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Drought effects on damage by forest insects and pathogens: a meta-analysis

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Abstract

In the context of climate change, the effects of prolonged or more severe droughts on pest and pathogen damage are a major concern for forest ecosystems. To date, there is great uncertainty about the direction, magnitude and sources of variation in responses to drought by insects and fungi. We report the outcomes of a meta-analysis of 100 pairwise comparisons of insect pest or pathogen damage to water-stressed and control trees from 40 publications. The type of feeding substrate for insects and fungi and the water stress severity emerged as the main factors influencing the level of damage in water-stressed trees. Overall, primary damaging agents living in wood caused significantly lower damage to the water-stressed trees compared with the control, whereas primary pests and pathogens living on foliage caused more damage to water-stressed trees, in all cases irrespective of stress severity. In contrast, damage by secondary agents increased with stress severity, which was best estimated by the ratio between the predawn leaf water potential in stressed trees and the xylem pressure inducing 50% loss in hydraulic conductance due to cavitation, a species-specific index of drought tolerance. Insect and fungus feeding behaviour, affected tree part, and water stress severity are therefore proposed as three important predictors of forest damage in drought conditions.

Keywords: drought, fungus, pest, risk analysis, tree

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Introduction

Extensive research has demonstrated that summer drought often affects tree growth and forest ecosystem functioning. The heat wave and the severe drought that Western Europe experienced in 2003 had serious consequences for forest health and productivity [see Annals of Forest Science, special issue 63 (6) 2006]. More recently, Allen *et al.* (2010) reported on many cases of drought-induced tree mortalities all around the world. These catastrophic events are raising a large concern among foresters about the resistance and resilience of forests in the context of climate change. Since the mid-1950s, a trend towards increasing drought has been reported for many Northern Hemisphere land areas including Europe (Dai *et al.*, 2004). While future changes in precipitation or moisture patterns are more difficult to forecast than mean changes in temperature, most of the models used to predict changes in climatic conditions indicate decreases in summer precipitation and increases in winter precipitation across Europe (Blenkinsop & Fowler, 2007) and the US (Cayan *et al.*, 2010). The main changes are expected at the lower latitudes of the continents where areas affected by drought are very likely to increase (Planton *et al.*, 2008).

Severe or prolonged droughts not only have direct adverse effects on tree growth or survival, but they may also trigger more frequent or severe outbreaks of forest insects (Ayres & Lombardero, 2000; Breshears *et al.*, 2005; Logan *et al.*, 2003; Netherer & Schopf, 2010) and epidemics of forest pathogens (Ayres & Lombardero, 2000; Moore & Allard, 2008). Insect outbreaks and pathogen epidemics may interact with carbon starvation or hydraulic failure to facilitate mortality under drought conditions (McDowell *et al.*, 2008). Climate change may then bring forest ecosystems into a vicious circle where increased drought would enhance insect and pathogen epidemics that cause tree growth loss and mortality, resulting in carbon starvation (McDowell *et al.*, 2008) and then higher carbon concentration in the atmosphere, reinforcing the global warming. There is therefore a need to better understand the impact of drought not only on pest performances (Huberty & Denno, 2004) but also on their damage to trees. Using damage as response variable has two main advantages: (i) it is a more integrative measure than herbivore performance,

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incorporating both tree sensitivity and pest or pathogen aggressiveness and (ii) it is a proxy of biomass consumption and hence has a more direct link to the carbon balance.

Several textbooks (Speight & Wainhouse, 1989; Wainhouse, 2005) and review articles (Mattson & Haack, 1987; Koricheva *et al*., 1998; Huberty & Denno, 2004) have listed examples of forest pest responses to drought. They revealed considerable variation in the magnitude and direction of responses to water stress most of which was related to insect feeding guild. Generally, bark beetles and wood borers benefit from severe drought (Koricheva *et al*., 1998; Huberty & Denno, 2004). Sap sucking insects also perform better on water-stressed trees (Koricheva *et al*., 1998; Björkman & Larsson, 1999), at least under moderate stress condition (Huberty & Denno, 2004), whereas the effect of drought on leaf miners, leaf chewers and gall makers is more uncertain. Similarly, depending on the pathogen species, e.g. *Armillaria* spp. (Wargo & Harrington, 1991), *Collybia fusipes* (Camy *et al*., 2003), *Heterobasidion annosum* (Woodward *et al*., 1998), *Phytophthora cinnamoni* (Desprez-Loustau *et al*., 2006), pathogenicity may be either reduced or enhanced with increased drought. Furthermore, according to Huberty & Denno (2004), the magnitude and direction of herbivorous insects' response to drought would depend on the severity of water stress. Desprez-Loustau *et al.* (2006) also suggested that the duration of drought periods can be critical as more infections are likely to develop during or after prolonged drought stress, and many pathogen outbreaks can only occur following a particular sequence of dry and wet conditions (e.g. *Phytophthora* sp.). Finally, many different methods have been used to quantify drought or water stress, including soil or tree water content, leaf water potential and loss in hydraulic conductivity, and even more approaches have been used to estimate forest pest and pathogen damage in root, stem or tree crowns.

This diversity in both methodological approaches and individual pest and pathogen species responses to drought makes it difficult to summarize the pattern of damage in water-stressed trees. And yet, we need to go beyond the species-specific analyses and draw more general conclusions about the drought–damage relationships if we want to better predict the effects of climate change on forest ecosystem functioning (Volney & Fleming, 2000; Luyssaert *et al*., 2010). To make a step forward in this direction, we conducted a meta-analysis of published primary studies that addressed the impact of water stress on forest pest or pathogen damage. Meta-analysis is a set of statistical tools that allows combining the outcomes of independent studies to evaluate the overall effect of a particular factor and also to test the influence of covariates on this effect (Gurevitch & Hedges, 1999). Our main objectives were:

1. To estimate the overall effect of water stress on insect pest and fungal pathogen damage in forest trees;
2. To investigate the variation of response to water stress among functional groups of pests and pathogens;
3. To explore the relationship between the magnitude of pest or pathogen damage and the severity of drought.

Material and methods

Data collection

Published studies that compared pest or disease damage on water-stressed vs. control trees were compiled using bibliographic databases including ISI Web of Science and CAB abstracts. Keyword searches were conducted using various combinations of relevant terms such as: (*tree* or *forest* or *Abies* or *Acer* or *Betula* or *Eucalyptus* or *Fagus* or *Picea* or *Pinus* or *Populus* or *Quercus*) and (*insect* or *pest* or *fungi* or *pathogen*) and (*drought* or *water stress*). We also examined the cited references in relevant articles we retrieved. Studies were included in the meta-analysis if they met the following specific criteria:

1. The study assessed tree damage caused by an insect or a fungal pathogen, not just on herbivore performance or abundance. We considered as damage variables all measures that quantified impact on tree survival or tree growth via two main proxies, (i) the amount of damaged or consumed tree tissues and (ii) the number of attacks per tree or the percentage of infested or killed trees (see Appendix S1 for details). We included in the meta-analysis studies reporting on any insect and fungal species that were observed to affect tree tissues or organs whether they are usually considered as pest and pathogen or not. We also retained studies focusing on trees or woody shrubs that were not in forests, but in savanna or urban areas.
2. The mean of the response variable (tree damage), a measure of the variance (standard deviation, standard error, or confidence interval) and the sample size for both 'control' and 'drought' treatments (as defined by authors) were reported (in the text, tables or graphs) to allow calculation of effect sizes.
3. The water conditions in the control and stressed group of trees were quantified using predawn leaf water potential (Ψ_p), most often with a pressure chamber. This was to ascertain that the two groups of trees were under different water supply conditions and that the methodology of water stress assessment was consistent across studies. For example, we discarded studies in which different watering treatments or different natural precipitations were compared, but without any check of the water tree status, as well as studies where it was assessed through soil humidity or tree organ water con-

tent. The Ψ_p values were used as indicators of water stress severity (Delzon *et al.*, 2004) and we included all studies reporting Ψ_p values even if the authors did not find any significant differences in water potential between stressed and unstressed trees.

4. The reported paired comparison between water-stressed and unstressed (control) trees was made under the same environmental conditions (besides water supply), on the same date and in the same area.

Calculating effect sizes and documenting explanatory variables

The effect of water stress on forest insect and disease damage was estimated by computing Hedges' *d* as a measure of the effect size (Appendix S1). A positive value of *d* indicates higher damage on water-stressed trees than on control trees.

When several damage variables (response variables) were available, we selected only one variable per comparison between water-stressed and unstressed trees to avoid pseudoreplication. We chose as response variable the variable documented with the largest sample size or the variable that allowed the highest number of possible paired comparisons. When results for a damage variable were reported for several years in the same sample, we only used data from the first year to avoid confounding factors such as the effects of cumulative previous biotic damage. Similarly, when watering or drought treatments were applied several times, with damage assessment in between, we only considered the first application. When results of an experiment were reported for 2 years but from two different, independent tree samples, data for each year were used as two separate comparisons. Likewise, two independent experiments (different sites, insects, fungus or tree species) reported in the same paper were considered as two separate comparisons.

To quantify water stress severity, we calculated four variables. The first two variables were calculated with the information provided in the retained papers as the difference or the ratio between the mean predawn leaf water potential in water-stressed ($\Psi_{P\ \mathrm{Stress}}$) and control trees ($\Psi_{P\ \mathrm{Control}}$). Predawn leaf water potential conventionally takes negative values and has higher absolute value in water-stressed trees. The other two variables, representing the hydraulic failure (level of native embolism), were calculated as the difference or the ratio between the mean predawn leaf water potential in water-stressed trees in the study ($\Psi_{P\ \mathrm{Stress}}$) and the xylem pressure inducing 50% loss in hydraulic conductance (P_{50}) due to cavitation in the same tree species. P_{50}, a proxy of cavitation resistance, has been shown to be highly variable between species (Delzon *et al.*, 2010) and well correlated with plant drought tolerance (lethal water stress) (Brodribb & Cochard, 2009; Brodribb *et al.*, 2010). We could retrieve P_{50} values for all but one tree species (*Pinus yunnanensis*) involved in our review (Appendix S3).

We split the dataset into subsets of different functional groups of insects or fungi depending on their feeding substrate as described in the literature. First, we considered insect or fungal species colonizing foliar organs involved in photosynthetic processes (leaves, needles) vs. those living in woody organs responsible for tree structure (bark, wood, roots). Second, we distinguished insect or fungal species that can usually develop on healthy trees (primary agents) from those that only exploit trees in poor physiological conditions (secondary agents) (Wainhouse, 2005). For example, endophytic fungi (endophytes) were considered as falling into the category of secondary agents as they are latent in healthy trees, surviving asymptomatically within tree tissues and they turn pathogenic in stressed trees (Slippers & Wingfield, 2007). By combining these two classifications, we expected four theoretical functional groups of insects and fungi; however, the species included in our survey could only match with three groups, as we were not able to find examples of secondary agents damaging foliar organs (Table 1). In some studies, disease symptoms caused by endophytes (*Sphaeropsis sapinea* and *Botryosphaeria dothidea*) were recorded on leaves or needles, but we considered them living on woody organs because these are their main trophic substrate. We also classified damaging agents according to their trophic guild: chewing, boring, sucking and galling insects, leaf pathogens, root and bark rot, bluestain fungi and endophytes.

We also considered the type of drought comparison. Studies were classified into observational vs. experimental depending on whether the drought was due to natural site conditions or controlled water supply (irrigation or soil covering). In both experimental and observational studies, we used as control treatment the one proposed by authors; i.e. with highest mean water potential (i.e. less negative). We also distinguished between comparisons made in the field (forest or nursery) vs. in protected conditions (greenhouse or climatic chamber), i.e. in the absence of natural enemies.

In 14% of the cases, several water stress treatments of different severity were compared with the same control within the same publication. This means that these particular comparisons were not truly independent. In the case of multiple comparisons, it is recommended to create an average of the publication-level effect sizes to estimate the mean effect (Lipsey & Wilson, 2001; Little *et al.*, 2008). To conduct this test, we used the method proposed by Borenstein *et al.* (2009) for multiple comparisons within a study (Bertheau *et al.*, 2010). The outcome with the reduced dataset ($n = 76$ comparisons) was almost identical to that obtained with the complete dataset ($n = 100$). For example, the nine mean effect sizes accounting for the combination of feeding guilds/disease types and type of damaged organs did not significantly differ when calculated from the whole and from the reduced datasets (Kolmogorov–Smirnov test, $P = 0.99$). To keep the maximum of information and benefit from higher statistical power, we therefore decided to use all pairwise comparisons.

Effect sizes across all comparisons were combined using the random effects model (Gurevitch & Hedges, 1993) to provide the grand mean effect size (d_{++}). The effect was considered statistically significant if the bootstrap confidence interval, calculated with 9999 iterations, did not include zero. The mean effect size (d_{+}) and 95% bias-corrected bootstrap confidence

Table 1 Classification of forest insect and fungus species retrieved in the review according to the affected tree organ and the physiological status of affected trees

Primary agent		Secondary agent	
Insect	Fungus	Insect	Fungus
Foliar organs			
Asphondylia spp.	*Septoria musiva*		
Chrysomela populi			
Corytucha arcuata			
Elatobium abietinum			
Leaf aphid sp.			
Lymantria dispar			
Malacosoma disstria			
Neodiprion autumnalis			
Neodiprion fulviceps			
Neodiprion sertifer			
Schizolachnus pineti			
Woody organs			
Dioryctria sylvestrella	*Armillaria ostoyae*	*Dendroctonus frontalis*	*Biscogniauxia mediterranea*
Matsucoccus feytaudi	*Phytophthora cinnamomi*	*Ips acuminatus*	*Botryosphaeria dothidea*
Pissodes strobi	*Fusarium solani*	*Oncideres cingulata*	*Botryosphaeria stevensii*
Pissodes validirostris	*Thyronectria austro-americana*	*Scolytus ventralis*	*Cystospora chrysosperma*
Rhyacionia buoliana			*Leptographium wingfieldii*
			Leptographium yunnanense
			Ophiostoma ips
			Ophiostoma polonicum
			Sphaeropsis sapinea

interval were calculated for each functional group of forest insect or fungi combining affected tree organ and its physiological status. We used a mixed effect model to test the between-classes heterogeneity and evaluated the significance of the class effect (Gurevitch & Hedges, 1999). To account for the problem of multiple comparisons, we used the more conservative $P = 0.001$ value for statistical significance (Gates, 2002). We also used a mixed model to test the relationship between difference in damage on stressed vs. control trees (effect size) and severity of water stress (as continuous variable).

The so-called 'file drawer problem' was addressed by calculating a fail-safe sample size that represents an estimate of the number of non-significant, unpublished or missing studies that would need to be added to the analysis to make the overall test of an effect statistically non-significant. The weighted method proposed by Rosenberg (2005) was used to calculate the fail-safe number for our dataset and this number was compared with Rosenthal's conservative critical value of $5n + 10$ (Rosenberg *et al.*, 2000), where n is the total number of individual comparisons. We double checked the dataset for publication bias with a Spearman rank-order correlation (between effect size and sample size) and we drew and visually assessed funnel plots to identify potential publication bias and abnormalities in data structure (Rosenberg *et al.*, 2000).

All analyses were carried out using METAWIN 2.0 software (Rosenberg *et al.*, 2000).

Results

Our literature search yielded 100 comparisons of forest pest and disease damage on water-stressed vs. unstressed trees, derived from 40 publications and reports that were published between 1975 and 2010 (see the list of references in Appendix S2). They involved 27 insect and 14 fungus species (Appendix S1). The most frequently studied species were *Biscogniauxia mediterranea*, *Phytophthora cinnamomi* and *Neodiprion autumnalis*, which accounted for 12%, 9% and 8% of the comparisons respectively. A total of 26 tree or shrub species were studied, of which 46% were broadleaves and 54% conifers. *Pinus sylvestris*, *Pinus ponderosa*, *Larrea tridentata*, *Quercus rubra* and *Populus nigra* were the most frequent tree species with 14%, 12%, 8%, 6%, and 6% of the comparisons respectively.

Overall water stress resulted in higher forest pest and disease damage as the grand mean effect size equalled 0.23 and was significantly different from zero (95% CI = 0.06–0.41; $n = 100$, $P < 0.0001$). However, according to Cohen (1988), an effect size of 0.2 is considered a small effect, as in this case. Furthermore, 40% of the individual effects were negative, indicating lower damage in water-stressed trees (Fig. 1).

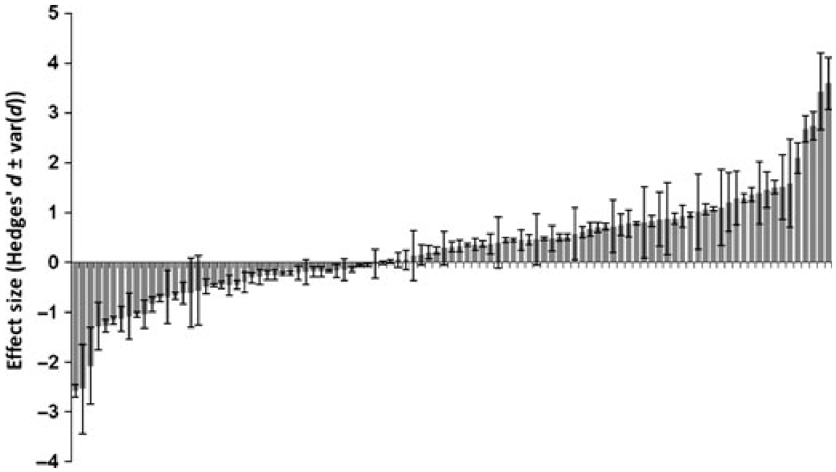

Fig. 1 Hedges' *d* effect size (and variance) of 100 individual studies on forest pest and disease damage in water-stressed vs. unstressed trees. Negative effect sizes indicate that drought resulted in lower damage. More information on each study is given in Appendix S1.

The weighted fail-safe sample size was 788, thus a greater value than the conservative critical value of 510 (5 × 100 + 10). Furthermore, the Spearman rank order was not significant (*R*s = −0.08, *P* = 0.43) and the funnel plot did not reveal any outliers, with no gap in the lower values of the effect size. Thus, these results were unlikely to be affected by publication bias.

Effect of pest and pathogen functional groups

The type of trophic substrate used by forest pest and pathogens had a highly significant effect on the difference in damage between water-stressed and unstressed trees [df = 2, Q between (QB) = 43.4, *P* = 0.0001]. For primary damaging agents living on foliar organs, the mean effect size was significantly positive (*d* = +0.31), indicating higher damage in water-stressed trees (Fig. 2). For pest insects and pathogens developing on woody organs, the drought effect differed between the primary and the secondary agents. Drought had negative effects on damage caused by primary agents (*d* = −0.63), but significantly increased damage caused by secondary agents (*d* = +0.65).

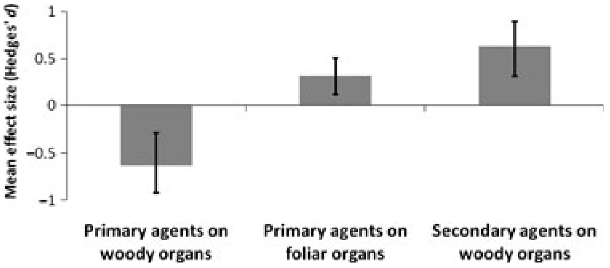

Fig. 2 Mean Hedges' effect size (*d* ± 95% bias corrected bootstrap CI) per functional group of forest pest and pathogen.

Within each functional group of forest pests and pathogens, the effects of trophic guild were never significant (Table 2). Effect sizes were consistently negative for sucking and boring insect and root and bark rot fungus species developing in woody organs in healthy trees (primary agents). Mean effects were consistently positive for leaf pathogens living in foliar organs in healthy trees (but only one species was tested, *Septoria musiva*) and galling and chewing insects, although marginally significant for the latter guild. The pattern was less clear for pests and pathogens living on woody organs of weakened trees (Table 2) with positive mean effect size for endophytic fungi, but mean effect sizes not significantly different from zero for boring insects and associated blue-stain fungi (although the sample size was low).

These results clearly indicate that the effect of water stress on the level of damage by forest pests and pathogens depends more on the type of substrate they use than on their feeding guild.

Effect of water stress application

We tested the effect of the type of water stress application on level of damage for each functional group of forest pests and pathogens separately. We did not detect any significant difference in mean effect size between observational and experimental studies (*n* = 39, QB = 0.12, *P* = 0.72 for primary agents feeding on foliar organs, *n* = 22, QB = 0.35, *P* = 0.60 for primary agents feeding on woody organs; no sufficient data for secondary agents), nor between studies made in the field or in protected conditions (greenhouses or

Table 2 Effects of drought on mean effect size (damage) by different types of forest pest and pathogens

Class variable*	Sample size	Hedges' $d^{\dagger}$	Bias corrected bootstrap 95% confidence interval
Primary agents living on woody organs (QB = 1.87, $n = 22$, $P = 0.46$)			
Sucking insects	2	**−0.14**	−0.22 to −0.05
Boring insects	8	**−0.84**	−1.60 to −0.29
Root and bark rot fungi	12	**−0.61**	−0.97 to −0.25
Primary agents living on foliar organs (QB = 2.13, $n = 38$, $P = 0.36$)			
Chewing insects	20	+0.24	−0.05 to +0.55
Galling insects	12	**+0.33**	+0.04 to +0.61
Leaf pathogens	6	**+0.67**	+0.37 to +1.01
Secondary agents living on woody organs (QB = 2.34, $n = 39$, $P = 0.07$)			
Boring insects	6	+0.29	−0.49 to +1.57
Blue-stain fungi	5	+0.35	−0.26 to +1.04
Endophytic fungi	28	**+0.80**	+0.49 to +1.17

Note that the mean effect size could not be calculated for the only case of insect sucking on tree crown.

QB, Q between.

*Class effect (P).

†In bold: Hedges' d effect size significantly differs from zero, based on a bootstrap CI.

climatic chambers) for any functional group ($n = 39$, QB = 0.33, $P = 0.58$ for primary agents feeding on foliar organs, $n = 22$, QB = 0.18, $P = 0.71$ for primary agents feeding on woody organs, and $n = 39$, QB = 0.10, $P = 0.15$ for secondary agents feeding on woody organs).

Effect of water stress severity

We tested the effect of water stress severity on level of damage for each functional group of forest pests and pathogens separately. We observed no significant effect of any water severity variables on level of damage in water-stressed trees for any primary damaging agent (Table 3). On the contrary, the effect of water stress severity significantly affected the level of damage caused by secondary agents living in woody organs (Table 3). The variable best explaining damage variation was the ratio between observed predawn leaf water potential in stressed trees ($\Psi_{\mathrm{P\ Stress}}$) and the species-specific index of drought tolerance (P_{50}) (Table 3). The level of damage increased linearly with this ratio (Fig. 3). A threshold value of 30% was detected below which damage in water-stressed trees may be lower than in unstressed trees (negative effect size), whereas damage were consistently higher in stressed trees with predawn leaf water potential higher than 30% of P_{50} (tree having a high native state of embolism; Fig. 3). Interestingly, a covariance analysis showed a significant effect ($P < 0.001$) of stress severity ($\Psi_{\mathrm{P\ Stress}}/P_{50}$), but no significant effect ($P = 0.22$) of the damaging agent type (fungus vs. insect) nor of the interaction between the two factors ($P = 0.54$) indicating a similar response of secondary pest and pathogen damage to stress severity. Finally, we found no significant effect of the tree species-specific drought resistance (P_{50}) and the mean damage for any functional group of damaging agent ($P = 0.25$, 0.35 and 0.11 respectively for primary agents feeding on foliar organs, primary agents feeding on woody organs and secondary agents feeding on woody organs respectively).

Discussion

Our meta-analysis provides the first comprehensive overview of effects of water stress on damage made by both forest pests and pathogens. It confirms that drought does not systematically result in higher biotic damage. Type of feeding substrate for forest insect and pathogens as well as water stress severity emerged as the two key factors explaining differential response to drought. Primary damaging agents living in woody organs caused significantly lower damage on water-stressed trees, whereas those living on foliar organs made significantly higher damage, in all cases irrespec-

Table 3 Relationships between water stress severity and forest pests and pathogens level of damage in stressed trees

	$\lvert \Psi_{\mathrm{P\ Stress}} - \Psi_{\mathrm{P\ Control}} \rvert$	$\lvert P_{50} - \Psi_{\mathrm{P\ Stress}} \rvert$	$\Psi_{\mathrm{P\ Control}}/\Psi_{\mathrm{P\ Stress}}$	$\Psi_{\mathrm{P\ Stress}}/P_{50}$
Primary agents on woody organs	ns	ns	ns	ns
Primary agents on foliar organs	ns	ns	ns	ns
Secondary agents on woody organs	$P = 0.007$ $R^2 = 0.31$	$P = 0.015$ $R^2 = 0.33$	ns	$P = 0.0002$ $R^2 = 0.47$

Water stress severity was calculated as difference or ratio between predawn leaf water potential in control trees ($\Psi_{\mathrm{P\ Control}}$), water-stressed trees ($\Psi_{\mathrm{P\ Stress}}$) and trees in which 50% of hydraulic conductivity is lost due to cavitation (P_{50}). Level of damage was estimated using Hedges' effect size. Relationships between water stress severity and damage level were tested with a mixed linear model.

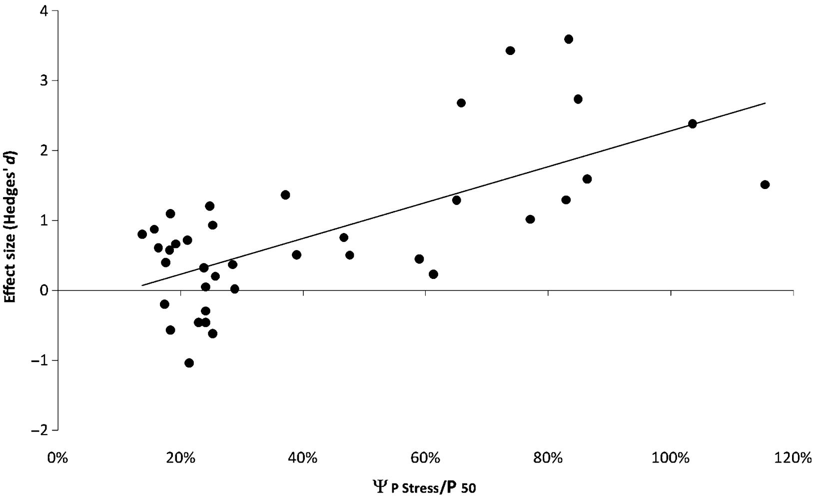

Fig. 3 Relationship between level of damage (effect size) made by secondary forest pests and pathogens living on woody organs and water stress severity ($\Psi_{\mathrm{P\ Stress}}/P_{50}$). ($y = -0.28 + 2.57x$, $n = 39$, $P = 0.0002$, $R^2 = 0.47$.

tive of stress severity. In contrast, damage made by secondary agents on water-stressed trees increased with stress intensity. In some cases, trees under mild water stress conditions were less damaged than unstressed trees, whereas above a threshold of stress severity, all stressed trees were more damaged by these secondary agents. The difference in response to tree conditions we found in our study between primary and secondary agents is not surprising as the definition of these two groups of pests and pathogens is based on their ability to colonize and survive in healthy vs. weakened host trees (Wainhouse, 2005; Sinclair & Lyon, 2005).

Forest pest and pathogen performances under drought conditions

Damage can be considered as a function of tree resistance and pest or pathogen performances, which may be both affected by drought conditions. Koricheva *et al.* (1998) and Huberty & Denno (2004), using the same meta-analysis approach, demonstrated that the magnitude and direction of insect performance response to water stress depend on their feeding traits. In both studies, they found that borers performed better on stressed plants, whereas gall makers and leaf chewers were negatively affected in their performance. However, there were also discrepancies between the outcomes of the two reviews. In particular, sap suckers were considered as performing better on stressed trees in Koricheva *et al.* (1998), whereas Huberty & Denno (2004) found the opposite. In contrast, direct effects of drought on forest pathogens are expected to be mainly negative, irrespective of the development substrate, as fungi require high humidity conditions for spore dispersal, germination and infection. However, indirect effects through host physiology may be predominant, such as for endophytic pathogens (Desprez-Loustau *et al.*, 2006). The combination of effects on the performance of the biotic agent and effects on tree response may explain discrepancies in the results of different studies, when either performance or damage is being considered. For example, primary boring insects caused lower damage in severely water-stressed trees, whereas secondary boring insects caused higher damage. These examples clearly illustrate that plant–pathogen relationships are to be considered for predicting the effect of water stress on level of damage.

Drought and tree resistance to forest pests and pathogens

Drought can affect the nutritional quality of host trees for herbivorous insect and fungal pathogens through changes in water, carbohydrates and nitrogen contents (Rouault *et al.*, 2006; Netherer & Schopf, 2010). Water supply is critical for primary metabolism of plant and thus greatly influences carbohydrate photosynthesis and hence the provision of sugars for herbivorous insects and parasitic fungi. Obligate biotrophic foliar parasites only develop on vigorous hosts (Desprez-Loustau *et al.*, 2006). As a consequence of drought, reduced concentration of carbohydrates in conifer bark tissues has been proposed as an explanation for the reduced development of bark beetles and of the blue-stain fungi they carry into their gallery (Speight & Wainhouse, 1989).

During drought period, reduced water content and proteins hydrolysis (i.e. the 'Plant Stress Hypothesis' White 1969) lead to higher nitrogen concentration in tree organs. As nitrogen is generally limiting for many insects, increase in available plant nitrogen during water stress could result in improved growth of phytophagous insects (Mattson & Haack, 1987), and particularly of folivorous species as water stress increases nitrogen allocation to crown vs. stem (Martin *et al.*, 1998). For example, defoliator performances are higher in moderately water-stressed trees due to higher concentration of soluble nitrogen in foliage (White, 1984; Mattson & Haack, 1987; Larsson, 1989; Larsson & Björkman, 1993). Sap feeding insect would also benefit from this increase in nitrogen concentration (Huberty & Denno, 2004). Some amino-acids, such as proline, asparagine and alanine, were found in increased concentrations in water-stressed plantlets of *Populus tremuloides* and stimulated the hyphal growth of the bark canker fungus *Entoleuca mammata* (Belanger *et al.*, 1990). As a result, the concentrations of carbohydrates and nitrogen are expected to decrease in the stem of trees under moderate water stress. This would limit the performances and then the damage of primary pest living on woody organs as we found in our analyses (Table 2, Fig. 2). For the same reasons, performance and damage made by primary pests living on foliar organs, benefiting from higher nitrogen content, would increase as confirmed by our results (Table 2, Fig. 2).

Besides nutritional quality of host tissues, water stress also affects host metabolism involved in resistance to pest and pathogen damage. On the one hand, some resistance mechanisms might be increased. Secondary metabolites (e.g. tannins – Forkner *et al.*, 2004), involved in tree resistance, are often in higher concentrations in foliage of water-stressed trees, which were shown to affect larval performance of Lepidoptera such as *Operophtera brumata* on *Quercus robur* (Buse & Good, 1996). Leaf chewers such as lepidopteran, sawfly larvae and beetles would be more susceptible to increased defence compounds in leaf tissues of water-stressed trees than sap feeders (e.g. aphids), phloem and cambium feeders as vascular tissues contain lower amount of allelochemicals (Mattson & Haack, 1987; Larsson, 1989; Awmack & Leather, 2002; Huberty & Denno, 2004). On the other hand, resistance mechanisms might be less effective in water-stressed trees, as summarized by Schoeneweiss (1986) in the predisposition concept. Phytoalexins produced in cypress and inhibiting the development of *Diplodia pinea* f. sp. *cupressi*, were found to accumulate more slowly and at lower concentrations in water-stressed plants as compared with controls (Madar *et al.*, 1995). The formation of the necrophylactic periderm, an active defence barrier against pathogen colonization, was shown to be delayed in water-stressed tissues (Puritch & Mullick, 1975). More generally, mechanisms involved in resistance to canker pathogens, such as compartmentalization and callusing, were shown to be less effective in stressed trees than in well-watered trees (Bevercombe & Rayner, 1980; McIntyre *et al.*, 1996).

Water stress severity

Lower water supply affects not only sap flow but also oleoresin production and pressure. This results in lower constitutive resistance to primary attacks of many bark beetles (Lieutier, 2004; Rouault *et al.*, 2006). Furthermore, infection of pathogenic blue-stain fungi by scolytids often results in the development of necrotic lesions containing high concentration of terpenoid and phenolic chemicals that are toxic to both insects and fungi. Water-stressed trees would lack carbohydrates reserve to fuel the secondary metabolism involved in these induced resistance processes (Lieutier, 2004). As a consequence, severely water-stressed trees are likely to be more damaged by secondary pest and pathogens like wood boring insects and associated bleu-stain fungi, just as we observed in our review (Table 2 and Fig. 2).

However, while tree resistance to secondary pests such as scolytids is likely to be impaired by severe stress, moderate water stress would lead to increased resistance. According to the 'growth–differentiation balance' hypothesis (Herms & Mattson, 1992), in normal conditions, carbohydrates produced by photosynthesis are mainly allocated to growth and development of new foliage, whereas a lower priority is given to production of defensive chemicals. Under moderate water stress, the carbohydrate pool still increases, but can be diverted to the synthesis of defensive secondary chemicals (such as phenolic and terpenoid compounds) so that trees become more resistant to insect attacks (Speight & Wainhouse, 1989; Herms & Mattson, 1992; Lieutier, 2004). It is then expected that secondary pests living in woody organs, like bark beetles, would cause less damage in moderately water-stressed trees, thus explaining the presence of negative effect sizes in our meta-analysis (Figs 1 and 3). We found a significant and positive relationship between the level of damage by secondary pests and pathogens and the stress intensity (Fig. 3). This is consistent with the prediction that water-stressed trees would shift from more resistance to more sensitivity (than unstressed trees) with increasing stress severity.

Furthermore, in severely stressed trees, decreased water content may lead to tougher foliage, resulting in lower herbivory by chewing insects such as defoliating Lepidoptera (Hodar *et al.*, 2002; Tikkanen & Lyytikäinen-Saarenmaa, 2002; Henriksson *et al.*, 2003) or Hymenoptera (Pasquier-Barre *et al.*, 2001). As expected, we did find negative effect size for chewing insects on foliar organs (lower damage in water-stressed trees, Table 2), but we were not able to show a negative correlation between damage level and stress severity (Table 3).

We found the ratio between leaf water potential in water-stressed trees and P_{50} in the same tree species to be a better predictor of secondary pest and pathogen damage than the difference between leaf water potential in water-stressed and control trees. Two main reasons might explain this result. First, unstressed trees in the retrieved studies may not have been in the optimal water supply conditions and thus did not provide the best control situation. Second, P_{50} is now considered as a reliable species-specific index of drought tolerance (Brodribb & Cochard, 2009), thus offering a more accurate reference when compared with the realized water stress in the study. For example, when leaf water potential in water-stressed trees goes beyond the P_{50} threshold, trees are at least cavitated at 50%.

Conclusion

Insect and pathogen status (primary vs. secondary pest and pathogens), affected tree part (foliar vs. woody organs) and water stress severity clearly are three important predictors of biotic damage in water-stressed trees. We therefore propose to use a combination of these three factors to assess the potential risk of tree damage in response to prolonged or more frequent droughts that are expected to come along with climate change (Table 4). The type of trophic substrate at both organ (leaf vs. wood) and tree (weakened vs. vigorous) levels seems a more relevant criterion than feeding guilds to rank forest pest and pathogen according to their potential impact on water-stressed trees. Moreover, our results suggest that water stress severity should not be considered an absolute value, but relative to the intrinsic drought resistance of a given tree species, which can be evaluated through the xylem pressure inducing 50% loss in hydraulic conductance (P_{50}). However, further investigations are needed, particularly in field conditions, to substantiate this risk analysis. For example, little is known about the effects of water stress on tree damage during pest or pathogen outbreaks, whether more frequent droughts might increase the magnitude or the recurrence of epidemics. It would also be of interest to investigate drought consequences for top-down regulation of pest and pathogen populations as very few studies have so far addressed the direct and indirect effects of reduced precipitation on parasitoid, predator or antagonist species.

Table 4 Conceptual Table showing that the risk of damage due to drought depends on three components: (i) insect or fungus trophic behaviour (primary vs. secondary agents), (ii) type of affected tree part (foliar vs. woody organs) and (iii) water stress severity (relative to P50, the species specific index of drought tolerance)

	Mild water stress	Severe water stress
Primary agents		
Foliar organs	↘	↘
Woody organs	↗	↗
Secondary agents		
Woody organs	→	↗

↘ Reduced damage in water-stressed trees.
↗ Increased damage in water-stressed trees.
→ Unchanged damage in water-stressed trees.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Summary of data included in the meta-analysis.
Appendix S2. List of references used in the meta-analysis.
Appendix S3. P_{50} values (in MPa) of tree species retrieved in the review.