Rouault, Jean-Noël Candau, François Lieutier, Louis-Michel Nageleisen, Jean Claude Martin, et al.. Effects of drought and heat on forest insect populations in relation to the 2003 drought in western Europe. Annals of Forest Science, 2006, 63 (6), pp.613-624. 10.1051/forest:2006044 . hal-02666012

HAL Id: hal-02666012
https://hal.inrae.fr/hal-02666012

Submitted on 31 May 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Copyright

Ann. For. Sci. 63 (2006) 613–624
© INRA, EDP Sciences, 2006
DOI: 10.1051/forest:2006044

Review

Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe

Gaëlle ROUAULT[a], Jean-Noël CANDAU*, François LIEUTIER[b], Louis-Michel NAGELEISEN[c], Jean-Claude MARTIN[a], Nathalie WARZÉE[d]

[a] Unité de Recherches Forestières Méditerranéennes, INRA, Domaine St-Paul, Site Agroparc, 84914 Avignon Cedex 9, France
[b] Université d'Orléans, Rue de Chartres, BP 6759, 45067 Orléans Cedex, France
[c] Ministère de l'agriculture, de l'alimentation, de la pêche et des affaires rurales, Département de la Santé des Forêts, Centre INRA de Nancy, 54280 Champenoux, France
[d] Lutte biologique et Écologie spatiale (LUBIES), CP 160/12, Université Libre de Bruxelles, 50 avenue FD Roosevelt, 1050 Bruxelles, Belgium

(Received 14 January 2006; accepted 21 June 2006)

Abstract – Although drought affects directly tree physiology and growth, the impact of secondary factors (insect pests, pathogens and fire) is often greater than the impact of the original stress and can lead to important tree mortality. In 2003, Western and Central Europe experienced a drought and heat waves that led to extensive forest damage. This paper reports on the impacts of drought and high temperatures on forest insect populations in the context of this exceptional event. Observations of changes in population levels of the main European forest insect pests during and after the drought are presented and discussed in the light of current knowledge and theories of interactions between drought and insects. We investigated the direct effects of drought on life history traits and indirect effects through physiological changes experienced by host trees. Forest pest insects were separated in 4 feeding guilds: woodborers, leaf-chewers, leaf-miners and leaf-suckers. The impact of water stress varied according to feeding guilds. Woodborers were positively influenced by prolonged water stress and the decline of host resistance. In contrast, defoliators profited better from the increased nitrogen in plant tissues linked to moderate or intermittent water stress. Field observations showed the importance of the soil water status in tree resistance against pest attacks. Thus, the 2003 drought confirmed observations from earlier droughts that, is case of bad choice of tree species in some plantations, site matching becomes a prominent and primary cause of the development of pest outbreaks. This exceptional drought may give us some indication of the impacts of extreme climatic events. However, observations of the performance at the individual level were not sufficient for predicting long-term insect population dynamics, which depends on complex interactions between biotic and abiotic factors.

climate change / drought / heat wave / forest pest insect / population dynamic

Résumé – Effet de la sécheresse et de la canicule de 2003 sur les populations d'insectes ravageurs forestiers en Europe centrale et occidentale. Bien que la sécheresse affecte directement la physiologie et la croissance des arbres, l'impact de facteurs secondaires (insectes ravageurs, pathogènes et feu) est souvent plus important que le stress original et peut conduire à la mortalité des arbres. En 2003, une sécheresse et des vagues de chaleur ont provoqué des dégâts importants dans les forêts d'Europe centrale et occidentale. Cet article rend compte de l'impact de la sécheresse et de la canicule sur les populations d'insectes forestiers dans le contexte de cet évènement exceptionnel. Les observations des fluctuations de populations des principaux insectes ravageurs des forêts européennes sont présentées et discutées en regard des connaissances actuelles et des théories des interactions entre sécheresse et insectes. Nous avons recherché les effets directs et indirects de la sécheresse, respectivement sur les traits d'histoire de vie et au travers des modifications physiologiques induites chez les arbres hôtes. Les insectes forestiers ont été séparés en 4 groupes : xylophages, phyllophages, mineuses et suceurs de sève. L'impact du stress hydrique a été différent selon la guilde considérée. Les xylophages ont été positivement influencés par le déclin de la résistance de l'hôte suite à un stress hydrique prolongé. Au contraire, les phyllophages ont mieux profité de l'augmentation de l'azote dans les tissus de la plante sous un stress hydrique modéré ou intermittent. Des observations de terrains ont montré l'importance du statut hydrique du sol sur le niveau de résistance des arbres contre les attaques de ravageurs. En certains sites, la sécheresse de 2003 a d'ailleurs mis en évidence des choix d'essences inappropriés. Cette sécheresse exceptionnelle peut nous donner des indications sur les impacts des événements climatiques extrêmes. Cependant les observations des performances au niveau individuel ne permettent pas de prédire à long terme les dynamiques des populations, lesquelles dépendent d'interactions complexes au niveau local entre facteurs biotiques et abiotiques.

changement climatique / sécheresse / canicule / insecte ravageur forestier / dynamique des populations

1. INTRODUCTION

Current climate change scenarios are predicting an increase in the frequency and intensity of summer drought and heat waves in western and central Europe [66]. Such extreme, large scale climatic events will likely be important drivers of change in the organization and functional attributes of forest ecosystems. Water stress and high summer temperatures have direct effects on tree physiology, phenology and ultimately, on the distribution and abundance of tree species [11, 37]. Indeed, temperature and soil moisture are the primary limiting factors of the natural range of most European forest tree species [13]. Prolonged drought and heat may also impact forest ecosystems

---

* Corresponding author: jean-noel.candau@avignon.inra.fr

Article published by EDP Sciences and available at http://www.edpsciences.org/forest or http://dx.doi.org/10.1051/forest:2006044

indirectly by interacting with natural disturbances such as insect pests, pathogens and fire. The impact of these secondary agents on tree mortality may be larger than the impact of the initial stress [6, 29, 90]. This may, however, greatly vary, especially according to the general condition of the forest and its management regime. Consequently, understanding the interactions between drought, heat, and natural disturbances may be critical in predicting the overall impact of future drought on forest ecosystems.

Historical archives suggest that the summer of 2003 was likely the warmest since 1500 [59]. In France, average monthly temperatures were greater than normal temperatures, calculated over the period 1976–2002, for every month from March to September [16, 78]. In addition to a general increase in mean monthly temperatures, two heat waves affected most of Western Europe, first in the beginning of June, then in the first half of August. At the same time, the soil moisture remained in deficit from April to November [16, 17]. This combination of extreme drought and very high temperatures made the 2003 event unprecedented. However, such event can be seen as a "shape of things to come" as it is predicted to occur with higher frequency under climate change [12, 46, 63].

In general, insects experience the effects of drought and heat directly through changes in life history traits, and indirectly through trophic feedbacks and interactions with other species and abiotic components of their environment. Consequently, insect responses are likely to be complex and dependant on host plant physiology and site characteristics. In addition, water stress impacts differently according to feeding guilds. While a moderate water-stress is thought to limit woodborer performances [53], in contrast, defoliator performances are usually enhanced in response to the increase in concentration of soluble nitrogen in foliage [50, 51, 60], either during drought or the following year. For both guilds, performances decline with severe stress because of the deterioration of host quality.

Many reviews have looked at the direct or indirect impacts of drought on insects at the individual level [45, 48, 50, 53, 60]. However, whether responses at this level will translate into effects at the population or community level will depend on the net result of complex interactions. The occurrence of the 2003 drought and heat wave over Western Europe has put a new emphasis on this question while giving the opportunity to observe the result of water stress and high temperatures on a variety of forest insects. The aim of this paper is to review the current observations of the impacts of the 2003 drought and heat wave on the major European forest insect species and discuss these observations in the light of current knowledge and theories of interactions between drought and insects. The study makes extensive use of the data collected by the French Forest Health program and therefore focuses on French forests although observations made in other European countries are reported when they were available. Two original research data about the pine processionnary moth and the spruce bark beetle and its parasitoid are reported. We hypothesize that the nature and the severity of these impacts will depend on regional characteristics (in relation to the severity and duration of climatic stresses), site characteristics, insect type (in relation to the feeding guild, ecology and population levels the previous years), and host type (in relation to its tolerance to stress).

2. DIRECT EFFECTS OF DROUGHT AND HEAT ON INSECT PERFORMANCES

Insect populations can often respond rapidly and dramatically to changes in climatic condition. In temperate forest ecosystems, warmer, drier weather is generally thought to promote per capita growth rates leading, in some cases, to population outbreaks [60, 89, 95]. An increase in temperature towards species optima will usually accelerate egg and larval development and, consequently, increase the chances of survival by reducing the time spent at development stages most susceptible to predation and parasitism. For multivoltine species, shorter development times may also lead to additional generations within a year [3, 95, 99]. High temperatures such as those experienced during the 2003 heat waves may have negative effects on insect populations. The relation between temperature and insects performances is usually dome-shaped. Hence, when temperatures increase above the optimal, growth rates will start to decrease [7, 88] as well as fecundity and survival [5, 45, 48]. In addition, changes in phenology that may allow a species to escape from predation may also desynchronize it with the phenology of its host plant leading to starvation [36, 55, 92, 100].

Water stress may increase the effects, whether positive or negative, of temperature as the temperature in and on drought-stressed plants are usually higher that ambient temperature [60]. In addition, low air humidity may shorten the life of insects through dehydration [3, 39, 95] but little is known about the effects at the population level.

The direct effects of temperature and drought on insects are likely to vary among species depending on the sensitivity of individual growth rates to increase temperatures [7], the life-stage at which they experience high temperatures and drought [3, 26, 42], their adaptation to warm, dry environments and climate extremes [27, 67], and their capacity to escape unfavourable environmental conditions [58].

2.1. Effects of summer heat on the survival of early instars of defoliators and aphids

Thaumetopoea pityocampa (Denis & Schiffermuller), the pine processionary moth, is one of the most damaging defoliator of conifers in France. Population levels of this insect are primarily related to the survival of first-instar larvae [27, 41, 99]. Eggs and young larvae are sensitive to high temperatures; an excess of heat or exposition to intense solar radiations may induce high levels of mortality [26]. The mortality of some larvae of *T. pityocampa* can also have an impact on the survival of the entire batch (group of larvae hatched from the same egg mass) because the ability to construct nests and consequently to survive over the winter, is dependent on the number of larvae per batch that reach late

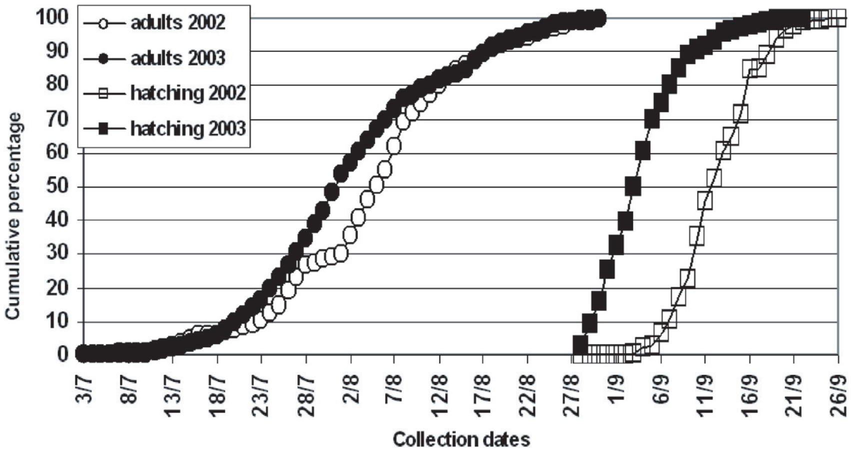

Figure 1. Daily distribution of adult flight and egg hatch for the pine processionary caterpillar, *Thaumetopoea pityocampa*, at Sainte Victoire (France, 5° 37" 21'; 43° 31" 23') in 2002 and 2003. Adult were captured with pheromonal traps charged with 1mg of pheromone. Egg masses were collected at the end of the adult flight period and placed individually in a 22 °C-climatized chamber until the end of egg hatch. An egg masse was considered as hatched when at least five eggs had hatched. During 2002 and 2003, temperatures were recorded daily in July and August.

instars [27, 42]. A large-scale survey carried by the French Forest Health Department in 2003–2004 [14, 15] reported an overall increase in egg and larval mortality, particularly in continental zones where winter-nests are essential to survive winter temperatures; whereas the Atlantic coast, under oceanic influence, was less concerned [14, 15]. This mortality may have stopped the outbreak that was expected from the population levels recorded during the winter of 2002–2003. In addition to this large-scale survey, an intensive study was conducted in southeastern France by a team of the Institut National de la Recherche Agronomique (INRA) in Avignon. Egg masses (1387 in 2002 and 1507 in 2003) were collected at the end of the flight period (end of August) and reared individually at 22 °C. The number of larvae hatching from these egg masses was recorded daily. Results showed that egg mortality rate in 2003 was low (9%) but significantly higher than in 2002 ($\text{Chi}^2 = 120.71$; $p < 0.01$). These differences could have resulted from differences in July and August mean temperatures. Mean temperatures during both months were below 25 °C in 2002; while in 2003 means exceeded 25 °C with a long period close to 30°C (mean daily temperatures were on average 4 °C higher in 2003 than in 2002). Despite higher mean temperatures in 2003, adult flight preceded the beginning of adult flight in 2002 by only 3 days, and the length of adult flight periods was quite similar. In 2003, egg hatch occurred before the first sample date and finished 6 days before what was observed in 2002 (Fig. 1). In 2003, 50% of the egg masses had hatched on August 3, preceding by 9 days the hatching date in 2002. Egg incubation period, calculated as the time between 50% hatch and 50% adult flight, was 33 days in 2003 and 38 days in 2002 (Fig. 1). After the 2003 drought, high levels of infestations, although not outbreak levels, were locally observed in the fall of 2004 in the West and Southwest of France, in the Southern Alps and in Corsica [15]. A mild 2003–2004 winter may have allowed remaining larvae to survive despite the overall bad quality of winter nests.

The impact of the 2003 summer drought and heat on gypsy moth (*Lymantria dispar* L.) populations is difficult to assess from the observations made to this day. Overall, the drought didn't seem to have affected populations of this insect [10].

Populations of broadleaf defoliators such as the small winter moth (*Operophtera brumata* L.) and the oak leaf roller moth (*Tortrix viridana* L.) increased in 2003 in France [31], Switzerland [65], the Czech Republic [23], and southeastern Sweden [57]. In 2004, populations were still increasing. These species accomplish their larval development early in the season (April-May). Consequently, they may have benefited from the warm spring of 2003 without suffering from the summer heat. This is particularly true for geometrids such as *O. brumata* as these species spend most of the warmest period of the year as nymphs in the ground. In 2005, high increase in population levels was reported in early defoliators [70].

Observations of aphid populations during and after 2003 reveal varying effects of drought on these insects. For the poplar woolly aphid, *Phloemyzus passerinii* (Sign.), climatic conditions in 2003 seemed to have favored its installation and outbreak, particularly in the NE of France [62]. However, the outbreak that was expected in 2004 in the same region did not materialize. Conversely, exceptionally high population levels of the beech woolly aphid, *Phyllaphis fagi* L. were observed in 2004 (Fig. 2) following a period of latency of several years. Vigorous host, i.e. poplar stands with elevated temperatures, high moisture and no direct light, usually favors aphid development [5, 62]. However, direct solar radiations and low moisture may impact negatively aphid populations.

2.2. Effects of elevated temperatures and drought on bark beetle development

Bark beetle populations were generally high since the 1999 "Lothar" storm that affected Western Europe, but were starting

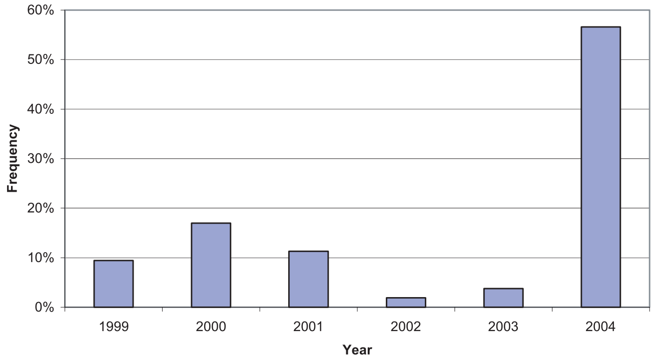

Figure 2. Frequency of reports of beech woolly aphid, *Phyllaphis fagi* L., damage in France between 1999 and 2004 (total number of records = 53). Data were extracted from the database of the French Forest Health Department.

to decrease prior to 2003. The spruce bark beetle (*Ips typographus* L.) and the pine bark beetle (*Pityogenes chalcographus* L.) accounted for most of the damage. In Northeastern France, the volume of wood affected reached 380 000 m^3 in 2003, an increase of 29% from 2002 (Fig. 3). In Switzerland, damages reached a record level of 2 000 000 m^3 of wood infested [99]. Record levels of damage were also recorded in Germany [4] and Austria [49]. In the Czech Republic, the volume of timber infested reached 1 246 000 m^3, five times the volume recorded in 2002 [23].

Bark beetle development is directly affected by phloem temperature, which in turn is dependent on air temperature and direct solar radiation [95]. Although the increase in temperature observed in 2003 generally favoured woodborers, extreme temperatures experienced during the heat waves may have had negative effects on their performance and dispersal [3].

High spring temperatures lead to early flights of wintering adults and, in most locations, to an extra generation in the year. The minimum temperature threshold for the development of *I. typographus* is 16.5 °C with an optimum between 22–26 °C [94]. In 2003, captures of *I. typographus* in Northeastern France (Fig. 4) began earlier in the season than usually. In France and Switzerland, *I. typographus* developed two generations at low altitude and three generations in some stands in the plains instead of respectively one or two usually observed [64, 68]. However, at the beginning of August the number of adults captured had decreased, probably due to the effect of the heat wave that prevented adult from flying [3].

The French Forest Health Department also observed that the heat wave during the first two weeks of August 2003 stopped the development of most woodborer species [97]. Surveys indicated high levels of egg and larval mortality. Temperature inside the egg galleries exposed to direct sunlight has been shown to exceed 50 °C, a fatal temperature for larvae, pupae and adults [3, 68]. The same level of mortality did not seem to have occurred in *I. typographus* populations. Damages from this insect continued to increase in 2004 (Fig. 3).

The increase in temperature enhances the development rate of *Pityokteines curvidens* (Germ.) which may result in the development of a second generation the same year [1]. In Switzerland, where even a third generation was observed in some areas, populations of *P. curvidens* reached outbreak level for the first time in 40 years [71]. This insect was responsible for damages on 100 000 m^3 of timber in Switzerland and more than 50 000 m^3 in Northeastern France [68]. In addition, populations of the silver fir weevil, *Pissodes piceae* (Illiger) were reported on the rise in France in 2003 [68]. *P. piceae* oviposits on trunk within cavities [1]. Adults and larvae undergo a period of summer dormancy during summer heat. Larvae located in galleries under the bark usually develop slowly in summer and autumn and then resume their development in spring. Increase of heat in galleries may have accelerated the development and allowed larvae to enter winter at more advanced and resistant instars, then resulted in higher population levels the following year. However, for this species of secondary pest, outbreaks occur only if increase in insect population are associated with a weakening of the host tree and a decrease of its resistance level [68].

2.3. Impacts on insect phenology in interaction with host phenology

For many defoliators of temperate forests synchrony in phenology between budburst and larval development is determinant to growth and survival of these defoliators [83, 91, 92]. A good synchronization between hatching and budburst allows larvae to feed on soft and young foliage, with high food quality [5, 30, 36]; see also indirect effects).

For geometrids, generalist defoliators of broadleaf trees such as *O. brumata*, larvae feeding on ageing foliage show declining growth rates and increasing dispersal with a dramatic increase in mortality since this dispersal is passive [19, 82, 83]. Consequently, a differential effect of warmer temperatures on budburst and larval phenology would have marked effects on the abundance of this species in extreme years such as 2003. However the potential for increased temperature to desynchronize *O. brumata* phenology with its host's is still controversial [19, 91]. In France, an outbreak of *O. brumata* had already started in 2002. Defoliation due to this insect, locally in association with *Tortrix viridana* L., continued to increase in 2003 and 2004 in the north-eastern regions [21, 32]. In Switzerland, the extent of the defoliation observed in 2004 indicated that the 2003 conditions were favourable to the survival and growth of *O. brumata* populations [65]. Noticeable levels of defoliation by this insect were also recorded in the Czech Republic [23] and in Germany [4]. These observations tend to indicate that the 2003 drought and heat did not have a negative effect on *O. brumata* or other geometrids populations.

2.4. Impacts on distribution

The impact of an increase in mean temperature on the distribution of forest insects has been well documented (e.g. [6, 7, 9, 15, 41, 86]). The geographic distribution of many forest insects is more limited than their host distribution; therefore,

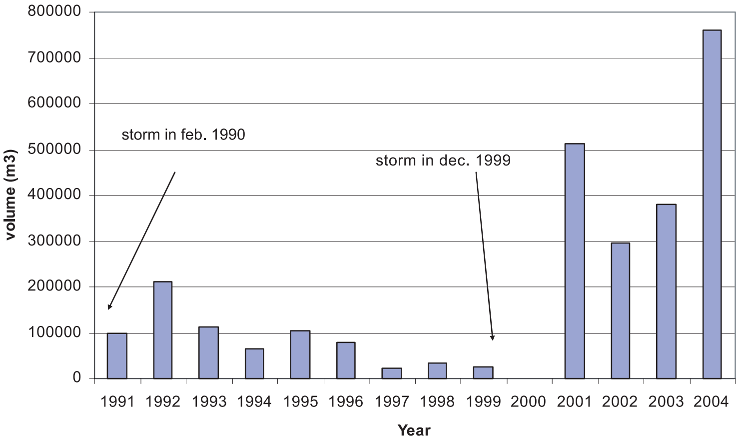

Figure 3. Annual volume of spruce timber salvaged from bark beetle infestation in France reported by the French Forest Health Department [97].

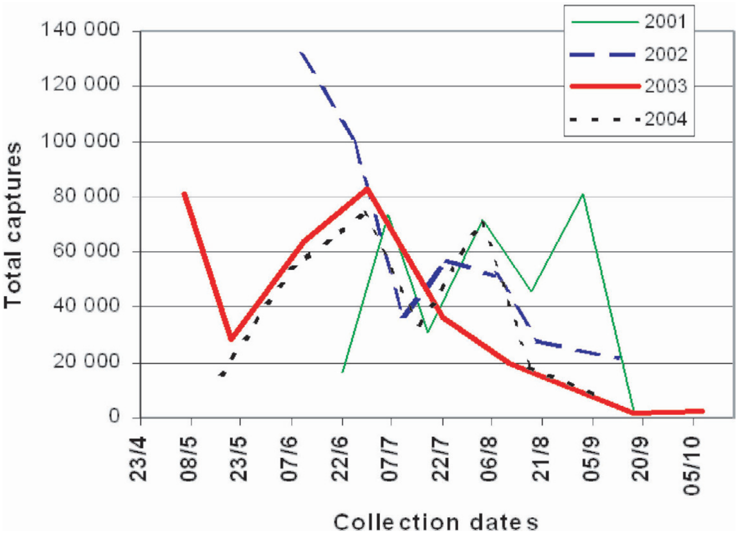

Figure 4. Total captures of *Ips typogaphus* on spruce in 5 sites in northeastern France from 2001 to 2004. On each site, captures were realized with 10 bottle-traps each equipped with "Pheroprax" (Cyanamid) (*cis*-verbenol et methyl-butenol), Ipsdienol (PheroTech) and *exo*-brevicomine (PheroTech) diffusers. Traps were collected every two weeks. (A color version of this figure is available at www.edpsciences.org.)

insect distribution could change very rapidly in response to climatic variations. Species distributions are often limited in their northern range by winter temperatures [6, 89] and increase in mean annual temperature means may favor populations to extend their geographic distribution.

The pine processionary moth, previously limited at about the Loire valley in France, moved 90 km north in the last 30 years [9, 26]. In 2003, this insect was negatively impacted by high summer temperatures in the continental areas [14, 15], however an increase of the winter temperature may have allowed the survival of remaining larvae and the progress of the migration front.

Similarly, the poplar woolly aphid was recorded for the first time in the Northeast of France in 2002 and lead to severe damages in 2003 [62]. Temperature increase of foliage may enhance performances of some defoliators that usually live under their optimal temperature regime [89] and allow the progression of the populations. However positive effect of temperature is often modulated by decrease of foliage quality [5]. Interaction between both factors (increase of temperature and foliage quality) could explain in part insects' migration and the development of outbreaks [60].

3. INDIRECTS EFFECTS ON TREE RESISTANCE AND INSECT PERFORMANCES

Extreme climatic events such as those observed in 2003 may also have indirect impacts on forest insect populations through plant-insect relationships and other trophic interactions. Drought and high temperatures have an effect on virtually every plant process. Impacts on tree physiology, biochemistry and phenology will affect the nutritional quality of wood, foliage and sap, and plants mechanical and chemical defenses against pest attacks.

Among the different theories that have been successively put forward to explain plant defense mechanisms (reviewed in [81, 98]) and how they can be impacted by water stress, the Growth – Differentiation Balance theory (GDB; [40, 56]) appears today as the most mature. According to the GDB theory, a moderate water stress would stimulated tree defenses. In contrast, severe water stress would decrease tree resistance to pest attacks [40, 53, 56, 85].

Drought may also affect the nutritional quality of plants, positively by increasing the level of foliar nitrogen which may, in turn, stimulate insect feeding [60, 97], or negatively through low leaf water content and increased concentrations of secondary metabolites (e.g. [45, 79, 80]). The net effect of water stress on insect populations is often hard to grasp because effects on host physiology and phenology can be contradictory. In drought conditions leaf maturation may become unsuitable food tissues earlier in the season due to the accumulation of defense compounds. However at the same time, their concentration in nitrogen increases which may enhance insect performances [28, 45, 48, 60]. Drought effects also depend on the insect feeding guild. Leaf-chewers such as moths, sawflies and beetle, are often more susceptible to the increase in defense compounds in leaf tissues than sap-feeders (aphids) feeding on vascular tissues containing less of these compounds [45, 60].

Finally, not all forest insects are immediately concerned by local drought conditions [62] and some, like aphids, must wait for the trees to recover better living conditions [45] to exploit the physiological modifications of the host due to drought. Sometimes tree decline is not visible until several years after the stress period or the drought may be preceded by defoliation, a freezing period or a windstorm that could already negatively impacted host trees. Then it becomes hard to determine what environmental factors were really responsible for tree dieback [10, 16].

3.1. Effects of water stress on host attractiveness to woodborers

Water stress may modify the acoustical, thermal, mechanical, visual or chemical cues used by insects to recognize their host [60]. After a prolonged stress, the vibrations that result from the cavitation of xylem tissues could attract insects such as bark beetles or woodborers [8, 60, 75]. First mechanical defense of conifers against woodborer attacks, the constitutive resin flow is reduced under severe water stress but is increased under a moderate drought [75]; and see references in [53]). In severely stressed hosts, the concentration of secondary metabolites implicated in host resistance is also reduced. Short range host attractiveness is then higher for woodborers (ref. in [53]), however intrinsic mechanisms implicated in long range attraction is still unstudied. Usually, a reduction of food quality occurs at the same time due to a decrease of the water content in tree tissues [52, 53]. Wood tissues in stress trees also emit chemical compounds that attract secondary pest insects [47].

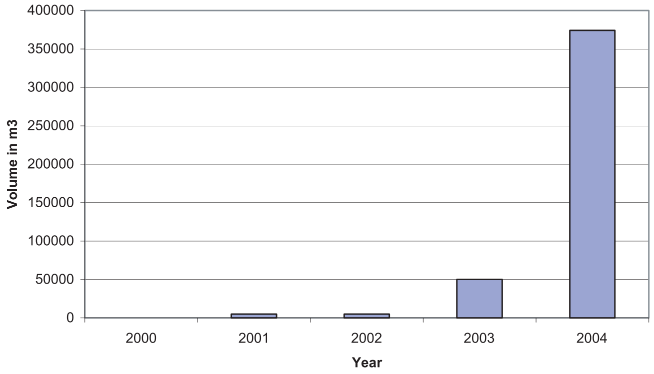

Figure 5. Annual volume of fir timber salvaged from bark beetle infestation in France reported by the French Forest Health Department [97].

3.2. Impacts of prolonged drought on bark beetles

The success of the establishment of bark beetle populations on their host tree depends, on the level of the insect populations and the ability of pioneer individuals to attract congeners, on the levels of tree natural defense mechanisms and the efficacy of beetle associated fungi to stimulate these defenses [20, 52, 72, 76]. Water stress may impact the emission of aggregation pheromones. Indeed, most Scolytid pheromones are derived from host's monoterpenes [20].

In 2004, populations of *I. typographus* have increased compared to the levels recorded in 2003 (Fig. 3). If this increase is indeed related to drought, one can expect it to continue in 2005, since tree susceptibility to bark beetles is usually maximum 1 or 2 years after a stress event [53, 69, 77]. Serious damages caused by bark beetle were reported in 2005 [70].

Recent studies showed that moderate water stress increased tree level of resistance to fungi associated with scolytids while a severe or long stress decreased it [24, 53, 94]. In contrast, several successive, short cycles of water stress may decrease resistance [53].

Consequently, if normal summers in temperate regions may stimulate conifer stand resistance to bark beetle attacks, it is possible that exceptionally dry summers increase tree susceptibility to these insects. This was confirmed by observations of increased damages by bark beetles on spruce (Fig. 3) and fir (Fig. 5) following the 2003 drought (conversely species associated to pine remained at endemic levels). In the fall of 2003, drought had weakened most conifers and broadleaves resulting in the infestation by most species (*Pityokteines* on fir, *Pityogenes chalcographus* on spruce, buprestids on broadleaf trees...). This illustrates differences between parasites that seems to be indifferent to the status of their hosts, and those that needs a weakened host to be successful.

Although conifers may become susceptible during a period of extreme drought, experiments have suggested that they can recover rapidly and resistance level return to normal as soon as water is available [22, 25, 69]. Thus, good conditions of rain during winter following a severe summer drought, could allow trees to recover their resistance and then to limit attacks

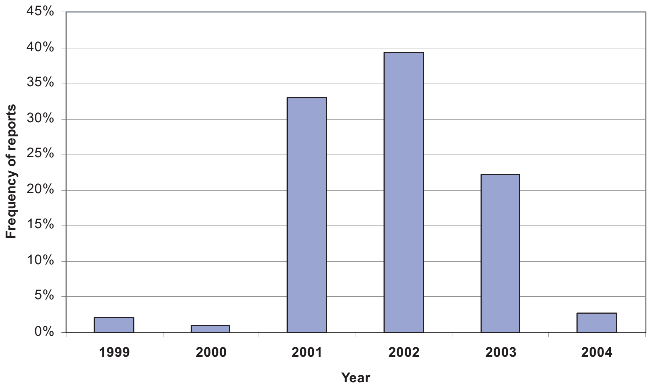

Figure 6. Frequency of reports of *Ips acuminatus* damage in France between 1999 and 2004 (total number of records = 662). Data were extracted from the database of the French Forest Health Department.

the following year. Nevertheless, in case of several consecutive years of severe water stress, bark beetle populations could outbreak and extensive attacks on healthy trees could become possible.

In contrast with *I. typographus* and *P. chalcographus* on Norway spruce or *P. curvidens* on fir, whose populations increased in 2004, populations of *I. acuminatus* on Scots pine have decreased (Fig. 6). According to Bréda et al. [16, 17], *Pinus sylvestris* was one of the conifers species least weakened by drought at the end of August 2003. One may suppose that in 2003, Scots pines were not stressed enough to attract *I. acuminatus* and even that their resistance was increased, because usually outbreaks of this insect are related to drought episodes [54]. Following the 2003 drought, other minor woodborers populations have also increase in France in 2004, on fir, oak and beech [32, 68].

Bark beetle propagation was also triggered in Switzerland and Germany [63]. During the 2003 drought episode, hosts were already stressed in the spring [16] and severe cold during the winter had damaged some crowns [61]. The addition of all these climatic factors weakened spruce stands thus promoting the increase of bark beetle population observed in 2003. The first generation of beetle dispersing at this time thus certainly found suitable sites for oviposition [61]. Two factors may have modified locally the impact of drought and bark beetles. First, conifers react differently to water stress. For example, Norway spruce is the conifer least resistant to water stress, particularly on unfavourable sites [16, 17]. Second, sufficient precipitations in the winter of 2002 may have allowed trees to enter the 2003 drought with a good resistance level in favourable sites [16].

3.3. Host attractiveness and defoliator performances

Leaf water content is the most important factor correlated with the larval growth of the geometrids *E. autumnata* and *O. brumata* (e.g. [39, 82]) and for the pine processionary moth (*T. pityocampa*) and the pinyon sawfly (*Diprion pini* L.). Young instars are usually the most sensitive to foliage quality [26, 42, 73], which may also have a negative effect on hatching rate [73, 80, 91, 100]. For the pine processionary, mortality observed in 2003 [14, 15] in young larvae could be the result of starvation because of a decrease in needle quality [42, 43]. Lepidoptera hatching during a drought period are negatively affected by leaf texture changes; leaves become tougher because of the decline in water content (see ref. in [5, 60, 74]. However, senescing foliage also provides insects with high quality food containing high nitrogen concentration [44]. For some insects, nutrient compounds in non-stressed plant are below the insect optimum of development so even a moderate stress can change foliage quality and increase insect performances [50, 60]. During, drought, the increase in nitrogen concentration usually stimulates insect feeding [60], but despite an increase in consumption rates, growth may be slowed down because the nutrition is less efficient due to low water content and high secondary metabolite concentration in the stressed foliage [19, 36, 79, 80].

In contrast with bark beetles that are known to perform better under prolonged drought, most evidence suggest that leaf chewers are negatively affected by continuous or high water stress, while performances increase under moderate and intermittent water stress [6, 45, 60, 93]. Mopper & Whitham [66] propose that the optimum host for *D. pini* would be a tree that had undergone a moderate stress followed by abundant precipitation while the larvae are feeding. In France, defoliators damages (e.g. *L. dispar* and *T. pityocampa*) observed in 2004 and 2005 show variable intensity according to the location [21, 32]. Differences in damage level may be related to host vigor and ability to resist and recover from a drought episode. During drought, leaf miners show better performance than leaf-chewers because of their ability to avoid compartmentalized secondary metabolites while in the same time benefiting from nitrogen elevation [5, 50]. Intermittent and moderate drought would promote defoliators performances, with higher performances from aphids and leaf-miners, while prolonged drought would decrease defoliators outbreaks.

3.4. Impacts on interspecific interactions

Drought stress may also have indirect effects on forest insect populations through biotic interactions such as competition, facilitation or predation. In this case, changes in insect populations that were directly affected by drought will in turn have effects on other insect species. These effects, often mediated through changes in plant chemistry and physiology induced by the feeding of primary pests [28], may immediately impact co-occurring species or persist for several growing seasons. Indirect effects are often negative: drought-increased performance of early defoliators often induces long-lasting plant resistance that will have negative effects on insect species occurring later in the season [96].

Severe defoliation due to drought together with defoliator proliferation may also lower tree resistance and facilitate secondary pest attacks the year after the drought. Heavy defoliation of *Picea sitchensis* (Bong.) Carr. by the aphid *Elatobium abietum* Walker (more than 90%) increases significantly the host susceptibility to secondary pest attacks by reducing

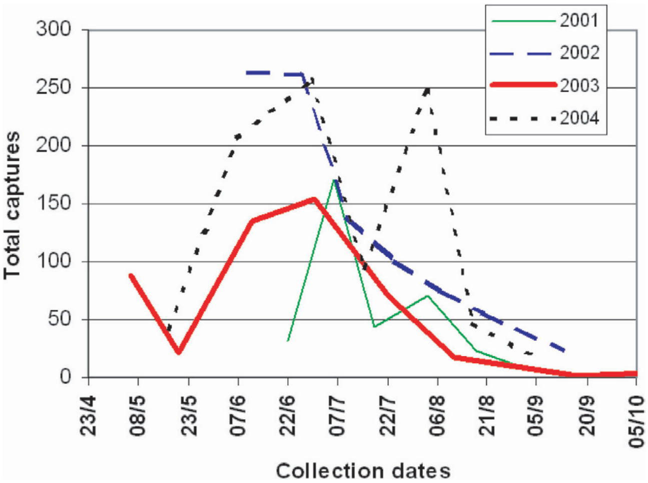

Figure 7. Annual captures of *Thanasimus formicarius* in 5 sites in northeastern France from 2001 to 2004. Capture methods are described in Figure 4. (A color version of this figure is available at www.edpsciences.org.)

both preformed and induced defense mechanisms [53, 77]. Increase of bark beetles attacks has been also demonstrated after defoliation by *Zeiraphera diniana* Guenée and *T. pityocampa* (ref. in [53]). In 2004, oak defoliation caused by geometrids reached 60% of the foliage [32]. This defoliation is expected to increase oak susceptibility to secondary pest attacks.

Drought may also indirectly impact forest pest insect population dynamics through impact on parasitism. Low plant quality reduces the development rate of defoliators, lengthening growth period thus increasing exposition period to parasitoid attacks [34, 38, 55].

During drought, performance of *D. pini* parasitoids are affected by the decrease in host size and quality in response to the low nutritional content of water-stressed trees [33, 38, 79].

It has been hypothesized that the combined action of changes in host plant quality due to drought stress and insect's response to increased temperature could allow insect populations to escape natural enemies [35, 84]. This hypothesis was not verified for *I. typographus* and other Scolytidae during the 2003 drought: in Northeastern France, captures of *Thanasimus formicarius* L., a parasitoid of these Scolytids occurred earlier in 2003 than usually recorded (Fig. 7). Captures increased in 2004, following the increase of host populations, but occurred later in the season.

4. DISCUSSION

We have compiled various observations of changes in forest pest populations during the 2003 drought and heat waves. Although it is difficult to establish unambiguously a causal relationship, it seems reasonable to assume that most changes were related to drought. Indeed, the observed impacts were often consistent with the nature and the timing of the stress. In some instances, insects might have tried to escape from stressful conditions through migration or behavioral changes; however the spatial extent and the duration of the stress were such that they were likely unsuccessful. Moreover, in several cases, insects were at a developmental stage that was not mobile enough to escape stress.

As expected, there were regional differences in the impacts of drought and heat waves (Tab. I). For early instars of defoliators and aphids, these differences were related to regional differences in the severity of the climatic stress and the direct impacts of this stress on insect performance. For other defoliators (e.g. *L. dispar*) and woodborers, regional differences can be explained by differences in host species composition. On spruce and fir that were severely impacted by drought (especially at low elevation), populations of woodborers increased. On host species more tolerant to drought (e.g. *Pinus sylvestris*), populations actually decreased. Field observations by The French Forest Health Department have also showed site differences. Damages were essentially located in sites with shallow soils, poor moisture-holding capacity or direct exposition to solar radiations [10, 31, 32, 68]. These observations illustrate the importance of soil water status in the level of tree resistance to pest attacks. Indeed, the drought and the heat waves had more impact on trees already weakened by other biotic or abiotic factors. In some cases, the 2003 drought revealed a poor choice of tree species in some plantations [10].

Overall, forest insects responded differently according to their feeding guild. Woodborers infestations showed a significant increase in 2003, while defoliators reacted rather in 2004 (Tab. I). Woodborer populations had already increased after the 1999 windstorm and were still at epidemic levels at the beginning of 2003. Populations increased in 2003 because of the association between a severe water deficit that lowered tree resistance and high mean temperatures that increased insect development rates [68]. Plurivoltine insects are also able to react faster to better life conditions than univoltine insects. Woodborers perform better under moderate but prolonged stress while defoliator performances are increased under moderate but intermittent stress. Increases of defoliator populations occurred when the leaves recovered their water content. Aphids would usually outbreak after a mild winter, on trees with both high nitrogen content and high water content. Consequently, drought followed by a warm winter will likely promote outbreaks.

The impacts of the 2003 drought reported in this study illustrate the sensitivity of most of the major Western European forest insect species to extreme drought and heat waves. The immediate and short term impacts appear fairly conspicuous. The long term impacts, however, are more difficult to predict for several reasons. First, drought can have a significant effect on plant and insect populations but a few years of lower temperatures and higher rainfall may reverse the changes induced by the drought [67]. Second, delayed effects on the insects themselves, on their hosts and on trophic relations can be important, but the complexity of the trophic structure in which a particular insect is imbedded may prevent one from predicting the trajectory of its population's response and its capacity to return to its original state. Finally, the correlations between

Table I. Damage intensity from the major European forest pest insects observed in France in 2003–2004 recorded by the French Forest Health Department (DSF). Abbreviations and symbols (regions correspond to DSF regions : (SE) = southeast, (SW) = southwest, (NW) = northwest, (MC) = centre, (NE) = northeast, (+++) = important damages with high population level or population increase; (++) = important but local damages or no changes in population level; (+) = local damages with low population level; (–) = population decrease; (n) = no data available; empty cell = no damage or outside insect geographic distribution.

							Damage location and intensity				
Guild	Order	Family	Species	Common names	Hosts	Pest level	SE	SW	MC	NW	NE
Chewing insect											
Woodborer	Coleoptera	Scolytidae	*Ips typographus* L.	European spruce bark beetle	*Picea*	Secondary or primary	+++/++	+++/+++	+/+++		+++/+++
	Coleoptera	Scolytidae	*Ips sexdentatus* Boern.	Pine stenographer beetle	*Pinus, Picea*	secondary	+/n	+++/–		+/–	++/–
	Coleoptera	Scolytidae	*Ips acuminatus* Gyll.	Engraver beetle	*Pinus*	Secondary			++/–		
	Coleoptera	Scolytidae	*Pityokteines curvidens* Germ.	Bark beetle P.c.	*Abies*	Secondary	/+	+/++	++/++		++/+++
			Pityokteines spinidens		*Pseudotsuga*	Secondary			/++		/++
	Coleoptera	Scolytidae	*Dendroctonus micans* Kug.	Great spruce bark beetle	*Picea*	Primary	/+	++/++	+/+	+/++	+/+
	Coleoptera	Scolytidae	*Pityogenes chalcographus* L.	Small spruce bark beetle	*Picea*	Secondary	+/+	++/+++	+/+		+++/+++
	Coleoptera	Scolytidae	*Tomicus piniperda* L.	Common pine shoot beetle	*Pinus*	Secondary		++/++		++/++	+/+
	Coleoptera	Curculionidae	*Pissodes notatus* Fabr.	Pine weevil	*Pinus*	Secondary		+/	/+	/+	
	Coleoptera	Curculionidae	*Pissodes piceae* Ill.	Fir weevil	*Abies*	Secondary	/+	/+	++/+++		+/+
Free-living	Lepidoptera	Thaumetopoeidae	*Thaumetopoea pityocampa* Schiff.	Pine processionary moth	*Pinus*	Primary	++/++	+++/+++	+++/++	++/++	
	Lepidoptera	Thaumetopoeidae	*Thaumetopoea processionnea* L.	Oak processionary moth	*Quercus*	Primary				+/+	+++/+++
	Lepidoptera	Tortricidae	*Zeirapheira diniana* Gn.	Larch bud moth	*Larix, Pinus*	Primary	n/+				
	Lepidoptera	Tortricidae	*Tortrix viridana* L.	Green oak leaf-roller moth	*Quercus*	Primary		+++/++	/++	/+	+/+++
	Lepidoptera	Lymantriidae	*Lymantria dispar* L.	Gypsy moth	*Quercus*	Primary	+/+++	/+		+/+	++/–
	Lepidoptera	Geometridae	*Operophtera brumata* L.	Winter moth	*Quercus*	Primary		+/–	+/+++	/++	+/ +++
Leaf-miners	Lepidoptera	Curculionidae	*Rhynchaenus fagi* L.	Beech leaf miner	*Fagus*	Primary		++/+++	/+	/++	+/+
Sap-feeder											
Phloem-feeder	Homoptera	Margarodidae	*Matsucoccus feytaudi* Duc.	Maritime pine bast scale	*Pinus*	Primary	+/+				
	Homoptera	Aphididae	*Elatobium abietinum* W.	Green spruce aphid	*Picea*	Primary				++/–	
	Homoptera	Aphididae	*Phyllaphis fagi* L.	Beech woolly aphid	*Fagus*	Primary		/+++	/+	/++	/+++
	Homoptera	Aphididae	*Phloeomyzus passerinii* Sign.	Poplar woolly aphid	*Populus*	Primary		+++/–	++/		+++ /+

drought stress and the variations of insect populations are not always easy to interpret. In particular, it is often difficult to separate the effects of a particular climatic event from the normal fluctuations of insect populations and, consequently, to assess the real impact of the event.

The most important effects of climate change on temperate forests will probably be mediated through changes in disturbance regimes such as fire, insects and pathogens. Hence, it is useful to consider how climate change will affect these disturbances. Already, considerable efforts have been put towards the description of the effects of changes in mean climate parameters on insect populations through the use of equilibrium biogeographic models (e.g. [85, 87, 98]). However, for many species, it is expected that performance and survivorship will not be affected by slight, progressive changes in climatic conditions, but by the likelihood of catastrophic events. Extreme droughts in association with bark beetle infestations have already revealed the potential to cause rapid changes in forest composition [2, 18]. A clearer understanding of how climatic extremes affect insect populations will enable better predictions of the impacts of climate change on forest ecosystems.

We suggest that, in order to better understand the effects of climatic extremes on forest insect populations, we need to: (1) Quantify the basic relationships between extreme climatic events and key processes including: per capita rate of development, population growth, phenology and voltinism. This question remains one of the most outstanding that prevent from predicting the long term impacts of climate change on forest insect populations. The controlled experimental approach that has been used in trying to quantify these relationships in agricultural systems is not always suited for forest species [92]. In addition, there is a need to better relate small scale experimental results to population processes. (2) Take into account phenotypic and genotypic variability in the quantification of these relationships. (3) Develop process-level understanding of the dynamics of forest insect populations. It is often difficult to disentangle density dependent and density independent processes involved in the dynamics of forest insect populations. Climate may interact with these processes or, conversely, limitation or facilitation of climate impacts on populations may come from indirect factors such as trophic interactions. One difficulty relates to the complexity induced by the interaction of the various factors influencing insect performance and population dynamics. (4) Continue and expand forest health survey programs. Qualitative surveys should be maintained and augmented with quantitative assessments of populations' levels using appropriate sampling protocols. Survey and monitoring programs should also better take into account site and host plant conditions.

Acknowledgements: The authors thank M.J. Lombardero for information and references she provided on plant stress hypothesis, L. Bouhot-Delduc for sending her two manuscripts on the pine processionary moth, and J.-C. Grégroire for his comments on bark beetle. We are also grateful to G. Landmann for his constant support and comments on earlier version of the manuscript. GIP-ECOFOR (www.gip-ecofor.org) provided financial support for G. Rouault.

REFERENCES

[1] Abgrall J., Soutrenon A., La forêt et ses ennemis, Cemagref-DICOVA, Antony, France, 1991.

[2] Allen C.D., Breshears D.D., Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation, Proc. Natl. Acad. Sci. USA 95 (1998) 14839–14842.

[3] Annila E., Influence of temperature upon the development and voltinism of *Ips typographus* L. (Coleoptera, Scolytidae), Ann. Zool. Fenn. 6 (1969) 161–167.

[4] Anonymous, Annual Report 2003, in: Annual Report, Federal Biological Research Centre for Agriculture and Forestry, Berlin, Germany, 2003.

[5] Awmack C., Leather S., Host plant quality and fecundity in herbivorous insects, Annu. Rev. Entomol. 47 (2002) 817–844.

[6] Ayres M., Lombardero M., Assessing the consequences of global change for forest disturbance from herbivores and pathogens, Sci. Total Environ. 262 (2000) 263–286.

[7] Bale J., Masters G., Hodkinson I., Awmack C., Bezemer T., Brown V., Butterfield J., Buse A., Coulson J., Farrar J., Good J., Harrington R., Hartley S., Jones T., Lindroth R., Press M., Symrnioudis I., Watt A., Whittaker J., Herbivory in global climate change research: direct effects of rising temperature on insect herbivores, Glob. Change Biol. 8 (2002) 1–16.

[8] Barr B., Sound production in Scolytidae (Coleoptera) with emphasis on the genus *Ips*, Can. Entomol. 101 (1969) 636–672.

[9] Battisti A., Stastny M., Netherer S., Robinet C., Schopf A., Roques A., Larsson S., Expansion of geographic range in the pine processionary moth caused by increased winter temperatures, Ecol. Appl. 15 (2005) 2084–2096.

[10] Belrose V., Nageleisen L.-M., Renaud J.-P., Les conséquences de la canicule et de la sécheresse sur la santé des forêts : bilan à la fin de l'année 2003. La santé des forêts (France) en 2003, in: DSF, http://agriculture.gouv.fr/spip/IMG/pdf/canicule_secheresse.pdf, 2004.

[11] Beniston M., Innes J., The impacts of climate variability on forests, Springer-Verlag, Berlin, 1998.

[12] Beniston M., Diaz H., The 2003 heat wave as an example of summers in a greenhouse climate? Observations and climate model simulations for Basel, Switzerland,, Glob. Planet. Change 44 (2004) 73–81.

[13] Berninger R., Effects of drought and phenology on GPP in *Pinus sylvestris*: A simulation study along a geographical gradient, Funct. Ecol. 11 (1997) 33–42.

[14] Bouhot-Delduc L., La gradation de la chenille processionnaire du pin a culminé sur la façade atlantique lors de l'hiver 2003-2004., in: Les Cahier du DSF, 1-2005 (La santé des forêts (France) en 2003 et 2004), Min. Agri. Alim. Pêche Rur. (DGFAR, SDFB), Paris, http://www.agriculture.gouv.fr/spip/ressources.themes.foretbois.santedesforets_r314.html, 2005.

[15] Bouhot-Delduc L., Dynamique des populations de la processionnaire du pin et extension de son aire de colonisation de 1981 à 2004 en France, in: Les Cahier du DSF, 1-2005 (La santé des forêts (France) en 2003 et 2004), Min. Agri. Alim. Pêche Rur. (DGFAR, SDFB), Paris, http://www.agriculture.gouv.fr/spip/ressources.themes.foretbois.santedesforets_r314.html, 2005.

[16] Bréda N., Granier A., Aussenac G., La sécheresse de 2003 dans le contexte climatique des 54 dernières années : analyse écophysiologique et influence sur les arbres forestiers, Rev. For. Fr. 56 (2004) 109–131.

[17] Bréda N., Huc R., Granier A., Dreyer E., Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and log-term consequences, Ann. For. Sci. 63 (2006) 623–642.

[18] Breshears D.D., Cobb N.S., Rich P.M., Price K.P., Allen C.D., Balice R.G., Romme W.H., Kastens J.H., Floyd M.L., Belnap J.,

Anderson J.J., Myers O.B., Meyer C.W., Regional vegetation die-off in response to global-change-type drought, Proc. Natl. Acad. Sci. USA 102 (2005) 15144–15148.

[19] Buse A., Good J., Synchronization of larval emergence in winter moth (*Operophtera brumata* L.) and budburst in pedunculate oak (*Quercus robur* L.) under simulated climate change, Ecol. Entomol. 21 (1996) 335–343.

[20] Byers J., Chemical ecology of bark beetles in a complex olfactory landscape, Kluwer Academics Publishers, Dordrecht, 2004.

[21] Caroulle F., Recrudescence confirmée des défoliateurs de feuillus en 2004, in: Bilan de la Santé des Forêts en 2004, Min. Agri. Pêche, Paris, http://www.agriculture.gouv.fr/spip/IMG/pdf/2004_defoliateurs.pdf, 2005.

[22] Christiansen E., After-effects of drought did not predispose young *Picea abies* to infection by the bark beetle-transmitted blue-stain fungus *Ophiostoma polonicum*, Scand. J. For. Res. 7 (1992) 557–569.

[23] Communication Section of the Ministry of Agriculture, Summary report by the ministry of agriculture of the Czech Republic of the situation in agriculture, food-processing industry, forestry and water management in the year 2003, in: Ministry of Agriculture, Summary Report, Ministry of Agriculture, Prague, Czech Republic, 2004.

[24] Croisé L., Lieutier F., Effect of drought on the induced defense reaction of Scots pine to bark beetle-associated fungi, Ann. For. Sci. 50 (1993) 91-97.

[25] Croisé L., Lieutier F., Cochard H., Dreyer E., Effects of drought stress and high density stel inoculation with *Leptographium wingfieldii* on hydraulic properties of young Scots pine trees, Tree Physiol. 21 (2001) 427–436.

[26] Démolin G., Bioecologia de la processionnaria del pino, *Thaumetopoea pityocampa*. Incidencia de los factores climaticos, Bol. Serv. Plagas Forest. 23 (1969) 9–24.

[27] Démolin G., Bouhot-Delduc L., Abgrall J., Dynamique des populations de la chenille processionnaire du pin et climat, Min. Agri. Pêche (DERF), Paris, 1998.

[28] Denno R., Peterson M., Gratton C., Cheng J., Langellotto G., Huberty A., Finke D., Feeding-induced changes in plant quality mediate interspecific competition between sap-feeding herbivores, Ecology 81 (2000) 1814–1827.

[29] Desprez-Lousteau M.-L., Marçais B., Nageleisen L.-M., Piou D., Vannini A., Interactive effects of drought and pathogens in forest trees, Ann. For. Sci. 63 (2006) 595–610.

[30] Dewar R., Watt A., Predicted changes in the synchrony of larval emergence and budburst under climatic warming, Oecologia 89 (1991) 557–559.

[31] DSF, L'actualité phytosanitaire en forêt en 2003 : bilan de fin de saison de végétation, in: Information Santé des Forêts, Min. Agri. Alim. Pêche Aff. Rur., Paris, http://www.agriculture.gouv.fr/spip/IMG/pdf/actu_phytos2003.pdf, 2003.

[32] DSF, L'actualité phytosanitaire en forêt en 2004 : bilan d'automne, La Lettre du DSF 30 (2004) 3–9.

[33] Faccoli M., Winter mortality in sub-corticolous populations of *Ips typographus* (Coleoptera: Scolytidae) and its parasitoids in the south-eastern Alps, J. Pest Sci. 75 (2002) 62–68.

[34] Faeth S., Structural damage to oak leaves alters natural enemy attack on a leaf-miner, Entomol. Exp. Appl. 57 (1990) 57–63.

[35] Fleming R., Volney W., Effects of climate change on insect defoliator population processes in Canada's boreal forest: some plausible scenarios, Water Air Soil Pollut. 8 (1995) 445–454.

[36] Forkner R., Marquis R., Lill J., Feeny revisited: condensed tannins as anti-herbivore defences in leaf-chewing herbivore communities of *Quercus*, Ecol. Entomol. 29 (2004) 174–187.

[37] Greenbank D., The role of climate and dispersal in the initiation of outbreaks of the spruce budworm in New Brunswick, Can. Entomol. 34 (1956) 453–476.

[38] Havill N., Raffa K., Compounds effects of induced plant responses on insect herbivores and parasitoids: implications for tritrophic interactions, Ecol. Entomol. 25 (2000) 171–179.

[39] Henriksson J., Haukioja E., Ossipov V., Ossipova S., Sillanpää S., Kapari L., Pihlaja K., Effects of host shading on consumption and growth of the geometrid *Epirrita autumnata*: interactive roles of water, primary and secondary compounds, Oikos 103 (2003) 3–16.

[40] Herms D.A., Mattson W.J., The dilemma of plants: to grow or defend, Q. Rev. Biol. 67 (1992).

[41] Hodar J., Zamora R., Herbivory and climatic warming: a Mediterranean outbreaking caterpillar attacks a relict, boreal pine species, Biodivers. Conserv. 13 (2004) 493–500.

[42] Hodar J., Zamora R., Castro J., Host utilisation by moth and larval survival of pine processionary caterpillar *Thaumetopoea pityocampa* in relation to food quality in three *Pinus* species, Ecol. Entomol. 27 (2002) 292–301.

[43] Hodar J., Zamora R., Castro J., Baraza E., Feast and famine: previous defoliation limiting survival of pine processionary caterpillar *Thaumetopoea pityocampa* in Scots pine *Pinus sylvestris*, Acta Oecologia 26 (2004) 203–210.

[44] Holopainen J., Peltonen P., Bright autumn colours of deciduous trees attract aphids: nutrient retranslocation hypothesis, Oikos 99 (2002) 184–187.

[45] Huberty A., Denno R., Plant water stress and its consequences for herbivorous insects: a new synthesis, Ecology 85 (2004) 1383–1398.

[46] IPCC, Climate change. The IPCC Third Assessment Report, Cambridge Univ. Press, 2001.

[47] Kelsey R., Joseph G., Attraction of *Scolytus unispinosus* bark beetle to ethanol in water-stressed Douglas-fir branches, For. Ecol. Manage. 144 (2001) 229–238.

[48] Koricheva J., Larsson S., Haukioja E., Insect performance on experimentally stressed woody plants: a meta-analysis, Annu. Rev. Entomol. 43 (1998) 195–216.

[49] Krehan H., Borkenkäfer-Massenvermehrung 2003 – eine Folge der Sommerhitze und der Sturmschäden, in: Forstschutz Aktuell Nr. 29, Bundesamt und Forschungszentrum für Wald, Wien, 2003.

[50] Larsson S., Stressful times for the plant stress – insect performances hypothesis, Oikos 56 (1989) 277–283.

[51] Larsson S., Björkman C., Performance of chewing and phloem-feeding insects on stressed trees, Scand. J. For. Res. 8 (1993) 550–559.

[52] Lieutier F., Mechanisms of resistance in conifers and bark beetle attack strategies, Kluwer Academics Publishers, Dordrecht, 2002.

[53] Lieutier F., Host resistance to bark beetles and its variations, Kluwer Academics Publishers, Dordrecht, 2004.

[54] Lieutier F., Faure T., Garcia J., Les attaques de scolytes et le dépérissement du pin sylvestre dans la région Provence-Côte d'Azur, Rev. For. Fr. 40 (1988) 224–232.

[55] Lill J., Marquis R., The effects of leaf quality on herbivore performance and attack from natural enemies, Oecologia 126 (2001) 418–428.

[56] Loomis W., Growth-differentiation balance vs. carbohydrate-nitrogen ration, Proc. Am. Soc. Hortic. Sci. 29 (1932) 329–339.

[57] Lorenz M., Becher G., Mues V., Fischer R., Ulrich E., Dobbertin M., Stofer S., 2004 Technical Report, in: Forest Condition in Europe, United Nations Economic Commission for Europe, Geneva, Switzerland, 2004.

[58] Loxdale H.D., Lushai G., Slaves of the environment: the movement of herbivorous insects in relation to their ecology and genotype, Phil. Trans. R. Soc. London B 354 (1999) 1479–1495.

[59] Luterbacher J., Dietrich D., Xoplaki E., Grosjean M., Wanner H., European seasonal and annual temperature variability, trends, and extremes since 1500, Science 303 (2004) 1499–1503.

[60] Mattson W., Haack R., The role of drought stress in provoking outbreaks of phytophagous insects, Academic Press, London, 1987.

[61] Maugard F., Le gel, le vent, la grêle en 2003 et leur conséquences sur la santé des forêts, in: Bilan de la santé des forêts (France) en 2003, Min. Agri. Alim. Pêche Aff. Rur., Paris, http://www.agriculture.gouv.fr/spip/IMG/pdf/gel_vent_climat.pdf, 2004.

[62] Maugard F., Baudet O., Le puceron lanigère du peuplier accentue sa présence dans le Sud-Ouest et étend sa zone d'épidémie vers le Nord, in: Bilan de la santé des forêts (France) en 2003, Min. Agri. Alim. Pêche Aff. Rur., Paris, http://www.agriculture.gouv.fr/spip/IMG/pdf/puceron_lanigere.pdf, 2004.

[63] Meehl G., Tebaldi C., More Intense, more frequent, and longer lasting heat waves in the 21st century, Science 305 (2004) 994–997.

[64] Meier F., Engesser R., Forster B., Odermatt O., Protection des forêts – Vue d'ensemble 2003, in: Birmensdorf, http://www.wsl.ch/forest/wus/pbmd/artikel/fsub03f.pdf, 2004.

[65] Meier F., Engesser R., Forster B., Odermatt O., Protection des forêts – Vue d'ensemble 2004, in: Birmensdorf, Switzerland, http://www.wsl.ch/forest/wus/pbmd/artikel/fsub03f.pdf, 2005.

[66] Mopper S., Whitham T., The plant stress paradox: effects on pinyon sawfly ratios and fecundity, Ecology 73 (1992) 515–525.

[67] Morecroft M., Bealey C., Howells O., Rennie S., Woiwod I., Effects of drought on contrasting insect and plant species in the UK in the mi-1990s, Global Ecol. Biogeogr. 11 (2002) 7–22.

[68] Nageleisen L.-M., Recrudescence des insectes sous-corticaux à la suite des extrêmes climatiques de 2003, in: Bilan de la santé des forêts en 2003, Min. Agri. Alim. Pêche Aff. Rur., Paris, http://www.agriculture.gouv.fr/spip/IMG/pdf/ insectes_souscorticaux.pdf, 2004.

[69] Nageleisen L.-M., Les insectes sous-corticaux des résineux en 2002 : diminution inattendue des dommages dus aux scolytes, Min. Agri. Alim. Pêche Aff. Rur. (DGFAR), Paris, 2004.

[70] Nageleisen L-M., Quelques indicateurs de la santé des forêts françaises (1989–2005), in: Bilan de la Santé des Forêts. Min. Agri. Pêche, Paris, http://www.agriculture.gouv.fr/spip/IMG/pdf/ thermometre2005.pdf, 2006

[71] OFEFP, Rapport forestier 2005 – Faits et chiffres sur l'état de la forêt suisse, in: Office fédéral de l'environnement, des forêts et du paysage, Berne, Suisse, 2005.

[72] Paine T., Raffa K., Harrington T., Interactions among scolytids bark beetles, their associated fungi, and live host conifers, Annu. Rev. Entomol. 42 (1997) 179–206.

[73] Pasquier-Barre F., Palasse C., Goussard F., Auger-Rozenberg M.-A., Géri C., Relationship of Scots pine clone characteristics and water stress to hatching and larval performance of the sawfly *Diprion pini* (Hymenoptera: Diprionidae), Environ. Entomol. 30 (2001) 1–6.

[74] Quiring D., McKinnon M., What does early-season herbivory affect subsequent budburst? Ecology 80 (1999) 1724–1735.

[75] Raffa K., Mixed messages across multiple trophic levels: the ecology of bark beetle chemical communication systems, Chemoecology 11 (2001) 49–65.

[76] Raffa K., Berryman A., The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae), Ecol. Monogr. 53 (1983) 27–49.

[77] Raffa K., Krause S., Reich P., Long-term effects of defoliation on red pine suitability to insects feeding on diverse plant tissues, Ecology 79 (1998) 2352–2364.

[78] Rebetez M., Mayer H., Dupont O., Schindler D., Gartner K., Kropp J., Menzel A., Heat and drought 2003 in Europe: a climate synthesis, Ann. For. Sci. 63 (2006) 567–575.

[79] Roth S., McDonald E., Lindroth R., Atmospheric CO2 and soil water availability: consequences for tree-insect interactions, Can. J. For. Res. 27 (1997) 1281–1290.

[80] Scriber J., Slansky F., The nutritional ecology of immature insects, Annu. Rev. Entomol. 26 (1981) 183–211.

[81] Stamp N., Out of the quagmire of plant defense hypotheses, The Quarterly Rev. Bio. 78 (2003) 23–55.

[82] Tikkanen O.-P., Lyytikäinen-Saarenmaa P., Adaptation of a generalist moth, *Operophtera brumata*, to variable budburst of host plants, Entomol. Exp. Appl. 103 (2002) 123–133.

[83] Tikkanen O.-P., Julkunen-Tiitto R., Phenological variation as protection against defoliating insects: the case of *Quercus robur* and *Operophtera brumata*, Oecologia 136 (2003) 244–251.

[84] Tisdale R., Wagner M., Host tree influences oviposition preference and performance of a pine sawfly, Ecol. Entomol. 16 (1991) 371–376.

[85] Ungerer M., Ayres M., Lombardero M., Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmerman (Coleoptera: Scolytidae), J. Biogeogr. 26 (1999) 1133–1145.

[86] Virtanen T., Neuvonen S., Performance of moth larvae on birch in relation to altitude, climate, host quality and parasitoids, Oecologia 120 (1999) 92–101.

[87] Virtanen T., S N., Nikula A., Varama M., Niemela P., Climate change and the risks of *Neodiprion sertifer* outbreaks on Scots pine, Silva Fenn. 30 (1996) 169–177.

[88] Wagner T., Wu H., Sharpe P., Schoolfield R., Coulson R., Modeling insect development rates: A literature review and application of the biophysical model, Ann. Entomol. Soc. Am. 77 (1984) 208–225.

[89] Wallner W., Factors affecting insect population dynamics: differences between outbreak and non-outbreak species, Annu. Rev. Entomol. 32 (1987) 317–340.

[90] Wargo P., Consequences of environmental stress on oak predisposition to pathogens, Ann. For. Sci. 53 (1996) 359–368.

[91] Watt A., McFarlane A., Winter moth on sitka spruce: synchrony of egg hatch and budburst, and its effect on larval survival, Ecol. Entomol. 16 (1991) 387–390.

[92] Watt A., McFarlane A., Will climate change have a different impact on different trophic levels? Phenological development of winter moth *Operophtera brumata* and its host plants, Ecol. Entomol. 27 (2002) 254–256.

[93] Watt A., Leather S., Hunter M., Kidd N., Population dynamics of forest insects, Intercept Ltd., Andover, 1990.

[94] Wermelinger B., Ecology and management of the spruce bark beetle *Ips typographus*- a review of recent research, For. Ecol. Manage. 202 (2004) 67–82.

[95] Wermelinger B., Seifert M., Temperature-dependent reproduction of the spruce bark beetle *Ips typographus*, and analysis of the potential population growth, Ecol. Entomol. 24 (1999) 103–110.

[96] West C., Factors underlying the late seasonal appearance of the lepidopterous leaf-mining guild on oak, Ecol. Entomol. 10 (1985) 111–120.

[97] White T., The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants, Oecologia 63 (1984) 90–105.

[98] Williams D., Liebhold A., Forest defoliators and climatic change: potential changes in spatial distribution of outbreaks of western spruce budworm (Lepidoptera: Tortricidae) and gypsy moth (Lepidoptera: Lymantriidae), Environ. Entomol. 24 (1995) 1–9.

[99] Yamamura K., Kiritani K., A simple method to estimate the potential increase in the number of generations under global warming in temperate zones, Appl. Entomol. Zool. 33 (1998) 289–298.

[100] Zalucki M., Clarke A., Malcolm S., Ecology and behavior of first instar larval lepidoptera, Annu. Rev. Entomol. 47 (2002) 361–393.