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A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests

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ABSTRACT

Greenhouse gas emissions have significantly altered global climate, and will continue to do so in the future. Increases in the frequency, duration, and/or severity of drought and heat stress associated with climate change could fundamentally alter the composition, structure, and biogeography of forests in many regions. Of particular concern are potential increases in tree mortality associated with climate-induced physiological stress and interactions with other climate-mediated processes such as insect outbreaks and wildfire. Despite this risk, existing projections of tree mortality are based on models that lack functionally realistic mortality mechanisms, and there has been no attempt to track observations of climate-driven tree mortality globally. Here we present the first global assessment of recent tree mortality attributed to drought and heat stress. Although episodic mortality occurs in the absence of climate change, studies compiled here suggest that at least some of the world's forested ecosystems already may be responding to climate change and raise concern that forests may become increasingly vulnerable to higher background tree mortality rates and die-off in response to future warming and drought, even in environments that are not normally considered water-limited. This further suggests risks to ecosystem services, including the loss of sequestered forest carbon and associated atmospheric feedbacks. Our review also identifies key information gaps and scientific uncertainties that currently hinder our ability to predict tree mortality in response to climate change and emphasizes the need for a globally coordinated observation system. Overall, our review reveals the potential for amplified tree mortality due to drought and heat in forests worldwide.

1. Introduction

Forested ecosystems are being rapidly and directly transformed by the land uses of our expanding human populations and economies. Currently less evident are the impacts of ongoing climate change on the world's forests. Increasing emissions of greenhouse gases are now widely acknowledged by the scientific community as a major cause of recent increases in global mean temperature (about 0.5 8C since 1970) and changes in the world's hydrological cycle (IPCC, 2007a), including a widening of the Earth's tropical belt (Seidel et al., 2008; Lu et al., 2009). Even under conservative scenarios, future climate changes are likely to include further increases in mean temperature (about 2–4 8C globally) with significant drying in some regions

(Christensen et al., 2007; Seager et al., 2007), as well as increases in frequency and severity of extreme droughts, hot extremes, and heat waves (IPCC, 2007a; Sterl et al., 2008).

Understanding and predicting the consequences of these climatic changes on ecosystems is emerging as one of the grand challenges for global change scientists, and forecasting the impacts on forests is of particular importance (Boisvenue and Running, 2006; Bonan, 2008). Forests, here broadly defined to include woodlands and savannas, cover 30% of the world's land surface (FAO, 2006). Around the globe societies rely on forests for essential services such as timber and watershed protection, and less tangible but equally important recreational, aesthetic, and spiritual benefits. The effects of climate change on forests include both positive (e.g. increases in forest vigor and growth from CO2 fertilization, increased water use efficiency, and longer growing seasons) and negative effects (e.g. reduced growth and increases in stress and mortality due to the combined impacts of climate change and climate-driven changes in the dynamics of forest insects and pathogens) (Ayres and Lombardero, 2000; Bachelet et al., 2003; Lucht et al., 2006; Scholze et al., 2006; Lloyd and Bunn, 2007). Furthermore, forests are subject to many other human influences such as increased ground-level ozone and deposition (Fowler et al., 1999; Karnosky et al., 2005; Ollinger et al., 2008). Considerable uncertainty remains in modeling how these and other relevant processes will affect the risk of future tree die-off events, referred to hereafter as 'forest mortality', under a changing climate (Loehle and LeBlanc, 1996; Hanson and Weltzin, 2000; Bugmann et al., 2001). Although a range of responses can and should be expected, recent cases of increased tree mortality and die-offs triggered by drought and/or high temperatures raise the possibility that amplified forest mortality may already be occurring in some locations in response to global climate change. Examples of
recent die-offs are particularly well documented for southern parts of Europe (Penũelas et al., 2001; Breda et al., 2006; Bigler et al., 2006) and for temperate and boreal forests of western North America, where background mortality rates have increased rapidly in recent decades (van Mantgem et al., 2009) and widespread death of many tree species in multiple forest types has affected well over 10 million ha since 1997 (Raffa et al., 2008). The common implicated causal factor in these examples is elevated temperatures and/or water stress, raising the possibility that the world's forests are increasingly responding to ongoing warming and drying.

This paper provides an overview of recent tree mortality due to climatic water stress and warm temperatures in forests around the globe. We identify 88 well-documented episodes of increased mortality due to drought and heat and summarize recent literature on forest mortality and decline. From this review we examine the possibility of emerging mortality risks due to increasing temperatures and drought. Climate as a driver of tree mortality is also reviewed, summarizing our scientific understanding of mortality processes as context for assessing possible relationships between changing climate and forest conditions. Note that while climatic events can damage forests in many ways ranging from ice storms to tornadoes and hurricanes, our emphasis is on climate-induced physiological stress driven by drought and warm temperatures. The ecological effects of increased mortality in forests and the associated consequences for human society remain largely unassessed. We conclude by outlining key information gaps and scientific uncertainties that currently limit our ability to determine trends in forest mortality and predict future climate-induced forest die-off. Addressing these gaps would provide improved information to support policy decisions and forest management worldwide.

2. Methods

This paper emerged in part from collaborations and presentations developed in special sessions on climate-related forest mortality at two international meetings: the 2007 annual meeting of the Ecological Society of America in San Jose, California (Allen and Breshears, 2007), and the 2008 international conference entitled ''Conference on Adaptation of Forests and Forest Management to Changing Climate with Emphasis on Forest Health'' in Umea˚ , Sweden (Allen, 2009). In addition to citing contributions from these sessions, we conducted a systematic search for published accounts of climate-induced tree mortality since 1970 using the ISI Web of Science and Google Scholar. We used different combinations of the key words ''tree,'' ''forest,'' ''mortality,'' ''dieoff,'' ''dieback,'' ''decline,'' and ''drought'' in the searches. We also consulted regional forestry experts to find examples recorded in government documents and other sources outside the scientific literature.

From the extensive set of documents uncovered during these searches, we used two specific criteria to determine whether the reference was appropriate for this review. Criteria for inclusion were that the study included: (1) an estimate of area affected or amount of adult tree mortality at the stand or population level, based on ground measurements, aerial photography, or remote sensing, and (2) documentation of a strong correspondence between increases in mortality and increased water stress or high temperatures. We included examples where biotic agents were involved in the mortality, but excluded examples of fire-driven death. Studies of forest decline or partial canopy dieback without significant increases in mortality were also excluded, as were studies that documented only seedling mortality. To simplify presentation, we standardized study descriptors and combined references that describe impacts of the same event on the same tree species but used slightly different methods or were conducted at different spatial scales.

To estimate trends in the literature related to climate-induced forest mortality, we searched the ISI Web of

Science using the topic words ‘‘forest AND mortality AND drought’’ over the available interval from 1985 to 2009. We then controlled for increases in the general scientific literature related to forests by standardizing the number of target articles by the number of citations uncovered by a search using only the topic word ‘‘forest.’’

For each mortality event (listed as rows in Appendix Tables A1– A6) we tested the association between the forest type affected by mortality and the categorized duration of the mortality-triggering drought (seasonal event vs. multi-year drought) with a Chi-square analysis, comparing number of observed triggering droughts (by drought and forest type) versus expected number of triggering droughts. Forest types were grouped into four major biome types considering similar water limitations: (1) savannas, (2) conifer forests and Mediterranean woodlands, (3) temperate evergreen and deciduous forests, and (4) evergreen broadleaved tropical forests.

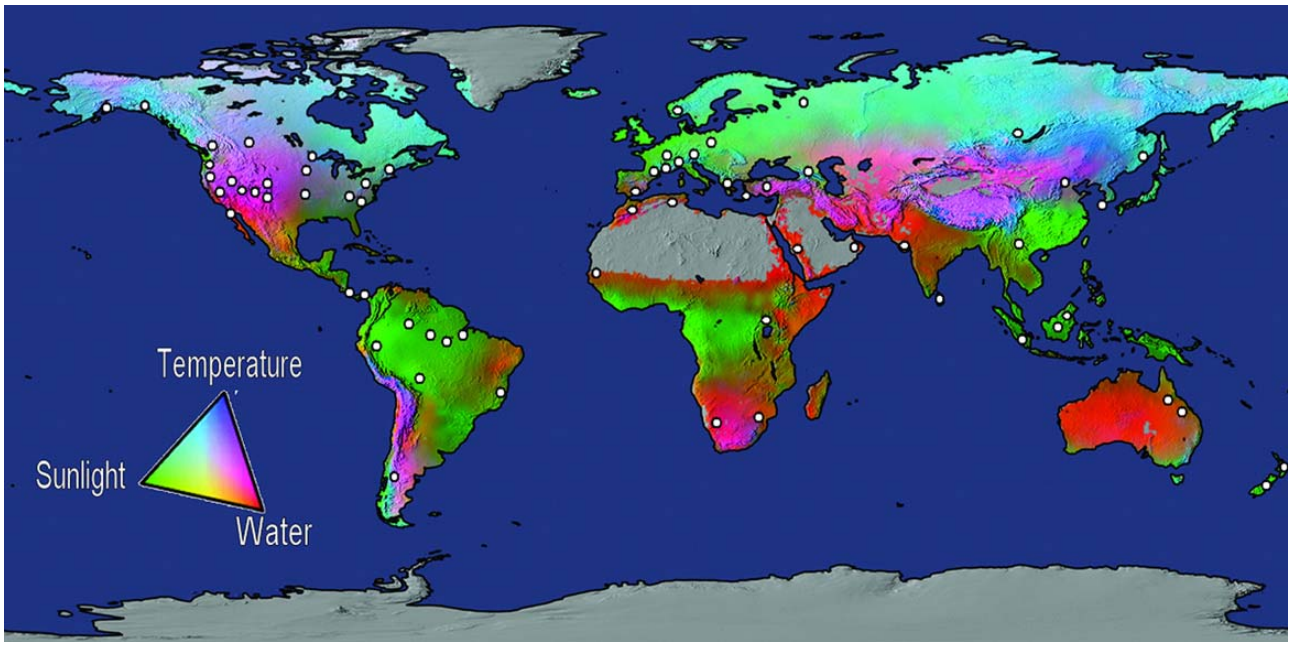


Fig. 1. White dots indicate documented localities with forest mortality related to climatic stress from drought and high temperatures. Background map shows potential environmental limits to vegetation net primary production (Boisvenue and Running, 2006). Only the general areas documented in the tables are shown—many additional localities are mapped more precisely on the continental-scale maps. Drought and heat-driven forest mortality often is documented in relatively dry regions (red/orange/ pink), but also occurs outside these regions.

3. Results

3.1. Examples of recent climate-induced forest mortality

More than 150 references that document 88 examples of forest mortality met our criteria of events that were driven by climatic water/heat stress since 1970. The examples range from modest but significant local increases in background tree mortality rates to climate-driven episodes of regional-scale forest die-off. We found examples from each of the wooded continents that collectively span diverse forest types and climatic zones (Figs. 1–8 and Tables A1–A6). Despite our collective efforts to secure references from non-English language sources, this review is clearly more comprehensive for North America, Europe, and Australia, and obviously incomplete particularly for some regions, including mainland Asia and Russia.

Our searches also reveal that published reports of climate related forest mortality in the scientific literature have increased markedly in recent decades. For example, a search of the ISI Web of Science (23 July 2009) using the topic words ‘‘forest AND mortality AND drought’’ showed 546 references for the period 1985 through 2009, with a steep increase in articles published since 2003 (Fig. 9), even when standardized for general increases in the forest-related scientific literature. The years of elevated mortality documented in the references that met our criteria also show a clear increase in mortality events with a jump in 1998 and marked accumulation of events in the 2000s, particularly the years 2003–2004. Although these trends could be coincidental or a reflection of greater scientific interest in the topic of tree mortality, recent increases in reported events also mirror warming global temperatures.

3.1.1. Continental-scale summaries

3.1.1.1. Africa. Increased tree mortality linked to drought and heat in Africa (Fig. 2; Table A1) includes examples from tropical moist forest in Uganda (Lwanga, 2003), mountain acacia (Brachystegia glaucescens) in Zimbabwe (Tafangenyasha, 2001), mesic savanna trees in South Africa's Kruger National Park (Viljoen, 1995), and centuries-old Aloe dichotoma in Namibia (Foden et al., 2007). In the Sahel, long-term decreases in precipitation linked to anthropogenic climate change (Biasutti and Giannini, 2006) have caused a die-off of mesic tree species in parts of Senegal (Gonzalez, 2001), especially following the severe drought of 1968–1973 (Poupon, 1980). Recent extreme drought in North Africa (Touchan et al., 2008) is linked to severe mortality of Atlas cedar (Cedrus atlantica) from Morocco to Algeria (El Abidine, 2003; Bentouati, 2008; Box 1, see also Fig. 3).



Fig. 2. Satellite map of Africa, with documented drought-induced mortality areas indicated with numbers, tied to Table A1 references. Upper photo: Cedrus atlantica die-off in Belezma National Park, Algeria; 2007, by Haroun Chenchouni. Lower photo: quiver tree (Aloe dichotoma) mortality in Tirasberg Mountains, Namibia; 2005, by Wendy Foden.

3.1.1.2. Asia. Reports of forest mortality in Asia (Fig. 4; Table A2) include death triggered by severe El Niño droughts in 1982/1983 and 1997/1998 in the tropical moist forests of both Malaysian and Indonesian Borneo (Leighton and Wirawan, 1986; Woods, 1989; Nakagawa et al., 2000; van Nieuwstadt and Sheil, 2005). Severe droughts are also associated with increased mortality among many tree species from tropical dry forests in northwest and southwest India (Khan et al., 1994), Abies koreana in South Korea (Lim et al., 2008), Juniperus procera from Saudia Arabia (Fisher, 1997), and pine and fir species in central Turkey (Semerci et al., 2008).

Recent droughts have triggered mortality of Pinus tabulaeformia across 0.5 million ha in east-central China (Wang et al., 2007), and across extensive areas of Pinus yunnanensis in southwest China (Li, 2003). The Russian Federal Forest Agency has mapped zones of forest health risk (''threat'') across the Russian Federation, showing 338 million ha as ''low threat'', 260 million ha as ''medium'' threat, and 76 million ha of ''high'' threat, predominantly in southerly portions of the country (Kobelkov, 2008), where forest health problems due to drought appear to be concentrated (Ermolenko, 2008).

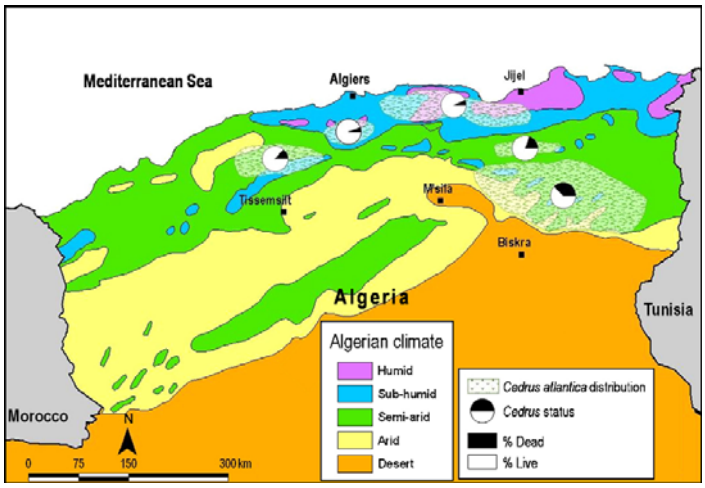


Fig. 3. Map of northern Algeria climate zones and mortality distribution of Cedrus atlantica. ''Box 1 - Atlas Cedar Die-off in Algeria'' serves as the full caption.

Box 1. Atlas Cedar Die-off in Algeria Atlas cedar (Cedrus atlantica) occurs in northern Algeria, distributed in scattered montane populations near the limits of its bioclimatic tolerance between the Sahara Desert and the Mediterranean Sea (Fig. 3). Since the onset of severe drought from 1999 to 2002 cedar forests have undergone mass mortality, affecting all age classes (Bentouati, 2008). While all Algerian cedar forests are affected, the magnitude of mortality varies along a steep moisture gradient (Fig. 3), with die-off greatest (up to 100%) in the drier mountains nearest the Sahara, dropping to much lower mortality levels in the moister coastal mountains (Chenchouni et al., 2008). Prolonged soil moisture deficits lead to decline and progressive death of cedar trees over a period of 1–3 years; a variety of insects and fungi have continued to kill weakened cedar trees since the drought eased after 2002 (Chenchouni et al., 2008). The Cedrus mortality began as small patches on drier aspects in the arid near-Sahara mountains, eventually coalescing into large patches affecting all ages on all exposures. In contrast, only small patches of old trees on dry aspects have died in more mesic regions near the coast. This recent drought also triggered substantial mortality in other Algerian tree species, including Pinus halepensis, Quercus ilex, Quercus suber, and Juniperus thurifera. Dendrochronological reconstructions of drought in Algeria show that this early 2000s dry period was the most severe drought since at least the middle of the 15th century (Touchan et al., 2008), consistent with climate change projections for a trend of increasing aridity in this region (Seager et al., 2007).

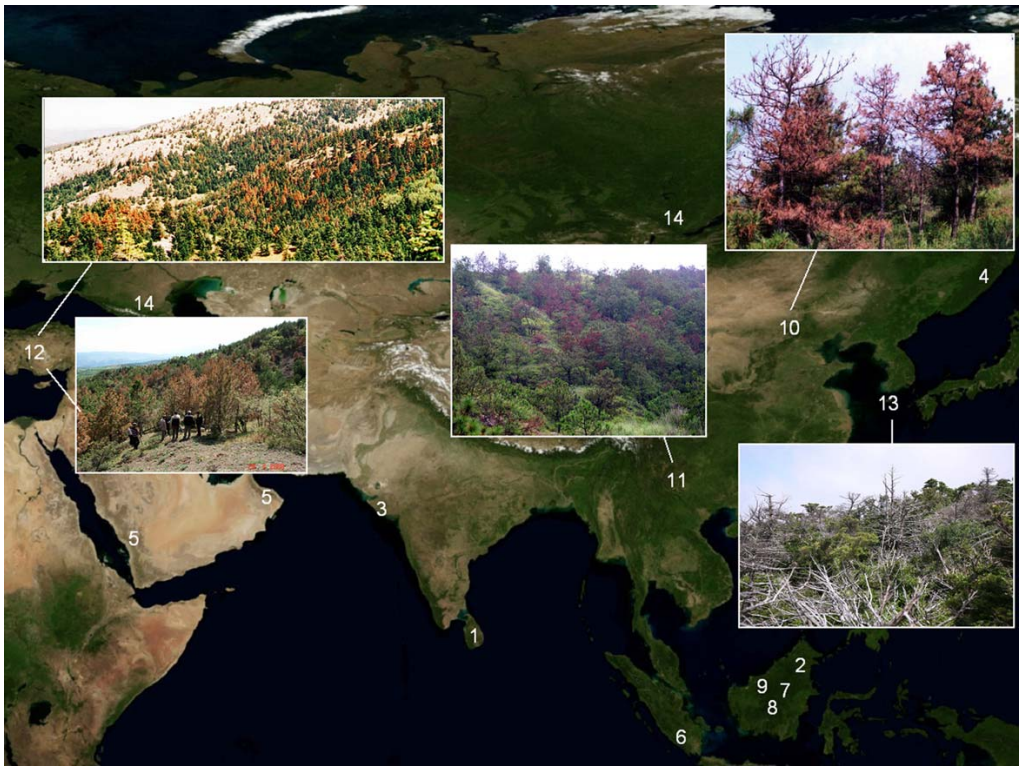


Fig. 4. Satellite map of Asia, with documented drought-induced mortality localities indicated with numbers, tied to Table A2 references. Lower R Photo: Dead Abies koreana, Mount Halla, South Korea; 2008, by Jong-Hwan Lim. Upper R photo: Pinus tabulaeformis mortality in Shanxi Province, China; 2001, by Yugang Wang. Center photo: Dying Pinus yunnanensis in Yunnan Province, China; 2005, by Youqing Luo. Upper L photo; Abies cilicica mortality in the Bozkir-Konya region, Anatolia, Turkey; 2002, by Orphan Celik. Lower L photo: Dying Pinus nigra near Kastamonu, Anatolia, Turkey; 2008, by Akkin Semerci.

3.1.1.3. Australasia. In the sub-humid environments of northeast Australia (Fig. 5; Table A3), multi-year droughts have repeatedly triggered widespread Eucalyptus and Corymbia mortality (Fensham and Holman, 1999; Rice et al., 2004; Fensham and Fairfax, 2007), and have also caused tree death in Acacia woodlands (Fensham and Fairfax, 2005). There is also documentation of drought-induced mortality in temperate Nothofagus forests in New Zealand (Hosking and Hutcheson, 1988).

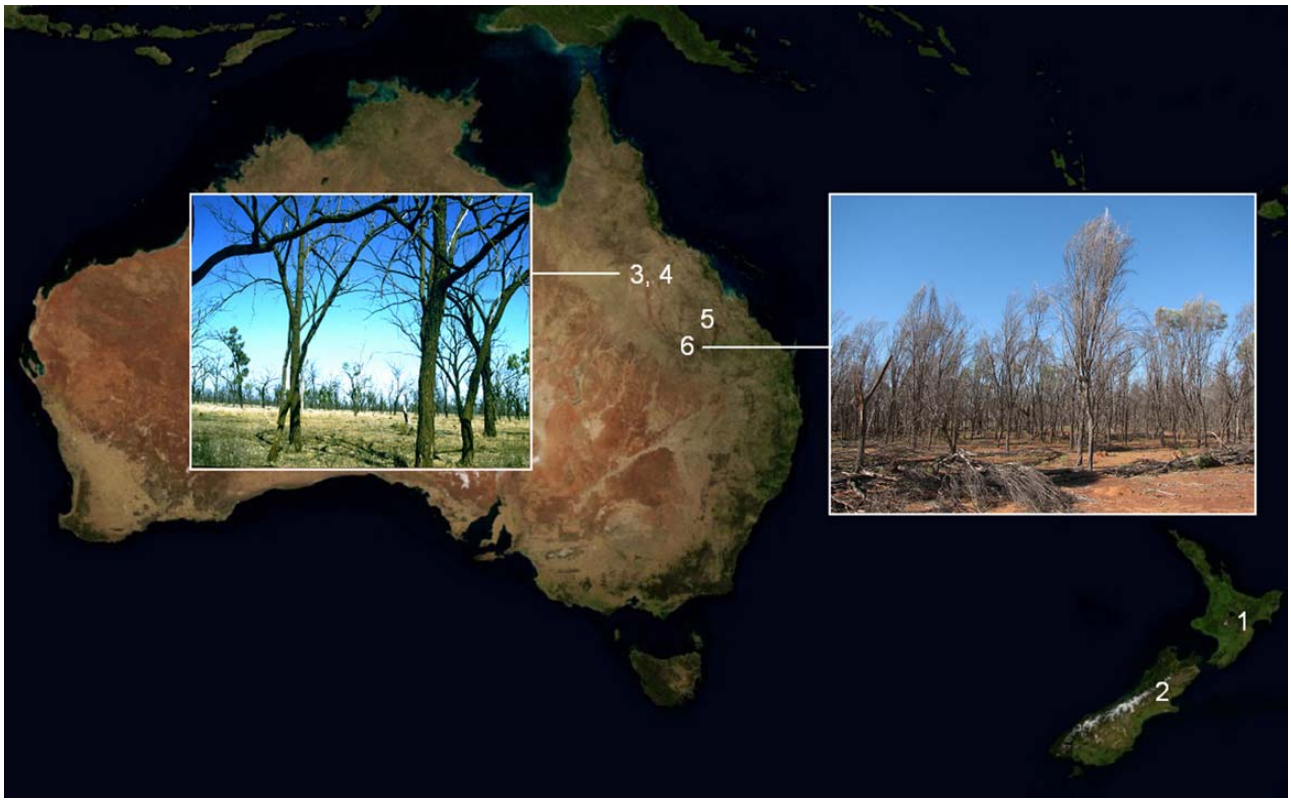


Fig. 5. Satellite map of Australasia, with documented drought-induced mortality areas indicated with numbers, tied to Table A3 references. R photo: Die-off of mulga, Acacia aneura, the dominant tree across large areas of semi-arid Australia; 2007, by Rod Fensham. L photo: Eucalyptus xanthoclada mortality in Queensland, northeastern Australia; 1996, by Rod Fensham.

3.1.1.4. Europe. In Europe (Fig. 6; Table A4), forest mortality due to dry and warm conditions in the 1990s and 2000s arcs across the Mediterranean regions, including increased death among many woody species in Spain (Peñuelas et al., 2001; Martinez-Vilalta and Piñol, 2002), increased mortality of oak, fir, spruce, beech, and pine species in France after the extreme heat wave and drought during the summer of 2003 (Breda et al., 2006; Landmann et al., 2006; Vennetier et al., 2007), and increases in mortality of Pinus sylvestris near the species' southern range limits in Switzerland and Italy (Dobbertin and Rigling, 2006; Bigler et al., 2006; Vertui and Tagliaferro, 1998).

A severe drought in 2000 killed many Abies cephalonica in mainland Greece (Tsopelas et al., 2004) and Pinus halepensis sub. brutia - the most drought tolerant of the Mediterranean pines - in eastern Greece (Körner et al., 2005). Farther north, summer drought paired with biotic stressors has been linked to mortality of Quercus robur in Poland (Siwecki and Ufnalksi, 1998), Picea abies in southeast Norway (Solberg, 2004), and with a severe die-off of Picea obovata in northwest Russia (Kauhanen et al., 2008; Ogibin and Demidova, in press).

3.1.1.5. North America. Climate-induced tree mortality and forest die-off is relatively well documented for North America (Fig. 7; Table A5). Drought and warmth across western North America in the last decade have led to extensive insect outbreaks and mortality in many forest types throughout the region, affecting □20 million ha and many tree species since 1997 from Alaska to Mexico (Raffa et al., 2008; Bentz et al., 2009). Examples of forest die-off range from >1 million ha of multiple spruce species in Alaska (Berg et al., 2006) and >10 million ha of Pinus contorta in British Columbia (Kurz et al., 2008a), to drought-induced Populus tremuloides mortality across a million hectares in Saskatchewan and Alberta (Hogg et al., 2008). In the southwestern U.S., die-off of Pinus edulis on over a million hectares was specifically linked to ''global-change-type drought'' (Breshears et al., 2005). In the eastern portion of the continent, declines and increased mortality among oaks, particularly in the red oak family, have been reported from Missouri (Voelker et al., 2008) to South Carolina (Clinton et al., 1993) in relation to multi-year and seasonal droughts in the 1980s–2000s. Drought during the 1980s followed by an unusual spring thaw in eastern North America also contributed to decline and mortality of maples in Quebec (Hendershot and Jones, 1989). In addition, recent increases in background rates of tree mortality across the western U.S. have been attributed to elevated temperatures (van Mantgem et al., 2009).

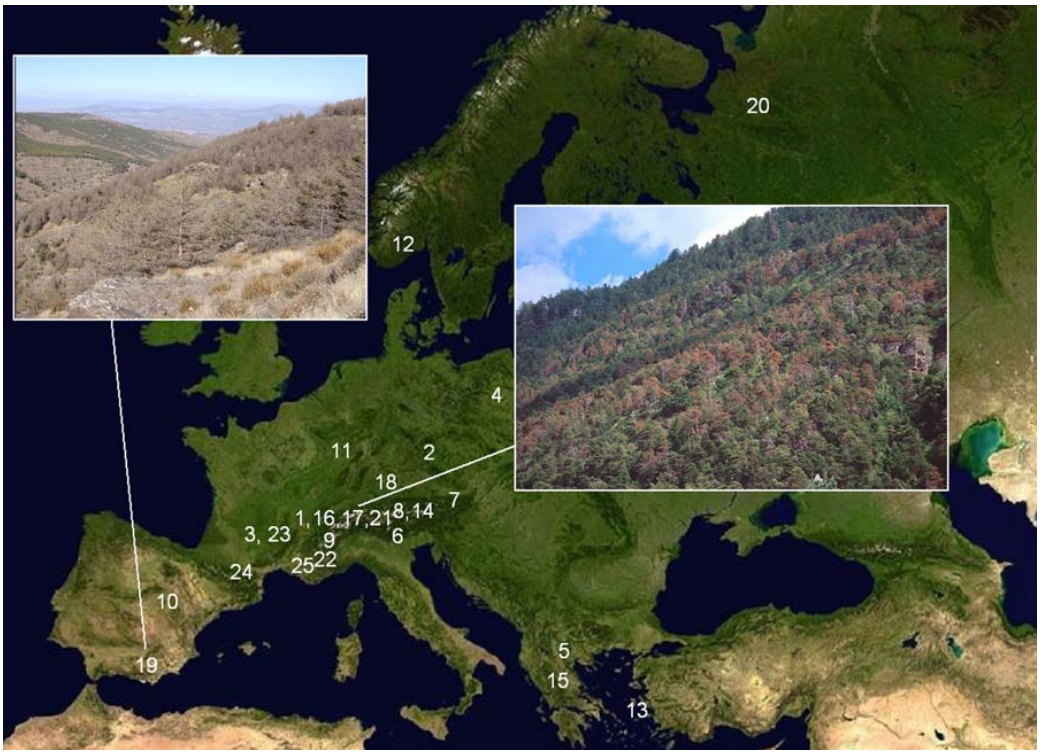


Fig. 6. Satellite map of Europe, with documented drought-induced mortality areas indicated with numbers, tied to Table A4 references. R photo: Pinus sylvestris mortality, Valais, Switzerland; 1999, by Beat Wermelinger. L photo: Pinus sylvestris die-off, Sierra de los Filabres, Spain; 2006, by Rafael Navarro-Cerrillo.

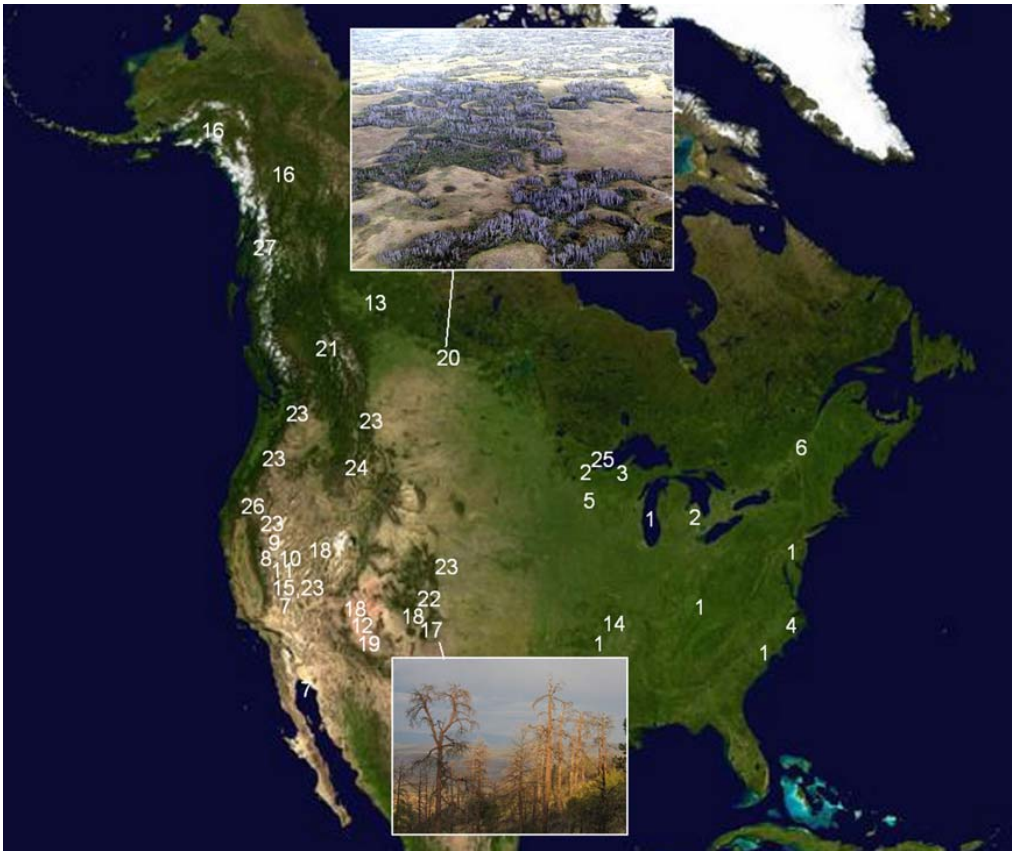


Fig. 7. Satellite map of North America, with documented drought-induced mortality localities indicated with numbers, tied to Table A5 references. Top photo: Aerial view showing severe mortality of aspen (Populus tremuloides) in the parkland zone of Alberta, Canada; 2004, by Michael Michaelian. Lower photo: Pinus ponderosa die-off, Jemez Mountains, New Mexico, USA; 2006, by Craig D. Allen.

3.1.1.6. South and Central America. In Latin America (Fig. 8; Table A6), ENSO-related seasonal droughts have amplified background tree mortality rates in tropical forests of Costa Rica (Chazdon et al., 2005), Panama (Condit et al., 1995), northwest Brazil (Williamson et al., 2000), and southeast Brazil (Rolim et al., 2005), and caused extensive mortality of Nothofagus dombeyi in Patagonian South America (Suarez et al., 2004). A hot and severe drought across the Amazon basin in 2005, linked to anomalously warm sea surface temperatures in the North Atlantic, has also recently been tied to regionally extensive increases in tree mortality rates and subsequent aboveground biomass loss, indicating vulnerability of Amazonian forests to moisture stress (Phillips et al., 2009) (Fig. 9).

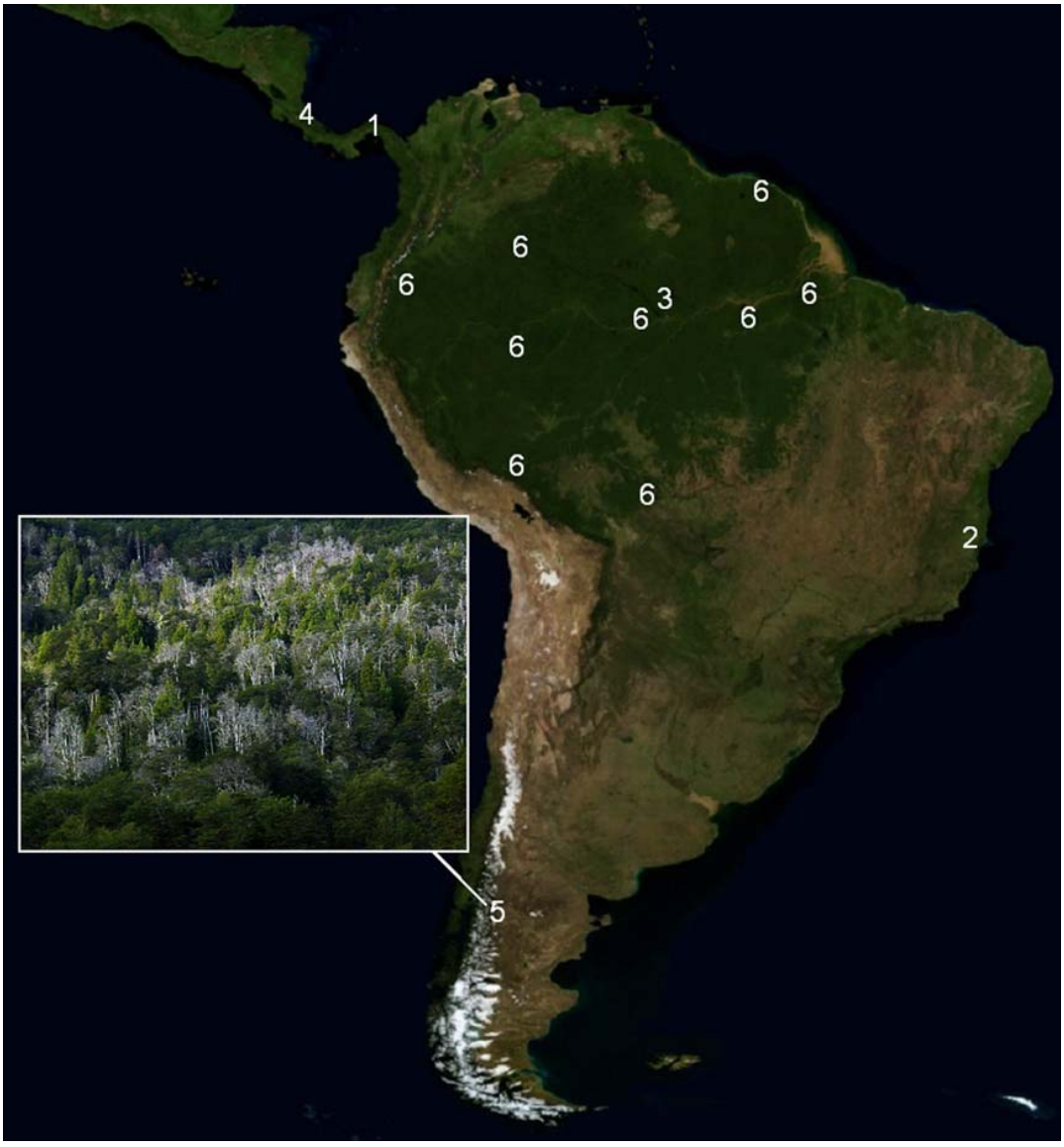


Fig. 8. Satellite map of South and Central America, with documented drought-induced mortality localities indicated with numbers, tied to Table A6 references. Photo: Nothofagus dombeyi mortality at Río Manso Inferior, northern Patagonia, Argentina; 2004, by Thomas Kitzberger.

3.1.2. Spatial and temporal patterns of mortality

Climate-induced mortality events in this review include examples that span a broad gradient of woody ecosystems, from monsoonal savannas with mean precipitation <400 mm/year, to subalpine conifer forests with a Mediterranean climate, to tropical rainforests with mean precipitation >3000 mm/year. These cases reveal a complex set of mortality patterns in response to drought and heat stress, ranging from modest and short-lived local increases in background mortality rates to episodes of acute, regional-scale forest die-off, which often (but not always) involve biotic agents like insect outbreaks.

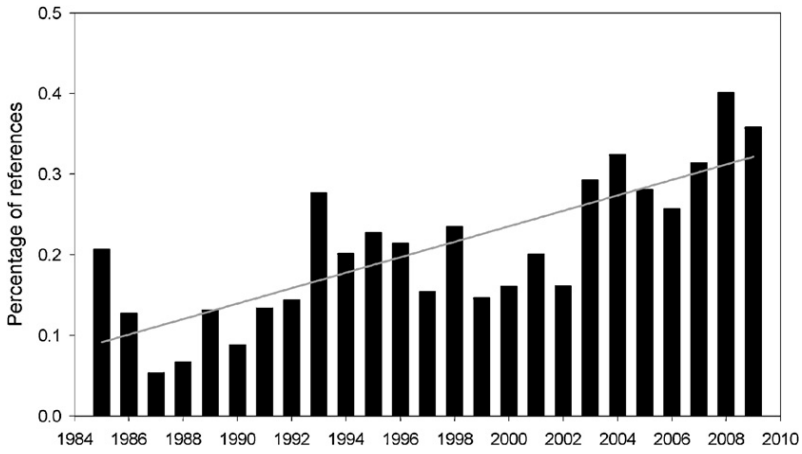


Fig. 9. ISI Web of Science search of the trend in published reports of climate-related forest mortality in the scientific literature, for the years 1985–2009. Plotted bars show the percent of references using the topic words ''forest AND mortality AND drought'', relative to all ''forest'' references. Line represents the linear regression model fitted to the data (R2 = 0.61; F = 35.73; p < 0.001).

At broad spatial scales, drought-related forest mortality has been reported near species geographic or elevational range margins where climatic factors (particularly water stress) are often presumed to be limiting (Allen and Breshears, 1998; Foden et al., 2007; Jump et al., 2009; Fig. 1; Fig. 3 and linked Box 1). Spatially extensive die-offs are commonly associated with prolonged water deficits, such as in savanna and temperate conifer forest vegetation types during multi-year droughts (Fensham et al., 2009; Fig. 10). Notably, however, drought-induced mortality is not restricted to forests typically thought to be water-limited, as highlighted by events in tropical rainforests of Borneo where stand-level mortality reached as high as 26% after the severe El Niño in 1997/1998 (van Nieuwstadt and Sheil, 2005), or the Amazon basin in 2005 (Phillips et al., 2009). Mortality in ever-wet and seasonally dry tropical rainforests appears to be relatively diffuse and incited most often by short but extreme seasonal droughts (Fig. 10). In temperate forests, short (seasonal) droughts may be more likely to induce dieback of broadleaved (deciduous angiosperm) trees (Fig. 10) than conifer (evergreen needleleaf) trees because of their increased vulnerability to xylem cavitation (Maherali et al., 2004).

Patterns of tree death are often quite patchy at finer spatial scales across the synoptic region where drought occurs. Although mortality is sometimes greatest in locally dry landscape positions (Oberhuber, 2001; Dobbertin et al., 2005; Worrall et al., 2008), ecosite variability (soils, elevation, aspect, slope, topographic position) may interact with density-dependent processes such as insect outbreaks, competition, or facilitation to produce complex spatial patterns of mortality at the stand and forest scale (Fensham and Holman, 1999; Lloret et al., 2004). Greater mortality can occur, for example, on more favorable sites within the middle of geographic and landscape distributions where higher tree density drives increased competition for water or elevated insect activity (Guarin and Taylor, 2005; Greenwood and Weisberg, 2008; Fensham et al., 2009; Horner et al., 2009; Klos et al., 2009). However, high severity drought can drive extensive forest mortality independent of tree density (Floyd et al., 2009). Higher mortality rates can also occur on favorable sites where trees do not invest in adequate root systems or where they otherwise become hydraulically overextended (Ogle et al., 2000; Fensham and Fairfax, 2007; Nepstad et al., 2007).

Spatial patterns of mortality at the stand and forest scale are also heavily influenced by life-history traits and tolerances of individual species within forests, with drought commonly triggering differential mortality rates between co-occurring tree species (Suarez et al., 2004; Gitlin et al., 2006; Fensham and Fairfax, 2007; Newbery and Lingenfelder, 2009; Phillips et al., 2009). Larger and/or older trees often appear more prone to drought-induced mortality (Mueller et al., 2005; Nepstad et al., 2007; Floyd et al., 2009), although this relationship is species-dependent, and in cases where stands are undergoing intense self-thinning, smaller sub-dominant trees and saplings are often more affected (Kloeppel et al., 2003; Elliott and Swank, 1994; Hanson and Weltzin, 2000).

Temporal patterns of drought-related tree mortality also can be difficult to interpret due to lagged responses in some species, in which mortality has been shown to occur years or even decades after drought stress (Pedersen, 1998, 1999; Bigler et al., 2007). Furthermore, the long-lived nature of trees and their ability to shift allocation of resources and change their hydraulic architecture throughout their lives can result in non-linear responses to drought stress in both space and time. Different sequences of climate events may also affect the risk of mortality (Miao et al., 2009).

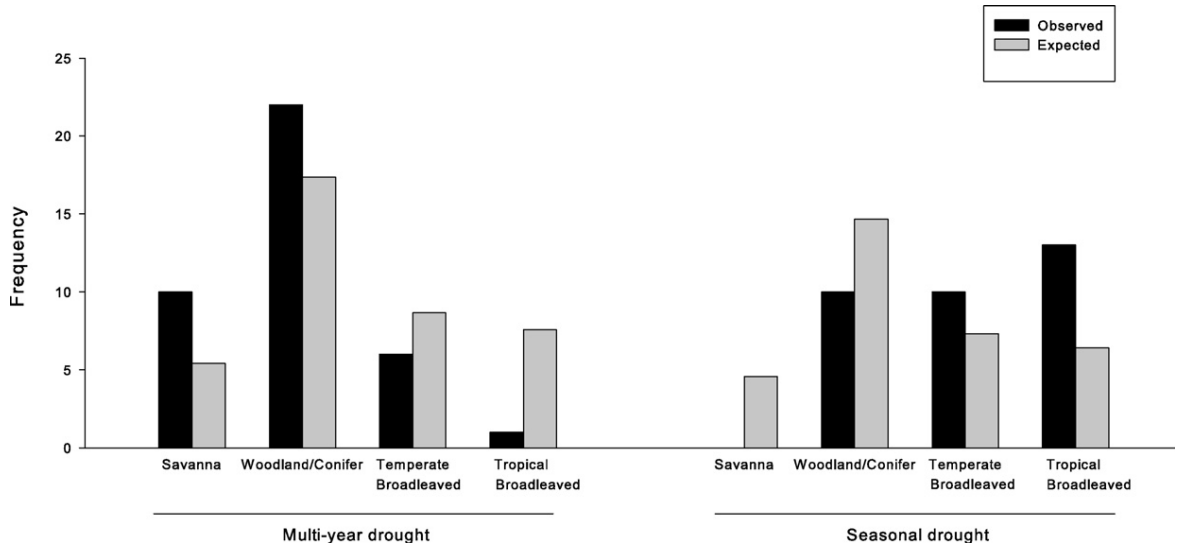


Fig. 10. Differences between observed and expected frequencies of reported forest mortality cases listed in Tables A1–A6, sorted by duration of associated drought events (seasonal vs. multi-year), with forests grouped into four major biomes. Mortality discriminated by forest type is dependent on drought duration, with more drought-adapted forest types showing mortality during long droughts and less drought-adapted forest types showing more mortality cases during short-term seasonal droughts. Pearson Chisquare = 23.46, df = 3, p = 0.000012.

4. Discussion

4.1. Climate-induced forest mortality : are new trends emerging?

The diverse instances of mortality reported here clearly illustrate that drought and heat can impact trees in many forest types. However awareness of, and interest in, climate-induced forest mortality and dieback is not new (Auclair, 1993; Ciesla and Donaubauer, 1994). Past die-offs have been extensively documented. Historic examples include: widespread death of Eucalyptus, Acacia, and Callitris species in the early 1900s triggered by the worst drought of the instrumental record in northeastern Australia (Fensham and Holman, 1999); Nothofagus mortality during 1914–1915 in New Zealand (Grant, 1984); Picea meyeri mortality during the 1920s in northern China (Liang et al., 2003); extensive tree mortality in the southern Appalachian Mountains and the Great Plains during the dust-bowl droughts of the 1920s– 1930s (Hursh and Haasis, 1931; Albertson and Weaver, 1945); Pinus sylvestris death during 1940–1955 in Switzerland (Dobbertin et al., 2007); oak mortality in many European countries following severe droughts episodes in 1892–1897, 1910–1917, 1922–1927, 1946–1949, 1955–1961 (Delatour, 1983); extensive tree mortality of Austrocedrus chilensis during El Nin˜o droughts in the 1910s, 1942–1943, and the 1950s in Argentina (Villalba and Veblen, 1998); and die-off of multiple pine species during the 1950s drought in the southwestern USA (Swetnam and Betancourt, 1998; Allen and Breshears, 1998). Furthermore, the overwrought perception of unprecedented forest decline and impending death due to air pollution in central Europe (where it was referred to as ‘Waldsterben’) and eastern North America that received much attention in the 1980s provides a cautionary example of exaggerated claims of widespread forest health risk in the absence of adequate evidence (Skelly and Innes, 1994).

So are recent occurrences of die-off simply well-documented examples of a natural phenomenon linked to climate variability, or is global climate change driving increases in forest mortality? We recognize that the available data on climate-induced forest mortality have many limitations: our examples represent a compilation of idiosyncratic case studies with uneven geographic coverage. The studies differed greatly in their goals, methods, and definitions of mortality, and inconsistently report mortality rates, spatial scale and patterns of mortality, and severity parameters of climate stress. The recent increase in forest mortality reports that we document could merely be an artifact of more scientific attention on climate change, perhaps in concert with a few high profile cases of climate-related forest die-off. These limitations, and the lack of any systematic global monitoring program, currently constrain our ability to determine if global changes in forest mortality are emerging.

Even though our review is insufficient to make unequivocal causal attributions, our data are consistent with the possibility that climate change is contributing to an increase in reported mortality. Documentation of climate-related forest mortality in association with recent warming and droughts is rising rapidly (Fig. 9), and in some of these cases the droughts have been the most severe of the last few centuries. Furthermore, recent research indicates that warmer temperatures alone can increase forest water stress independent of precipitation amount (Barber et al., 2000). In addition, new experimental results show that warmer

temperatures can greatly accelerate drought-induced mortality (Adams et al., 2009, and associated correspondence). If the recent increase in mortality reports is indeed driven in part by global climate change, far greater chronic forest stress and mortality risk should be expected in coming decades due to the large increases in mean temperature and significant long-term regional drying projected in some places by 2100, in addition to projected increases in the frequency of extreme events such as severe droughts, hot extremes, and heat waves (IPCC, 2007a; Jentsch et al., 2007; Sterl et al., 2008).

4.2. Climate and plant physiological interactions that drive forest mortality

Understanding complex spatial and temporal patterns of climate-induced tree death and forest die-off requires knowledge of the physiological drivers of tree mortality. The fundamental mechanisms underlying tree survival and mortality during drought remain poorly understood despite decades of research within the fields of forestry, pathology, entomology, and ecology (Waring, 1987; Manion, 1991; Mueller-Dombois, 1986,1988; Breda et al., 2006; Ogaya and Peñuelas, 2007; McDowell et al., 2008). Part of the challenge is that tree mortality commonly involves multiple, interacting factors, ranging from particular sequences of climate stress and stand life histories to insect pests and diseases (Franklin et al., 1987; Miao et al., 2009). Based on the decline spiral model (Manion, 1991; Manion and Lachance, 1992), drought can operate as a trigger (‘‘inciting factor’’) that may ultimately lead to mortality in trees that are already under stress (by ‘‘predisposing factors’’ such as old age, poor site conditions and air pollution) and succumb to subsequent stem and root damage by biotic agents (‘‘contributing factors’’ such as wood-boring insects and fungal pathogens). McDowell et al. (2008) build upon Manion’s framework to postulate three mutually non-exclusive mechanisms by which drought could lead to broad-scale forest mortality: (1) extreme drought and heat kill trees through cavitation of water columns within the xylem (Rennenberg et al., 2006; Zweifel and Zeugin, 2008); (2) protracted water stress drives plant carbon deficits and metabolic limitations that lead to carbon starvation and reduced ability to defend against attack by biotic agents such as insects or fungi (McDowell et al., 2008; Breshears et al., 2009; Adams et al., 2009); and (3) extended warmth during droughts can drive increased population abundance in these biotic agents, allowing them to overwhelm their already stressed tree hosts (Desprez-Loustau et al., 2006; Raffa et al., 2008; Wermelinger et al., 2008). Although these hypotheses have growing support, our physiological knowledge remains inadequate for confidently predicting patterns of regional die-off, as well as variation in survival for trees within the same stand.

The degree to which trees regulate water loss during drought may explain patterns of carbohydrate (and resin) production and subsequent susceptibility to drought or biotic attack (McDowell et al., 2008; Zweifel et al., 2009). A continuum of stomatal responses to drought exist from drought avoidance (isohydry), in which stomata close at a threshold water potential to minimize further transpiration, to drought tolerance (anisohydry), in which stomatal closure is less severe and transpiration continues at relatively high rates (McDowell et al., 2008). The isohydric response protects xylem from cavitation through avoidance of severe low water potentials, but can cause eventual carbon starvation as stomatal closure shuts down photosynthesis while respiration costs continue to deplete carbon stores. The anisohydric response can allow continued carbon gain through maintaining open stomata but at greater risk of cavitation, which might kill trees directly or could increase the likelihood of future carbon deficits. Plants that typify each response have associated traits consistent with their mode of stomatal regulation, such as deep rooting access to more reliable soil water and cavitation-resistant xylem for drought-tolerant species.

In addition to hydraulic failure and carbon starvation, a third physiological mechanism predisposing plants to mortality may exist—cellular metabolism limitation. This hypothesis suggests that low tissue water potentials during drought may constrain cell metabolism (Würth et al., 2005; Ryan et al., 2006; Sala and Hoch, 2009), thereby preventing the production and translocation of carbohydrates, resins, and other secondary metabolites necessary for plant defense against biotic attack. The common observation that trees which succumb to insect attacks have weak resin flow and are unable to pitch out attacking insects is consistent with constraints on photosynthetic carbon uptake, cellular carbon metabolism, and/or tree water relations. A likely sequence for many isohydric species that is consistent with Manion’s cascade (Manion, 1991) is that climate stressed trees starve for carbon, perhaps due to poor edaphic position combined with drought, which causes poor resin flow and an inability to defend against insect attack, which subsequently allows fungi that are symbiotic with the beetles to colonize and occlude the sapwood, causing transpiration to cease, drying of the canopy, and eventual mortality (McDowell et al., 2008, 2009).

The observation that climate-induced tree mortality is happening not only in semi-arid regions but also in mesic forests suggests that the global rise in temperature may be a common driver (van Mantgemet al., 2009; Adams et al., 2009). The mechanisms by which rising temperature in the absence of severe precipitation deficits may result in increased tree mortality include impacts on both host physiology and biotic agents. Increasing temperature raises the vapor pressure deficit and evaporation to the atmosphere. This results in increased water loss through transpiration and either stomatal closure in the case of isohydric species, or decreased margin of safety from hydraulic failure in the case of anisohydric species.

Rising temperatures may impact the carbon storage of trees in a particularly negative way because the rate of carbohydrate consumption required to maintain cellular metabolism (respiration) is strongly linked to temperature (Amthor, 2000). The first experiment under controlled climate to isolate the effect of temperature on drought-induced tree mortality, conducted on Pinus edulis, indicates a high degree of sensitivity to elevated temperature and indirectly implicates carbon starvation (Adams et al., 2009).

Warmer temperatures may also be important where cold winters are usual, in that abnormally warm winter temperatures maintain significant physiological activity after the growth season, with tree respiration costs wasting stored carbohydrates (Damesin, 2003). Even though CO2 uptake can occur during mild winters and partially compensate for carbon loss during summer droughts (Holst et al., 2008), the annual C balance often remains in deficit under these conditions. Therefore under climatic warming scenarios, drought-avoiding tree species may move closer to carbon starvation, and drought-tolerant species may come closer to hydraulic failure (McDowell et al., 2008).

Presumably, surviving individuals after a severe climate event would have some degree of genetic drought resistance that would be inherited by the next generation (Gutschick and BassiriRad, 2003; Parmesan, 2006; Millar et al., 2007a). But the adaptation of a tree species to a markedly different local climate, with only one or a few generations per century, may be too slow to successfully respond to the rapid present rate of climate change.

Warming temperatures also have direct effects on insect population dynamics—in particular, outbreaks of some aggressive bark beetle species are closely tied to temperature (Logan et al., 2003; Berg et al., 2006; Hicke et al., 2006; Rouault et al., 2006). Higher temperatures can accelerate insect development and reproduction, increasing infestation pressure directly (e.g., Wermelinger and Seifert, 1999; Bale et al., 2002; Caldeira et al., 2002; Gan, 2004), while at the same time heat-induced drought stress may reduce tree vigor and increase host susceptibility to insect attack (Mattson and Haack, 1987; Rouault et al., 2006). Warming temperatures and drought-stressed trees also may foster increased mortality from non-insect pathogens, particularly fungi (Ayres and Lombardero, 2000; Desprez-Loustau et al., 2006; Garrett et al., 2006). However, fungal responses to climatic factors are complex and uncertain because of interactions with tree host susceptibility and insect vectors, and some fungi-tree relationships are difficult to assess because important belowground interactions between fungi and tree roots are not well studied.

4.3. Consequences of broad-scale forest mortality

Due to the increasingly tight coupling of human and environmental systems, the consequences of broad-scale forest mortality are important to contemplate.

Trees grow relatively slowly but can die quickly: a 200-year-old tree may be killed by severe drought within a few months to a few years. Therefore, mortality of adult trees can result in ecosystem changes far more rapidly than a gradual transition driven by tree regeneration and growth (Fig. 11). If forests are forced to adjust abruptly to new climate conditions through forest die-off, many pervasive and persistent ecological and social effects will result. Major changes in understory species may occur (Rich et al., 2008), as well as the possible development of novel ecosystems due to new combinations of native and invasive exotic trees that, depending on the climatic tolerances of seedlings, eventually repopulate the overstory (Walther et al., 2005; Millar et al., 2007b; Suarez and Kitzberger, 2008).

Abiotic ecosystem impacts may include changes in solar energy fluxes reaching ground level and reflecting back to the atmosphere, with potentially large feedbacks to regional climate in some areas (Bonan, 2008; Chapin et al., 2008), aswell as alterations in hydrology and ecosystem water budgets due to increases in evaporation and reductions in transpiration (e.g., Huxman et al., 2005), and changes in groundwater recharge. Potential effects of extensive forest mortality on water resource availability could have large effects on human societies (Millennium Ecosystem Assessment, 2005).

In addition, broad-scale forest mortality could change local, regional, and global carbon budgets (Breshears and Allen, 2002; Jones et al., 2009). Forests store considerably more carbon than the atmosphere, and forest die-off could redistribute within-ecosystem carbon pools and release pulses of carbon back to the atmosphere. A recent modeling study simulated this type of transformation in managed forests of Canada, where climate-related increases in fire and insect disturbance are forecast to turn these forests into a net carbon source (Kurz et al., 2008b).

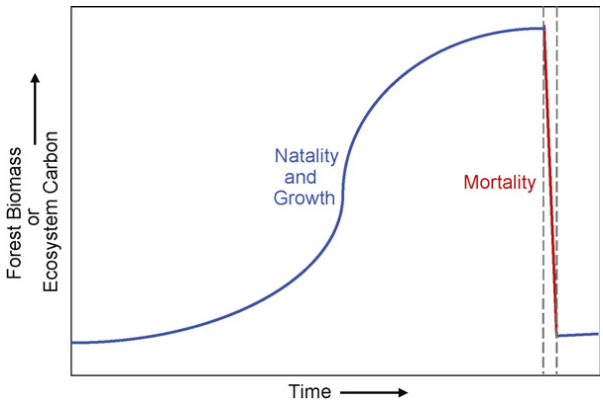


Fig. 11. Abrupt reductions in forest biomass (or ecosystem carbon) can result from drought-induced forest die-off and occur more rapidly than the relatively slow countervailing biomass increments from tree natality and growth. Trajectories of change vary with ecosystem, as do minimum biomass and carbon values, and are not to scale in this conceptual figure.

Meanwhile, climate-related increases in the spatial extent of mass tree mortality by insects, notably mountain pine beetle, have recently transformed some forests of interior British Columbia (Canada) from a net carbon sink into a net carbon source (Kurz et al., 2008a). Similarly, it is possible that ''widespread forest collapse via drought'' could transform the world's tropical forests from a net carbon sink into a large net source during this century (Lewis, 2006, p. 195; cf. Phillips et al., 2009; Jones et al., 2009). Land-use impacts such as anthropogenic fires and forest fragmentation, interacting with climate-induced forest stress, are likely to amplify these effects in some regions, including the Amazon Basin (Nepstad et al., 2008). Overall, climate-induced forest mortality and related disturbances will increase global carbon flux rates at least temporarily, potentially undermining the capacity of the world's forests to act as carbon sinks in the coming centuries.

Past forest management may have exacerbated recent mortality in some regions. In portions of western North America, over a century of fire suppression has fostered the buildup of unusually high tree densities. Trees in these unnaturally dense forests can have decreased vigor, which can increase their vulnerability to multiple mortality factors (Savage, 1997). Extensive reforestations with pine plantations in regions such as China and the Mediterranean Basin (e.g., ~3.5 million ha reforested with conifers since 1940 in Spain alone; J. Castro - from agency statistical sources) may be particularly vulnerable, especially because some of these plantations are on marginal sites given the excessive densities and unknown genetic provenances of the trees.

In summary, given the potential risks of climate-induced forest die-off, forest managers need to develop adaptation strategies to improve the resistance and resilience of forests to projected increases in climate stress (Seppala et al., 2009). Options might include thinning stands to reduce competition, selection of appropriate genotypes (e.g., improved drought resistance), and even translocation of species to match expected climate changes (e.g. Millar et al., 2007b; Joyce et al., 2008; Richardson et al., 2009).

4.4. Key information gaps and scientific uncertainties

The conclusions that can be drawn about recent trends in tree mortality and the predictions that can be made about future climate-induced forest die-off are limited by a number of key information gaps and scientific uncertainties.

(1) Accurate documentation of global forest mortality patterns and trends requires the establishment of a worldwide monitoring program. Despite many national and regional forest-monitoring efforts (e.g., the European Union's intensive forest health monitoring EU/ICP-Forests Level II network), there is an absence of adequate data on forest health status globally (FAO, 2006, 2007). Existing permanent sample plot networks can detect large scale events or a generalized background mortality increase, but are not designed to detect and assess patchy mortality, even at rather high rates, as is common when forest landscapes are heterogeneous and inmost of the cases of biotic agent outbreaks. Reliable, long-term, global-scale forest health monitoring, likely combining remote-sensing and ground-based measurements in a methodologically coordinated and consistent manner, is needed to accurately determine the status and trends of forest stress and mortality on planet Earth. Regional and global maps of actual patterns of climate-induced tree mortality are also vitally important for the development and validation of models for predicting forest die-off in response to climate change.

(2) Understanding the mechanisms by which climate change may affect forests requires quantitative knowledge of the physiological thresholds of individual tree mortality under chronic or acute water stress (Fig. 12). With the exception of information for a few tree species (McDowell et al., 2008; Zweifel et al., 2009), there is surprisingly little species-specific knowledge on regulation of xylem water potentials; therefore, placing various species on the continuum of isohydry–anisohydry is difficult, and predicting how diverse species differentially experience carbon starvation or hydraulic failure is currently impossible.

Similarly, there is almost no knowledge on the patterns or mechanisms of carbohydrate storage in response to drought and heat. The potential effects of other components of changing atmospheric chemistry (e.g., elevated levels of nitrogen deposition and ground-level ozone) on the sensitivity of trees to drought remain inadequately known (Grulke et al., 2009). Research is also needed on how tree phenologies will respond to climate warming, because increasing winter temperatures may contribute to depletion of carbohydrate reserves relevant to carbon starvation thresholds. In addition, better knowledge is needed on within-species genetic variability and selection of trees related to drought and heat stress.

(3) More accurate global vegetation maps are needed as essential inputs to calibrate and validate dynamic global vegetation models. The extent of forest mortality can only be documented or modeled if there is precise information on the locations and extent of pre-die-off forests.

(4) Spatially explicit documentation of environmental conditions in areas of forest die-off is necessary to link mortality to causal climate drivers, including precipitation, temperature, and vapour pressure deficit. Given the difficulties in measuring precipitation and the absence of reliable soil datasets at adequate resolutions for continental-scale studies, a robust water availability index, possibly derived from remote sensing, is needed to help modelers simulate water stress in trees. In order to disentangle moisture deficit from temperature effects on tree mortality, more research is also needed to relate spatial gradients of mortality to variation in temperature. This research might utilize historical and dendrochronological records across spatial and temporal gradients where

variations in rainfall deficit and temperature increase are expressed.

(5) Mechanistic understanding of climate-induced tree mortality requires improved knowledge of belowground processes and soil moisture conditions (e.g. Brunner et al., 2009). Models often include detailed algorithms describing aboveground physiological processes but treat belowground processes as a ‘‘black box’’. Understanding of the impacts of increasing atmospheric CO2, nitrogen deposition, ground-level ozone, and drought on root dynamics, productivity, exudation fluxes, and mycorrhizal interactions would particularly improve belowground modeling.

(6) The direct effects of climate on the population dynamics of almost all forest insect pests and other biotic disturbance agents remain poorly understood but are important to modeling climate-induced forest mortality (Wermelinger and Seiffert, 1999; Logan et al., 2003; Desprez-Loustauetal.,2006; Bredaetal.,2006; Bentzetal.,2009). Generalization through synthesis of current knowledge on the dynamics of damaging biotic agents and tree response to attacks could improve existing mortality functions in forest models.

(7) Feedbacks between physiological stress (and tree mortality) driven by climate and other forest disturbance processes (e.g., insect outbreaks, fire) are poorly understood (Allen, 2007). These major disturbance processes may increasingly drive the mortality dynamics of forests in a rapidly changing climate, necessitating improved modeling of their cumulative and collective effects (Nepstad et al., 2008). Current models of vegetation response to climate change share weaknesses associated with the knowledge gaps identified here, including individual tree-based process models (Keane et al., 2001), species-specific empirical models (climate envelope models, e.g., Hamann and Wang, 2005; Thuiller et al., 2008), climate envelope threshold models linked to plant functional types in dynamic global vegetation models (Scholze et al.,2006),and earth system models (Ciais et al., 2005; Huntingford et al., 2008). The significant uncertainties associated with modeling tree mortality are reflected in ongoing debates about the magnitude of die-off risk to Amazon rainforests and boreal forests from climate change this century, the potential for dieoffs in forests more generally (Loehle and LeBlanc, 1996; Phillips et al., 2008; Soja et al., 2007), and the degree to which forests worldwide are likely to become a net carbon source or sink (e.g., Kurz et al., 2008b).

5. Conclusions

This overview illustrates the complex impacts of drought and heat stress on patterns of tree mortality, and hints at the myriad ways in which changes in drought and/or heat severity, duration, and frequency may lead to gradually increasing background tree mortality rates and even rapid die-off events. Many recent examples of drought and heat-related tree mortality from around the world suggest that no forest type or climate zone is invulnerable to anthropogenic climate change, even in environments not normally considered water-limited. Current observations of forest mortality are insufficient to determine if worldwide trends are emerging in part due to the lack of a reliable, consistent, global monitoring system. Although the effects of climate change cannot be isolated in these studies and clearly episodic forest tree mortality occurs in the absence of climate change, the globally extensive studies identified here are consistent with projections of increased forest mortality and suggest that some forested ecosystems may already be shifting in response to climate.

There are major scientific uncertainties in our understanding of climate-induced tree mortality, particularly regarding the mechanisms that drive mortality, including physiological thresholds of tree death and interactions with biotic agents. Recent advances in the understanding of tree mortality mechanisms suggest that forests could be particularly sensitive to increases in temperature in addition to drought alone, especially in cases where carbon starvation rather than hydraulic failure is the primary mechanism of tree mortality. However, we currently lack the ability to predict mortality and die-off of tree species and forest types based on specific combinations of climatic events and their interactions with biotic stressors and place-specific site conditions. The potential for broad-scale climate-induced tree mortality can be considered a nonlinear ‘‘tipping element’’ in the Earth’s climate system (Lenton et al., 2008), because forest die-offs from drought can emerge abruptly at a regional scale when climate exceeds species-specific physiological thresholds, or if climate triggers associated irruptions of insect pests in weakened forests. Such cross-scale mortality processes in forests remain poorly understood.

Collectively, these uncertainties currently prevent reliable determination of actual mortality trends in forests worldwide, and also hinder model projections of future forest mortality in response to climate change. As one consequence, the potential for climate change to trigger widespread forest die-off may be underrepresented in important assessments to date, notably including the latest major IPCC report (2007b). If extensive climate-induced tree mortality occurs, then substantial negative ecological and societal consequences can be expected. Determining the potential for broad-scale, climate-induced tree mortality is therefore a key research priority for ecologists and global change scientists, and is essential for informing and supporting policy decisions and forest management practices.

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Appendix A

These appendix tables (Tables A1–A6) accompany the continental-scale maps and associated text descriptions, and are the core compilation of documented examples of drought and heat-induced tree mortality. Organized by continent and year of mortality event, concisely listing key information for each documented example, including an identification number allowing easy visual linkage to the continental-scale map locations.

Table A1
Documented cases of drought and/or heat-induced forest mortality from Africa, 1970–present. ID numbers refer to locations mapped in Fig. 2.

ID	Location	Year(s) of mortality	Forest type/mean precip. [a]	Dominant tree taxa	Spatial concentration of mortality within geographic or elevational range	Climate anomaly linked to mortality	Stand/ population-level mortality (%)[b]	Scale of impact/area affected	Biotic agents associated with mortality?[c]	Reference(s)[d]
1	Senegal	1972–1973	Savanna (300)	*Acacia senegal*, *Guiera senegalensis*	Middle–lower edges of elevational range; arid edge of geographic range	Multi-year drought	50	Regional	None	Poupon (1980)
2	South Africa (Northern Province)	1988–1992	Savanna (366)	*Colophospermum mopane*	Patchy within range	Multi-year drought	13–87 (basal area)	Not reported	Not reported	MacGregor and O'Connor (2002)
3	Zimbabwe (Southeast)	1970–1982, 1991–1992	Savanna	*Brachystegia glaucescens*; other savanna species	Not reported	Multi-year droughts	Not reported	Subregional; ~500,000 ha affected	Elephants, scale insects	**Tafangenyasha (2001**, 1998, 1997)
4	Senegal	1945–1993	Savanna, deciduous broadleaf woodland (240–560)	*Anacardium occidentale*, *Cordyla pinnata*, *Ficus ingens*, many others	Arid edges of geographic range	Multi-year drought	23	Regional	None	Gonzalez (2001)
5	South Africa (Northern Province)	1991–1993	Woodland, deciduous broadleaf (500–600)	*Dichrostachys cinerea*, *Pterocarpus angolensis*, *Strychnos madagascariensis*, *Terminalia sericea*, *C. mopane*, many others	Patchy within range	Multi-year drought	1–78 (species-dependent)	Not reported	None	Viljoen (1995)
6	South Africa (Northern Province)	1982–1997	Savanna (240–500)	*C. mopane*, *Combretum apiculatum*, *Grewia* spp., *Ximenia americana*	Patchy within range	Multi-year drought	7	Not reported	None	O'Connor (1999)
7	Uganda (Western)	1999	Tropical Rainforest (1492)	*Uvariopsis* spp., *Celtis* spp.	Not reported	Seasonal drought	19	Not reported	Not reported	Lwanga (2003)
8	Namibia, South Africa	1904–2002	Savanna (100–200)	*Aloe dichotoma*	Arid edge of geographic range	Multi-year drought, high temperatures	2–71	Subregional	None	Foden et al. (2007)
9	Algeria	2000–2008	Med. conifer (348–356)	*Cedrus atlantica*	Arid edge of geographic range	Multi-year drought	40–80	Subregional	Insects	Bentouati (2008); Bentouati and Bariteau (2006); Chenchouni et al. (2008)
10	Morocco	2002–2008	Med. montane conifer (300–600)	*Cedrus atlantica*	Arid edge of geographic range	Multi-year drought	10–40	Subregional	Not reported	El Abidine (2003); Adil (2008)

[a] Mediterranean forest types are abbreviated as Med. in this column. Annual precipitation is in mm/yr in parentheses if reported.
[b] Severity of mortality is reported at the stand or population level as percentage of dead trees (depending on study design), unless otherwise noted in the entry. Other common units are annual mortality rate during drought (%/year), percent dead basal area, and dead wood volume in meters^3.
[c] If biotic agents are thought to have played a primary role in tree mortality, this is noted in bold type. If biotic agents were involved in mortality but their role was not evaluated or is secondary to climate, the agents are simply listed.
[d] Citations from which reported mortality data is derived are written in bold type. Other citations provide corroborating or secondary evidence. If there are multiple citations without no bold type, reported data reflects numbers compiled from all citations.

Table A2
Documented cases of drought and/or heat-induced forest mortality from Asia, 1970-present. ID numbers refer to locations mapped in Fig. 4.

ID	Location	Year(s) of mortality	Forest type/mean precip.[a]	Dominant tree taxa	Spatial concentration of mortality within geographic or elevational range	Climate anomaly linked to mortality	Stand/ population-level mortality (%)[b]	Scale of impact/ area affected	Biotic agents associated with mortality?[c]	Reference(s)[d]
1	Sri Lanka	1976–1980	Montane tropical rainforest	*Calophylluru* spp., *Syzygium* spp.	Upper-mid elevational range	Seasonal drought	50–100	Not reported	Not reported	Werner (1988)
2	Malaysia (Borneo)	1982–1983	Tropical rainforest (~2000)	*Dipterocarpus* spp., *Shorea* spp.	Not reported	Seasonal drought	12–28	Not reported	Not reported	**Woods (1989)**; Becker et al. (1998); Leighton and Wirawan (1986)
3	India (Gujarat)	1987	Tropical dry deciduous	*Acacia senegal*, *Holarrhena antidysenterica*, *Helicteres isora*, *Terminalia crenulata*, others	Not reported	Seasonal or single-year drought	37–82 (species-dependent)	~141,000 ha affected	Ungulates (*Cervus unicolor*)	Khan et al. (1994)
4	Russia (Far East)	1987–1988	Montane mixed conifer	*Picea jezoensis*, *Abies nephrolepis*	Mountain slopes and plateaus, variable aspects	Drought	14 M m^3 timber lost	~165,000 ha affected	Fungi	Man'ko and Gladkova (2001)
5	Saudi Arabia and Oman	Early 1990s	Woodland (559)	*Juniperus procera*, *J. excelsa*	Lower edges of elevational range	Possibly drought	30 (*J. excelsa*)	Landscape–subregional	None	**Fisher and Gardner (1995)**; Fisher (1997); Gardner and Fisher (1996)
6	Indonesia (Sumatra)	1997–1998	Tropical rainforest	Not reported	Not reported	Seasonal drought	9.8	Not reported	Not reported	Kinnaird and O'Brien, 1998
7	Indonesia and Malaysia (Borneo)	1997–1998	Tropical rainforest (~2100–3000)	*Dipterocarpus* spp., *Lauraceae*	Not reported	Seasonal drought	0.6–26.3	Not reported	Not reported	**van Nieuwstadt and Sheil (2005)**; **Potts (2003)**; **Aiba and Kitayama (2002)**; Slik (2004)
8	Indonesia (Borneo)	1997–1998	Tropical lowland swamp (2800)	*Anacardiacea*, *Dipterocarpaceae*, *Sapotaceae*, *Rutaceae*	Not reported	Seasonal drought	4.2–6.1	Not reported	Not reported	Nishimua et al. (2007)
9	Malaysia (Borneo)	1997–1998	Tropical rainforest (~2700)	*Dipterocarpaceae*, *Euphorbiaceae*, *Burseraceae*, *Myristicaceae*	Not reported	Seasonal drought	4.3–6.4	Not reported	Not reported	Nakagawa et al. (2000); Lingenfelder and Newbery (2009)
10	China (Shanxi, Hebei, Henan)	1998–2001	Temperate coniferous plantation	*Pinus tabulaeformia*	Not reported	Seasonal drought	~30	Subregional; 500,000 ha affected	Bark beetles (*Dendroctonus valens*)	Wang et al. (2007)
11	China (Yunnan)	1986–1988; 1998–2000; 2003–2005	Subtropical coniferous plantation	*Pinus yunnanensis*	Not reported	Seasonal drought	Varied in different plantations	Landscape; ~26,700–113,000 ha affected	Bark beetles (*Tomicus yunnanensis*, *T. minor*)	Li (2003)
12	Turkey (Central Anatolia)	2002–2007	Temperate conifer and mixed (400–600)	*Qercus* spp., *Juniper* spp., *Pinus nigra*, *P. sylvestris*, *Abies cilicicia*	Southern edge of geographic range for *P. sylvestris*	Drought	Not reported	Not reported	Insects	Semerci et al. (2008)
13	South Korea	2003–2008	Temperate montane mixed (1400–2000)	*Abies koreana*	Not reported	Warm winters/ springs, possibly drought	20–50	Landscape	Not reported	Lim et al. (2008); Woo et al. (2007)
14	Russia	2005–2008	Boreal and temperate	*Picea* spp., *Pinus* spp.	Southern portions of Russian forest zones	Drought	Not reported	>400,000 ha across the nation	Not reported	Ermolenko (2008)

Footnotes as in Table A1.

Table A3
Documented cases of drought and/or heat-induced forest mortality from Australasia, 1970–present. ID numbers refer to locations mapped in Fig. 5.

ID	Location	Year(s) of mortality	Forest type/ mean precip.[a]	Dominant tree taxa	Spatial concentration of mortality within geographic or elevational range	Climate anomaly linked to mortality	Stand/ population-level mortality (%)[b]	Scale of impact/ area affected	Biotic agents associated with mortality?[c]	Reference(s)[d]
1	New Zealand (West Coast)	1978–1980	Montane broadleaf	*Nothofagus fusca*	Not reported	Spring droughts	75	Landscape; ~5000 ha affected	Beech scale (*Inglisia fagi*); Fungi (*Hypocrella duplex*); Wood borer (*Platypus* spp., *Psepholax* spp.)	Hosking and Kershaw (1985)
2	New Zealand (Hawkes Bay)	1984–1987	Montane broadleaf	*Nothofagus solandri*	Not reported	Spring droughts	24–52	Not reported	Leafminer (*Neomycta pulicaris*); Fungi (*Nodulisporium* spp.)	Hosking and Hutcheson (1988)
3	Australia (Queensland)	1992–1996	Tropical savanna (480–2600)	*Eucalyptus* spp., *Corymbia* spp.	Patchy within ranges	Multi-year drought	29 (basal area)	Regional; ~5.5 M ha affected	None	**Fensham and Holman (1999)**; Fensham (1998); Rice et al. (2004)
4	Australia (Queensland)	1990–2002	Tropical savanna (500–850)	*Eucalyptus* spp., *Corymbia* spp.	Patchy within ranges	Multi-year drought	78 stand level; 17.7 across region	Regional; ~5.5 M ha affected	None	Fensham et al. (2003, 2009)
5	Australia (Queensland)	2004	Tropical savanna (500–850)	*Eucalyptus* spp., *Corymbia* spp.	Patchy within ranges	Multi-year drought	15.0 (basal area; unpublished data)	Not reported	None	Fensham and Fairfax (2007)
6	Australia (Queensland)	2005	Tropical savanna (500–850)	*Acacia* spp.	Widespread	Multi-year drought	Not recorded	~600 ha affected	None	Fensham and Fairfax (2005)

Footnotes are as given in Table A1.

Table A4
Documented cases of drought and/or heat-induced forest mortality from Europe, 1970–present. ID numbers refer to locations mapped in Fig. 6.

ID	Location	Year(s) of mortality	Forest type/ mean precip.[a]	Dominant tree taxa	Spatial concentration of mortality within geographic or elevational range	Climate anomaly linked to mortality	Stand/ population-level mortality (%)[b]	Scale of impact/ area affected	Biotic agents associated with mortality?[c]	Reference(s)[d]
1	Switzerland (Valais)	1960–1976	Temperate conifer (572)	*Pinus sylvestris*	Lower/southern edges of ranges	Multi-year drought	5–100	Landscape–subregional	Not reported	Kienast et al. (1981)
2	Europe (Western, Central)	1970–1985	Temperate conifer and broadleaf (600–1500)	*Abies* spp., *Picea* spp., *Pinus* spp., *Fagus sylvatica*	Lower edges of elevation range	Repeated droughts	1–20	Regional; patchy across <1 M ha	Bark beetles (*Scolytus*, *Ips*, *Pityogenes*, *Tomicus*, *Dendrochtonus*, *Pytiokteines*); Fungi	Schutt and Cowling (1985)
3	France	1980–1985	Temperate broadleaf (650–850)	*Quercus* spp,. mainly *Q. robur*	Patchy across ranges	Seasonal or single-year drought	10–50	Subregional; patchy across ~500,000 ha	Fungi; bark beetles (*Agriles*, *Scolytus*)	Nageleisen (1994); Nageleisen et al. (1991); Delatour (1983)
4	Poland	1979–1987	Temperate broadleaf (500–550)	*Quercus robur*	Not reported	Seasonal drought	111,000 m^3 timber lost	Landscape	Moths (*Tortrix viridiana*); pathogens (*Ophiostoma* spp.)	Siwecki and Ufnalksi (1998)
5	Greece	1987–1989	Mediterranean mixed conifer (1622)	*Abies alba* Mill. × *A. cephalonica* Loud.	Middle of elevation ranges	Multi-year drought	1.8/yr in drought years	Landscape–subregional	Bark beetles and other insects	Markalas (1992); Kailidis and Markalas (1990)
6	Italy (South Tyrol)	1992	Temperate mixed conifer (650)	*Pinus sylvestris*	Lower/southern edges of ranges	Multi-year drought	Not reported	Landscape–subregional	Various insects	Minerbi (1993)

7	Austria (Lower Austria)	1990–1996	Temperate mixed conifer (~650)	*Pinus sylvestris*, *Pinus nigra*	Lower edge of elevational range	Seasonal droughts	27.6–49.2	Stand–landscape	Various insects	Cech and Tomiczek (1996)
8	Austria (Tyrol)	1991–1997	Temperate mixed conifer (~840)	*Pinus sylvestris*	Lower edge of elevational range	Seasonal droughts	10.0–70.0	Landscape	Various insects	Cech and Perny (2000)
9	Italy (Aosta)	1985–1998	Temperate mixed conifer and broadleaf (~550)	*Pinus sylvestris*	Lower/southern edges of ranges	Multi-year drought	Not reported	Landscape–subregional	Fungi (*Armillaria* spp.); wood borers	Vertui and Tagliaferro (1998)
10	Spain (Northeast, Central, South)	1994, 1998	Mediterranean mixed conifer and broadleaf (537–605)	*Quercus* spp., *Pinus* spp., *Juniperus* spp.	Patchy within elevational range; southern edge of geographic range (*P. sylvestris*)	Multi-year drought, recurrent summer droughts	0.0–19.4 (species-dependent)	Landscape–subregional	Not reported	**Peñuelas et al. (2001)**; Lloret and Siscart (1995); Lloret et al. (2004); Martinez-Vilalta and Piñol (2002)
11	France (Ardennes, Vosges)	1998	Montane mixed conifer and broadleaf (800–1200)	*Fagus sylvatica*	Middle of ranges	Deep frost after an abnomally hot period	5–30	Subregional; patchy across ~200,000 ha	None	French Forest Health Department (1998–1999)
12	Norway	1992–2000	Temperate conifer	*Picea abies*	Patchy across ranges	Multi-year summer droughts, high summer temperatures	2–6.6	Landscape–subregional	Bark beetles (*Polygraphus poligraphus*)	Solberg (2004)
13	Greece (Samos)	2000	Mediterranean mixed conifer (~700–800)	*Pinus brutia*	Lower edge of elevational range	Multi-year drought	Not reported	Not reported	Not reported	Körner et al. (2005); Sarris et al. (2007)
14	Austria (Tyrol)	2001	Temperate mixed conifer (710)	*Pinus sylvestris*	Lower edge of elevational range	Seasonal droughts	Not reported	Landscape–subregional	Not reported	Oberhuber (2001)
15	Greece (South, Central)	2000–2002	Mediterranean mixed conifer (~700–1100)	*Abies cephalonica*	Not reported	Multi-year drought	5–10/yr in drought years vs. 0.17–0.50/yr in non-drought years	Landscape	**Primary role**, bark beetles (*Phaenops knoteki*, *Pityokteines spinidens*) mistletoe	Tsopelas et al. (2004); Raftoyannis et al. (2008)
16	Switzerland	2003	Temperate conifer and broadleaf	*Picea abies*	Not reported	Drought, high temperatures	~2.0 M m^3 timber lost	Landscape–subregional	Bark beetles (*Ips typographus*)	Forster et al. (2008)
17	Switzerland (Valais)	1973–1976, 1987–1993, 1996–2000, 2000–2004	Temperate mixed conifer and broadleaf (500–600)	*Pinus sylvestris*	Lower/southern edges of ranges	Seasonal and multi-year droughts, high temperatures	7–59	Landscape–subregional	**Primary role**, bark beetles (*Phaenops cyanea*, *Ips acuminatus*); nematodes; mistletoe	Wermelinger et al. (2008); Dobbertin et al. (2007); Bigler et al. (2006); Dobbertin and Rigling (2006); Rigling et al. (2006); Dobbertin et al. (2005); Rigling and Cherubini (1999)
18	Germany (Baden-Württemberg)	2003–2006	Temperate broadleaf	*Fagus sylvatica*	Not reported	Drought, high temperatures	~98,000 m^3 timber lost	Landscape–subregional	Bark, ambrosia beetles (*Taphrorychus bicolor*, *Trypodendron domesticum*); wood borer	Petercord (2008)
19	Spain	2004–2006	Temperate conifer plantations	*Pinus sylvestris*, *Pinus nigra*	Not reported	Multi-year drought	Not reported	Patchy across 13,404 ha	Not reported	Navarro-Cerrillo et al. (2007)
20	Russia (Northwest)	2004–2006	Boreal conifer	*Picea obovata*	Patchy	Drought, high temperatures	208 M m^3 timber lost	~1.9 M ha affected	Bark beetles (*Ips typographus*), fungi	Krotov (2007); Tsvetkov and Tsvetkov (2007); Chuprov (2007); Shtrakhov (2008); Kauhanen et al. (2008)

Table A4 (*Continued*)

ID	Location	Year(s) of mortality	Forest type/ mean precip.[a]	Dominant tree taxa	Spatial concentration of mortality within geographic or elevational range	Climate anomaly linked to mortality	Stand/ population-level mortality (%)[b]	Scale of impact/ area affected	Biotic agents associated with mortality?[c]	Reference(s)[d]
21	Switzerland (Grisons)	2003–2007	Temperate mixed conifer (750)	*Pinus sylvestris*	Lower edge of elevational range	Drought, high temperatures	6.3–16.0	Landscape–subregional	Not reported	Schilli et al. (in press)
22	France (Provence, Southern Alps)	2003–2008	Mediterranean conifer (750–950)	*Pinus sylvestris*	Lower/southern edges of ranges	Multi-year drought, high temperatures	20–80	Subregional; patchy across ~100,000 ha	Bark beetles (*Tomicus*, *Ips*, *Pissodes*)	Vennetier et al. (2007); Thabeet et al. (2009)
23	France	2003–2008	Temperate mixed conifer and broadleaf (650–1100)	*Quercus* spp. *Fagus sylvatica*, *Abies* spp., *Picea abies*, *Pinus* spp.	Lower and middle of elevational range	Spring and summer drought, scorching heat	1–3/yr	Regional	Bark beetles; fungi	Breda et al. (2006); Landmann et al. (2006); Rouault et al. (2006); French Forest Health Department (2003–2008)
24	France (Eastern Pyrénées)	2003–2008	Temperate mixed conifer (800–1000)	*Abies alba*	Lower edge to middle of ranges	Recurrent drought, high temperatures	10–30	Subregional; patchy across ~150,000 ha	Bark beetles (*Ips*, *Pissodes*)	French Forest Health Department (2003–2008)
25	France (Provence, Maures Mountains)	2006–2008	Mediterranean broadleaf	*Quercus suber*	Northern edge to middle of geographic range	Multi-year drought	10–70	Subregional; patchy across ~120,000 ha	Insects (*Platypus* spp., *Coroebus* spp.)	Vennetier et al. (2008)

Footnotes as in Table A1.

Table A5
Documented cases of drought and/or heat-induced forest mortality from North America, 1970–present. ID numbers refer to locations mapped in Fig. 7.

ID	Location	Year(s) of mortality	Forest type/ mean precip.[a]	Dominant tree taxa	Spatial concentration of mortality within geographic or elevational range	Climate anomaly linked to mortality	Stand/ population-level mortality (%)[b]	Scale of impact/area affected	Biotic agents associated with mortality?[c]	Reference(s)[d]
1	USA (Southeast, Northeast, Midwest)	Late 1970s–1980s	Upland temperate mixed	*Quercus* spp., *Cayra* spp.	Not reported	Multi-year droughts; high temperatures preceded by severe winters	16.6 in stands across Southeast; 1.2–6.3 in Missouri	Regional	Wood borers (*Agrilus bilineatus*); fungi; insect defoliators	**Stringer et al. (1989)**; **Starkey and Oak (1989)**; **Starkey et al. (1989)**; **Clinton et al. (1993)**; **Millers et al. (1989)**; Tainter et al. (1983); Law and Gott (1987); Kessler (1989); Jenkins and Pallardy (1995)
2	USA (Midwest)	1984	Temperate deciduous	*Acer* spp.	Not reported	Drought	Not reported	Landscape–subregional	Wood borers (*Agrilus* spp.)	Millers et al. (1989)
3	USA (Midwest)	1979–1986	Temperate deciduous	*Betula* spp.	Not reported	Multi-year drought	Not reported	Landscape–subregional	leafminers; wood borers; birch skeletonizers	Millers et al. (1989)
4	USA (North Carolina)	1984–1989	Temperate deciduous (1270–1520)	*Acer saccharum*, *Fagus grandifolia*, *Tilia americana*, *Aesculus flava*	Not reported	Multi-year drought	1.0–3.25/yr. in drought years	Not reported	Not reported	Olano and Palmer (2003)

Table A5 (*Continued*)

ID	Location	Year(s) of mortality	Forest type/ mean precip.[a]	Dominant tree taxa	Spatial concentration of mortality within geographic or elevational range	Climate anomaly linked to mortality	Stand/ population-level mortality (%)[b]	Scale of impact/area affected	Biotic agents associated with mortality?[c]	Reference(s)[d]
5	USA (Minnesota)	1987–1989	Savanna (726)	*Quercus ellipsoidalis*, *Q. macrocarpa*	Not reported	Multi-year drought	18.2	Not reported	Not reported	Faber-langendoen and Tester (1993)
6	Eastern North America	1980s	Temperate deciduous (900–1200)	*Acer saccharum*	Patchy within ranges	Drought, high temperatures preceded by winter thaw	10–15	Subregional; patchy across >1 M ha	Insect defoliator (*Malacosoma disstria*)	**Hendershot and Jones (1989)**; Payette et al. (1996); Auclair et al. (1996); Roy et al. (2004); Robitaille et al. (1982)
7	USA and Mexico (California and Baja California)	1985–early 1990s	Montane mixed conifer (~600–800)	*Pinus jeffreyi*, *Abies concolor*	Not reported	Multi-year drought	4–15	Landscape–subregional	Bark beetles (*Dendroctonus* spp.)	Savage (1997)
8	USA (California)	1986–1992	Montane mixed conifer (945)	*Pinus ponderosa*, *Calocedrus decurrens*, *Abies concolor*	Not reported	Multi-year drought, high spring and summer temperatures	23.3–69.2	Landscape	Bark beetles (*Dendroctonus* spp.)	Guarin and Taylor (2005)
9	USA (California)	1986–1992	Montane mixed conifer	Not reported	Not reported	Multi-year drought	13 (basal area)	Landscape–subregional; 56,000 ha affected	Engraver beetles (*Scolytus* spp.)	Macomber and Woodcock (1994)
10	USA (California)	1986–1992	Montane mixed conifer	*Pinus* spp., *Abies* spp.	Drier edge of local range; lower edges of elevational ranges	Multi-year drought	Not reported	Landscape–subregional	**Primary role**, bark beetles (*Dendroctonus* spp.); engraver beetles (*Scolytus* spp.)	Ferrell et al. (1994); Ferrell (1996)
11	USA (California)	1985–1995	Montane mixed conifer	*Pinus flexilis*	Lower edges of elevational range	Multi-year drought, high temperatures	50–75	Stand–landscape	Mistletoe (*Arceuthobium*) bark beetles (*Dendroctonus ponderosae*)	Millar et al. (2007a)
12	USA (Arizona)	1996	Woodland (~370)	*Pinus edulis*, *Juniperus monosperma*	Patchy within elevational range	Single-year drought	2.3–25.9	Landscape–subregional	Not reported	**Mueller et al. (2005)**; Ogle et al. (2000); Trotter (2004)
13	Canada (Alberta)	1990–1997	Boreal forest, prairie ecotone (450)	*Populus tremuloides*	Patchy within ranges	Drought preceding warm winter and spring	18–47	Subregional; patchy across ~1 M ha	Insect defoliator (*Malacosoma disstria*)	Hogg et al. (2002)
14	USA (Midwest, Southeast)	1990–2002	Upland temperate mixed	*Quercus* spp.	Patchy within ranges	Multi-year drought	15–50 basal area reduction	Regional; ~1.8 M ha affected	Wood borers (*Enaphalodes rufulus*, *Agrilus* spp.); fungi	**Starkey et al. (2004)**; **Oak et al. (2004)**; Voelker et al. (2008); Heitzman et al. (2004); Lawrence et al. (2002)
15	USA (California)	1983–2004	Montane mixed conifer (1100–1400)	*Pinus* spp., *Abies* spp.	Lower edges of elevational range	Drought, high temperatures	63% increase in annual mortality rate	Landscape–subregional	Insects, pathogens	van Mantgem and Stephenson (2007)
16	USA and Canada (Alaska, Yukon)	1989–2004	Coastal rainforest, boreal (485)	*Picea* spp.	Patchy within ranges	Drought, high summer temperatures	Not reported	Subregional; >1.2 M ha	**Primary role**, bark beetle (*Dendroctonus rufipennis*)	Berg et al. (2006)

Table A5 (*Continued*)

ID	Location	Year(s) of mortality	Forest type/ mean precip.[a]	Dominant tree taxa	Spatial concentration of mortality within geographic or elevational range	Climate anomaly linked to mortality	Stand/ population-level mortality (%)[b]	Scale of impact/area affected	Biotic agents associated with mortality?[c]	Reference(s)[d]
17	USA (Southwest)	2000–2004	Woodland, conifer (~250–750)	*Pinus ponderosa*, *Pinus edulis*, *Juniperus monosperma*, *Populus* spp.	Patchy within elevational range	Multi-year drought	3.3–41.4 (species dependant)	Landscape–subregional	Not reported	**Gitlin et al. (2006)**; Burkett et al. (2005)
18	Southwest, USA (New Mexico, Arizona, Colorado, Utah, Nevada)	2000–2004	Woodland (200–450)	*Pinus edulis*, *Pinus monophylla*, *Juniperus monosperma*, *Juniperus scopulorum*	Patchy within geographic and elevational range	Multi-year drought, high spring and summer temperatures	~6 region-wide, 0–90 stand-level for *Pinus* spp.; 4.5 stand-level for *J. monosperma*	Regional; ~1.2 M ha affected	**Primary role**, bark beetles (*Ips confusus*); twig beetles; pitch moths; root fungus; mistletoe	**Breshears et al. (2005)**; **Shaw et al. (2005)**; Swaty et al. (2004); Mueller et al. (2005); Allen (2007); Greenwood and Weisberg (2008)
19	USA (Arizona)	2001–2004	Coniferous (180)	*Pinus ponderosa*	Lower edges of elevational range	Multi-year drought, high temperatures	7 –21	Landscape–subregional	**Primary role**, bark and engraver beetles (*Ips* spp.)	Negron et al. (2009)
20	Canada (Saskatchewan and Alberta)	2002–2004	Boreal forest, prairie ecotone (360–460)	*Populus tremuloides*	Southern edge of geographic range	Multi-year drought	3.6/yr vs. 1.6/yr in non-drought yrs.	Subcontinental; patchy across ~10 M ha	Insect defoliators	Hogg et al. (2008)
21	Canada (British Columbia)	2000–2006	Montane mixed conifer (~250–1000)	*Pinus contorta*	Middle of geographic range	Drought, high spring and summer temperatures	>435 M m^3 (timber lost)	Regional – continental; ~13 M ha affected	**Primary role,** bark beetle (*Dendroctonus ponderosae*)	Kurz et al. (2008a)
22	USA (Colorado)	2005–2006	Montane mixed (380–1100)	*Populus tremuloides*	Patchy but concentrated at lower edges of elevational range	Multi-year drought, high spring and summer temperatures.	32 (stand scale); 5.62 (landscape scale)	Landscape–subregional; 58,374 ha affected	Wood borers; cytospora canker; bark beetles	Worrall et al. (2008)
23	USA (Western States)	1955–2007	All western forest types	Many species	Not reported	High temperatures	3.9-fold increase in annual mortality rate	Regional	Not reported	van Mantgem et al. (2009)
24	Western North America	1997–2007	Coniferous	*Pinus* spp., *Picea* spp., *Abies* spp., *Pseudotsuga menziesii*	Not reported	Drought, high temperatures	Not reported	Regional; 60.7 M ha affected	**Primary role**, bark and engraver beetles (*Dendroctonus*, *Ips*, *Dryocoetes*, *Scolytus* spp.)	Bentz et al. (2009)
25	USA (Minnesota)	2004–2007	Boreal and temperate mixed (480–900)	*Populus tremuloides*, *Fraxinus* spp.	Lower edges and middle of ranges	Drought	Not reported	Not reported	Insect defoliators	Minnesota Dept. Nat. Resources (2007)
26	USA (California)	1998–2001, 2005–2008	Not reported	Not reported	Not reported	Drought preceded by wet, warm episodes	423,000 dead tress in northern California	Landscape–subregional	**Primary role**, pathogen (*Phytophthora ranorum*)	Garrett et al. (2006)
27	Canada and USA (Alaska, British Columbia)	Long-term 1880–2008	Temperate coastal rainforest (1300–4000)	*Chamaecyparis nootkatensis*	Middle	Warmer winters and springs	70% of basal area lost	Subregional; ~200,000 ha affected	None	Beier et al. (2008); Hennon and Shaw (1997); Hennon et al. (2005)

Footnotes as in Table A1.

Table A6
Documented cases of drought and/or heat-induced forest mortality from South and Central America, 1970–present. ID numbers refer to locations mapped in Fig. 8.

ID	Location	Year(s) of reported mortality	Forest type/ mean precip.[a]	Dominant tree taxa	Spatial concentration of mortality within geographic or elevational range	Climate anomaly linked to mortality	Stand/population-level mortality (%)[b]	Scale of impact/ area affected (ha)	Biotic agents associated with mortality?[c]	Reference(s)[d]
1	Panama (Panama)	1982–1985	Tropical rainforest (2600)	205 different species	Not reported	Seasonal drought, high temperatures	2.75/yr vs. 1.98/yr in non-drought years	Not reported	Not reported	Condit et al. (1995); Leigh et al. (1990)
2	Brazil (Espírito Santo)	1986–1989, 1997–1999	Tropical rainforest (1200)	Not reported	Not reported	Seasonal drought	4.5/yr vs. 1.4/yr in non-drought years	Not reported	Not reported	Rolim et al. (2005)
3	Brazil (Amazonas)	1997	Tropical rainforest (2000)	Not reported	Not reported	Seasonal drought	1.9/yr vs. 1.21–1.23/yr in non-drought years	Not reported	Not reported	**Williamson et al. (2000)**; Laurance et al. (2001)
4	Costa Rica (Heredia)	1998	Tropical rainforest (3962)	Not reported	Not reported	Seasonal drought	3.1/yr vs. 1.6/yr in non-drought years	Not reported	Not reported	Chazdon et al. (2005)
5	Argentina (western Neuquén, Rio Negro)	1998–1999	Temperate steppe – Montane broadleaf (500–1500)	*Nothofagus dombeyi*	Arid edge of geographic range; lower elevations	Seasonal drought, high temperatures	11–57	Landscape–subregional	Wood borers; woodpeckers	**Suarez et al. (2004)**; Suarez and Kitzberger (2008); Bran et al. (2001)
6	Amazon Basin	2005	Tropical rainforest	Not reported	Not reported	Single year drought	1.2–1.6 Pg C lost	Subcontinental	Not reported	Phillips et al. (2009)

Footnotes as in Table A1.

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