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Review

Impact of summer drought on forest biodiversity: what do we know?

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Abstract – To date, very few studies have assessed the impact of summer droughts on forest biodiversity and ecosystem functioning. Decreased ecosystem productivity and increased mortality are general consequences of drought on biodiversity. Competitive species, species adapted to cold and wet conditions as well as species with low reproduction rates and/or limited mobility seem the more affected. However, species-specific effects are regulated by mechanisms allowing for resistance to drought. The short-term consequences of drought on biodiversity depend on species abilities to resist, and to recover after, drought, and on competitive interactions between species. Although the abundance of many species generally decreases during drought, some taxa may increase in number during drought or shortly after. The effects of recurrent droughts must be evaluated in the wider context of global climate and habitat change. Considering the predicted increase in drought frequency and intensity, interdisciplinary research initiatives on this issue are needed urgently.

drought impact / biodiversity / forests / ecosystem functioning / global change

Résumé – Impact de la sécheresse estivale sur la biodiversité forestière : que savons-nous ? On connaît mal les conséquences des sécheresses sur la biodiversité et le fonctionnement des écosystèmes forestiers. La productivité des écosystèmes semble diminuer et s'accompagne d'une mortalité accrue. Les espèces compétitives, liées à des habitats frais ou humides, avec un faible taux de reproduction et/ou une mobilité réduite semblent les plus sensibles à la sécheresse. La réponse spécifique dépend également des mécanismes de résistance à la sécheresse. Les conséquences à court terme dépendent de la capacité des espèces à résister et à se rétablir de la sécheresse, et de leurs interactions. Un nombre conséquent de taxons peuvent être plus abondants en période de sécheresse ou peu de temps après. Les effets de sécheresses récurrentes sont à replacer dans le cadre du changement climatique global et des modifications d'habitats. Sachant que la fréquence et l'intensité des sécheresses devraient croître dans l'avenir, il est urgent de lancer des recherches interdisciplinaires sur le sujet.

sécheresse / biodiversité / forêts / fonctionnement de l'écosystème / changement global

1. INTRODUCTION

The importance of natural hazards in shaping biodiversity has received renewed scientific attention. Experts agree that natural disturbances will increase in frequency and intensity over the next few decades in response to global warming [52]. Both empirical and theoretical work has shown that the frequency and intensity of disturbances influence biodiversity [80, 110].

The dramatic effects of the extreme summer drought in 2003 on trees in Western Europe (i.e. mortality, dieback, premature leaf fall) [23] highlight the need to assess the impact of drought on forest biodiversity. All levels of forest biota may be affected, including aboveground (e.g. trees, understory layer) and belowground (e.g. soil microbiota, edaphic invertebrates) species that are intimately related. Therefore, drought may have serious consequences for forest ecosystem functioning.

While scientific interest concerning the impact of global warming on terrestrial ecosystems has increased recently [85, 108], the effects of extreme climatic events on forest ecosystems are still poorly understood [42]. To date, only a few studies have focused on the effects of drought on forest biodiversity (e.g. forest trees [46, 104]). Even studies attempting to quantify the loss of wood volume following natural disasters have not considered the direct effects of droughts [89, 104].

Investigations on the biological impacts of drought events have focused mainly on arid, semi-arid, and Mediterranean biomes and are biased towards open habitats such as grasslands. Extrapolating results from these habitats to temperate forests is unlikely to be valid. A further limitation is that most existing studies have concentrated on plants (especially trees in temperate regions), pests and herbivorous insects. The conclusions drawn from a few well-studied groups (plants, insects) should not be 'blindly' extrapolated to other components of biodiversity. In addition, most data on which our current knowledge is based are derived from experiments rather than from observations. While experiments simplify the complex feedback systems found in natural conditions, observations generally lack replication and tend to be very short-term. Thus, both approaches are necessary to compensate for their respective shortcomings.

Herein, we summarize the literature on the impact of summer drought on terrestrial biodiversity, with emphasis on forest ecosystems. First, the factors predisposing an organism to

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Table I. Mechanisms of drought resistance.

Organism	Mechanisms
Animals	Thermo-regulation
	Moving to more protected areas
	Summer diapause
Plants	Stomatal closure
	Production of antioxidant and compatible compounds Changes in cell membrane composition
	Rapid defoliation
	Morphological adaptation (e.g. deep-rooting)
	Seed bank

drought or, conversely, conferring drought-resistance are reviewed. Second, the short- (one or two years after the drought event) and mid-term (a decade or so) consequences of drought on biodiversity are assessed. Third, the long-term (decades or more) consequences of drought combined with other global changes on biodiversity are considered. There is evidence that drought effects may be less severe during summer than during other seasons of the year [39]. However, this review examines the effects of summer drought events only. Intensity [35,91], duration [30] and frequency [79] of droughts also influence biodiversity, with data suggesting that the duration of a drought event may be more important than its intensity [30] and that the impact of a single extreme drought may depend on the overall temporal trend in drought intensity [54]. Extreme temperatures, usually associated with summer drought, also amplify environmental stress [5]. Unfortunately, these issues cannot be covered here due to the limited number of adequate studies (but see [11] for details on eco-physiology).

2. DROUGHT RESISTANCE AND PREDISPOSING FACTORS

Table I summarizes resistance mechanisms of animals and plants. Organisms can cope with drought/heat by escaping these conditions (e.g. by moving in shaded areas) and/or by alleviating the damaging effect of the physiological stress (e.g. by producing compatible compounds to limit the osmotic stress). Details on physiological adaptation to drought by plants can be found in [7, 11, 112], by insects in [4] and by vertebrates in [69]. Analogies can be drawn between diapausing insects and seeds stored in a seed bank. In insects, summer diapause aims primarily at escaping drought and may occur at all developmental stages (from larval to adult) and may be facultative or not. Different environmental factors such as number of daylight hours or temperature may lengthen or terminate the diapause in a species-specific way [4, 51, 59].

Many factors can predispose organisms to drought in the short- and mid-term (Tab. II). These factors are difficult to summarize because of sparse and sometimes conflicting evidence. Moreover, some of the supposed 'predisposing factors' have never been scientifically proven.

At the individual level, the effects of drought may be influenced by genotype, age and location. Indeed, very young or very old individuals are typically the primary victims of drought events. Furthermore, individuals at the southern limits of their geographical distribution may be particularly affected by drought, as a species range is often determined by its physiological tolerance. Forest management that maximises leaf area index and/or favours species in regions close to the maximal heat- or water stress-tolerance limits of the species may threaten entire forest stands [45]. At the species level, the effects of drought are influenced by life history and ecological traits, such as anatomical or morphological adaptations (e.g. leaf size, depth of roots, Tab. II). At the ecosystem scale, the main effects of drought may occur indirectly, with droughts promoting the occurrence and/or increasing the intensity of other natural or anthropogenic pressures. One of the most striking examples is the dramatic increase of Mediterranean forest fires during dry years. The higher likelihood of insect attacks on water-stressed plants or trees is not a universal phenomenon (e.g. [16, 44]), but boring and sucking insects usually perform better on stressed plants (the contrary has been reported for gall-making and chewing insects [24, 56]).

There seems to be a general consensus that species-poor ecosystems are usually more sensitive to perturbations, such as droughts, than species-rich ecosystems [50]. For instance, a positive relationship was found between total biomass and species richness of naturally co-occurring mosses and liverworts under experimental drought conditions but not under constant conditions [73]. One explanation for the positive relationship between species richness and overall drought resistance may be that impoverished ecosystems may host fewer species or groups that are capable of a differential functional response [70]. For instance, a decrease in both total abundance and species richness of Collembola communities is associated with a strong reduction in decomposition rate [82]. However, ecosystem resistance and resilience are often unrelated to total species richness, the number of plant functional groups or the number of trophic levels (e.g. [109]). For instance, high functional redundancy has been found among forest soil microarthropods, so that the positive relationship between species richness and ecosystem functions would appear only for very low values of species richness [62]. Several studies have even emphasized the species-specific drought response of plants [14, 66], root mycorrhizae [55] and butterflies [92]. Idiosyncratic responses suggest that simple physiological models may not be sufficient to predict the effect of drought on whole communities [21, 38]. Furthermore, response patterns at the community level are also regulated by complex interactions between the different components of trophic chains. For example, a greater abundance of insect parasitoids and arthropod predators of European corn borer larvae (*Ostrinia nubilialis* Hubner) in drought-stressed corn fields compensated for the corn's greater susceptibility to the larvae [38].

3. SHORT- AND MID-TERM EFFECTS OF DROUGHT

Observed and potential short- and mid-term impacts of a drought event are listed in Table III. Short-term responses may differ from mid- and long-term responses because (1)

Table II. Observed and potential (in italics) factors predisposing taxa to drought impact. A distinction is made between factors that may vary between individuals of the same species, between phylogenetically-related species (but not between individuals of the same species) or between ecosystems (but not between species within the same ecosystem).

Level	Predisposing factor	Taxa and references
Individual	Location near species' range boundary	Tree [22], butterflies [99]
	Location in a shaded place	Plants [76, 107]
	Age (young and old individuals)	Trees [28, 61, 79]
	Not entering diapause (when facultative)	Grassland flies [74]
	Drought intolerant genotype	Never demonstrated
Species	Large leaf-area	Trees [5, 18]
	Competitive	Temperate grassland herbs [25,72] but maybe not temperate forest understory plants [71]
	Preference for cool or wet habitats	Absence of ground reserves
		Forest plants [14, 106], temperate Carabids and butterflies but not moths [71]
		Temperate herbaceous plants [15]
	Shallow roots	Temperate grassland herbs [14, 25, 72]
	Low reproduction rate	Temperate and Mediterranean grassland herbs [15, 66, 72]
	Low mobility	Temperate butterflies but not moths [71]
	Specific competition	Temperate forest understory plants [33] but see [12, 26][1]
	Not diapausing	Never demonstrated
Ecosystem	Disturbed ecosystems	Temperate grassland herbs [14], temperate mosses [73], temperate forest Collembolans [82]
	Susceptibility to fire	Mediterranean shrubs [65], Mediterranean forest Carabids [31], Mediterranean birds [47]
	Susceptibility to chemicals	Temperate forest and boreal grassland Collembolans [48, 58] but see [61]
	Susceptibility to pest attack and disease	Various plants and trees [17, 90] but see [16, 44]
	Susceptibility to invasion	Never demonstrated

[1] This may depend on the soil properties [18], temperature [21] and level of water supply and on the aspect of plant performance examined [87].

the impact of a drought event may appear primarily during a prolonged recovery phase rather than during the event itself [25, 42], and (2) resistance and resilience to drought may be negatively linked, as was found for herbaceous plant communities [67]. In the latter study, five herbaceous communities representing a wide range of functional types were experimentally subjected to drought in Great Britain. Fast-growing (resilient) species tended to be more sensitive to damage by drought than slow-growing species [67].

Lower productivity (as measured as changes in biomass or cover over time) and higher mortality are the most widespread effects of drought on plants. In two prairie grasslands, a major drought caused the annual production, which had been nearly constant previously, to oscillate every two years for at least nine years after the event, showing that drought impact on ecosystem productivity may last far beyond the event itself [43]. More fertile, early-successional ecosystems may be more vulnerable to drought, as found for British grasslands [41].

As for plants, desiccation during drought periods may increase the mortality rate of some insects [111], while other species may remain largely unaffected [71, 88]. Drought may even favour some taxa [68, 71]. In fact, high temperatures usually stimulate an insect's growth, allowing multivoltine species (i.e. species that produce several broods in a single season) to produce more generations per year. Furthermore, with the exception of species whose diapause is under strict photoperiodic control [51], high temperatures may induce or extend summer diapause [4]. Diapausing individuals are known to enjoy better survival and fecundity than non-diapausing ones [74, 113]. Information on the effects of the 2003 drought on forest insect populations can be found in [86].

To date, data on the short- and mid-term consequences of drought on biodiversity are almost completely confined to studies in grasslands. Forest biodiversity, and especially vegetation, may be particularly resistant to drought. According to annual surveys on $124 \times 100\ m^2$ plots of the French RENECOFOR long-term monitoring programme, for instance, changes in community composition were small after the extreme 2003 drought (J.-L. Dupouey, pers. com.). A response, if any, is more likely to result from canopy opening after drought [79] than from the drought itself, with shifts in plant community composition becoming apparent only several years after the drought, until the canopy closes again. Current knowledge on the impact of thinning cuts on herbaceous vegetation suggests that small changes in canopy cover will probably increase the number, the abundance and the flowering rate of forest plant species [6, 100].

Another potential positive impact of drought on forest biodiversity relates to the increased amount of standing (snags) and lying deadwood (branches, logs) [105]. Managed forests are characterized by low deadwood volumes per ha compared

Table III. Short- and mid-term, observed and potential (in italics), consequences of drought on biodiversity. A distinction is made between factors operating primarily at the individual, species and ecosystem levels (see legend of Tab. II).

Level	Short-term consequences	Taxa and references
Individual	Reduced growth	Forest plants [39]
	Reduced fecundity	Plants [34], soil microarthropods [62], butterflies [84]
	Increased mortality	Trees [78] but see [71] for grassland herbs and insects
Species	Increase of deadwood-dwelling species	Saproxylic insect and fungi [24]
	Shift in species range	Never demonstrated
	Increase of drought-tolerant species	Never demonstrated
Ecosystem	Reduced productivity	Boreal forest understory plants [13], temperate forest Collembolans [82],
	Slower ecosystem functioning	boreal forest birds [8]
	Decrease in local species richness	Temperate grassland herbs with accumulation of litter [25]
	Shift in species interactions	Boreal forest understory plants [75], temperate forest Collembolans [82]
	Shift in species composition	Mountain grassland herbs [19]
		Temperate grassland soil microarthropods [63]
Level	Mid-term consequences	Organisms and references
Individual	Lasting growth reduction	Trees [76, 79, 97]
	Delayed mortality	Trees [11, 78]
	Susceptibility to pathogens and disease	Trees [110]
	Reduced offspring performance	Grassland moths (males that do not diapause [113])
Species	Increase of drought-tolerant species	Temperate forest understory plants [106]
	Microevolutionary changes	Tropical island birds [10]
	Increase of deadwood-dwelling species	Never demonstrated
	Shift in species range	Never demonstrated
Ecosystem	Oscillations in productivity	Temperate grassland herbs [43, 103]
	Shift in species composition	Mountain grassland herbs [95]
	Shift in species interactions	Never demonstrated
	Reduced species richness	Never demonstrated

to old-growth or primary forests [105]. Therefore, even a small increase in deadwood in managed forests may have considerable ecological consequences [37]. In Scandinavia, about 25% of all forest species depend on deadwood (including fungi, insects, mosses, vertebrates and nematodes) [93].

Due to the lack of a global, standardised assessment of drought susceptibility for even the most common animal and plant taxa, the increase in drought-tolerant species after drought events has never been proven scientifically. For instance, there is no Ellenberg-like [27] index for drought resistance in vascular plants. Only surrogates for species drought-tolerance such as preference for cool or wet habitats or morphological traits (e.g. ground reserves, root depth for plants) have been used to assess the impact of droughts (e.g. [14, 71]).

The assessment of species susceptibility to drought will be an important step for understanding the impact of drought on forest biodiversity but it probably will not be sufficient. The response of communities to drought likely is more than just the sum of the individual responses of species because drought effects often are mediated through biological interactions. For example, drought may reduce the cover of perennial plants (see above; [71]) or prevent colonisation of poor soils by dominant plants [83]. This provides refuges for tap-rooted plants [14] and allows rapid colonisation by annuals or biannuals [15] from dormant or newly-dispersed seeds [57]. In one alpine meadow site, dominant grasses decreased in cover following an extreme, 4-year drought period; they had not recovered their initial cover nine years later because other species with a higher regenerative capacity had colonised [95]. In some cases, the identity of the dominant species in the herb layer may be determined by drought-resistance and competitive ability, with the outcome depending on the relative importance of the two phenomena. For example, *Bromus erectus* Huds. is usually excluded from calcareous grasslands in France by competition with *Brachypodium pinnatum* (L.) Beauv., but dominates in areas with high water-stress due to the greater drought sensitivity

of the latter species [19]. Relaxed inter-specific competition probably explains why the richness of bryophytes in Southern Norwegian old-growth coniferous forests [75] and of vascular plants in British grasslands [71] increased shortly after drought. Thus, an initial decrease in richness immediately after drought may be followed by an increase in richness, both at very local (α diversity) and larger spatial scales (γ diversity), either in a few years' time and/or over a much longer time period.

4. LONG-TERM EFFECTS OF DROUGHT AND GLOBAL CHANGE

Drought frequency is thought to be the main driver of vegetation dynamics in Mediterranean [102], boreal [94, 101] and temperate forests [64]. For example, the decline of oak in Europe has been linked to the detrimental effects of recurrent droughts [60, 98]. Similarly, summer drought is thought to be one of the factors that helped hazel to out-compete oak in the southern Alps 11 000–10 500 cal yr BP [32]. Species can be expected to shift their distribution in response to the new selection pressures, adapt or become extinct. Current changes in geographic ranges of many species have been linked to global warming in general, but extreme weather events, such as droughts, provide an alternative explanation [77].

Extreme events such as droughts may generate intense episodes of natural selection [3, 42]. Selection for drought-tolerant genotypes may thus cause micro-evolutionary changes. However, evidence for natural selection acting upon a heritable variation in traits increasing drought tolerance is lacking (but see [10]), although populations exposed to different drought frequencies often have corresponding levels of drought–tolerance that are genetically fixed. Examples can be found in [1, 53, 81] for plants and in [92] for insects. The flora and fauna that still exists in the Northern Hemisphere survived extreme climatic episodes during the Pleistocene. Therefore, contemporary climatic changes can be expected to cause relatively few extinctions. However, most extant taxa in the Northern Hemisphere have been selected to resist winter cold rather than summer drought or extreme heat (see [96] for plants and [9] for birds). Furthermore, the genus-level conservatism in climatic requirements observed in Northern Hemisphere tree species [96] and the selection acting simultaneously on antagonistic traits (e.g. dispersal/survival and fecundity, stress-resistance and resilience) [29] may well prevent species from adapting to rapidly changing environmental conditions. Additionally, the combinations of conditions that exist today may change in the future, with past and present climatic conditions failing to provide a suitable analogue. These changes may lead to combinations of species that have never co-occurred before [2]. Finally, long-term impacts of droughts will depend not only on drought frequency and intensity, but will be intimately linked to the effects of other atmospheric, climatic and habitat changes also. Most of these changes interact in complex ways [36, 39]. For instance, high rates of atmospheric nitrogen deposition may reduce inter-specific plant competition whilst a slow climatic warming may have little effect [40].

Overall, therefore, we lack sufficient data for making reliable predictions on the adaptive potential of species to the simultaneous action of several drivers of global change [49].

5. CONCLUSION AND RESEARCH NEEDS

Drought is certainly a widely underestimated ecological stress and selection force [42]. Our review has revealed a number of issues that should have priority in future research:

1. Variations of factors such as drought intensity, duration and return frequency, species-specific phenotypic plasticity, adaptive potential and phylogenetic and physiological constraints must be experimentally identified in relation to drought events. This should lead to a concise classification of species according to their sensitivity to drought or to environmental features linked to drought. Particular focus must be on vulnerable species and ecosystems, because these will probably be the first to be seriously affected by drought.
2. The impact of drought on ecosystem processes must be studied to better understand how drought alters ecological functions and how these effects are influenced by species composition. Points 1 and 2 should help to define an indicator system for predicting drought sensitivity at the stand and forest levels.
3. Research should focus on the simultaneous effects of drought and other factors, such as forest management, pollution and global warming. This is essential for identifying the most relevant factors that mediate the impact of drought events on forest biodiversity. The impact of strategies that are being proposed to mitigate the effects of drought on trees on forest biodiversity should be rapidly evaluated, especially the impact of the plantation of drought-tolerant tree species and of the reduction of the rotation length [20].
4. Long-term monitoring programs should be continued or developed, since these are the only way for evaluating the impact of rare events on ecosystems. However, these programs should be coupled with integrative experimental and modelling approaches to enhance our understanding of complex drought effects.
5. The effects of drought events on forest biodiversity should be considered in both planning (e.g. tree species selection) and management (e.g. retention of deadwood).

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