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Review

# Mechanisms of Fire Seasonality Effects on Plant Populations

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**Altered fire regimes resulting from climate change and human activity threaten many terrestrial ecosystems. However, we lack a holistic and detailed understanding of the effects of altering one key fire regime component – season of fire. Altered fire seasonality can strongly affect post-fire recovery of plant populations through interactions with plant phenology. We identify seven key mechanisms of fire seasonality effects under a conceptual demographic framework and review evidence for these. We reveal negative impacts of altered fire seasonality and identify research gaps for mechanisms and climate types for future analyses of fire seasonality effects within the identified demographic framework. This framework and these mechanisms can inform critical decisions for conservation, land management, and fire management policy development globally.**

## Highlights

Seasonality of fire is changing globally due to increasing human ignitions and climate change.

There is concern that season of fire can strongly affect the persistence of plant populations and composition of plant communities, but our understanding of fire seasonality effects lags behind that for some of the other fire regime components, largely because such effects are often confounded with covarying fire intensity effects.

By focusing on the causes of post-fire demographic change in plant populations, mechanisms of fire seasonality effects can be identified and studied.

Improved understanding of fire seasonality effects is essential for policy development for fire management in fire-prone ecosystems.

## Altered Fire Seasonality

Lengthening **fire season** (see Glossary) due to global climate change and increased **anthropogenic ignition sources** have, collectively, altered **fire seasonality** – the timing of fire throughout the year – in many regions around the world (Box 1) [1–4]. Extensive winter wildfires in California and southeastern Australia in 2017 and 2018, respectively, provide clear and well-covered examples of this phenomenon [5] (see https://theconversation.com/drought-wind-and-heat-when-fire-seasons-start-earlier-and-last-longer-101663). Because terrestrial plant species are adapted to a particular **fire regime** rather than simply to fire itself, there is concern that many ecosystems may not be resilient to such changes [6,7]. Negative impacts of altered fire seasonality on plant populations (including elevated mortality and reduced fecundity) are increasingly being documented (e.g., [8–10]), despite limited understanding of the mechanisms that might drive these impacts. This knowledge gap may arise from a lack of research attention, but may also be due to complex interactions that exist between fire seasonality and other fire regime components, **fire intensity** and **fire severity** in particular [6]. To provide land managers and policymakers with information that can aid with the challenge of managing and conserving **fire-prone ecosystems** and to mitigate the negative impacts of fire, research needs not only to quantify the impacts of altered fire seasonality but also to identify the mechanisms behind resulting shifts in plant population abundance and plant community composition.

## Plant Responses to Fire Seasonality

Many plant species possess traits that enable their persistence under a particular fire regime. These include belowground energy storage organs that provide resources for rapid regrowth after fire and the accumulation of **seed banks** with seeds that require heat to break **dormancy** and/or smoke cues to promote germination [11]. However, many of these traits vary with the seasonal cycles that plants follow (i.e., plant phenology), meaning that their fire-persistence qualities may be less effective if fire occurs outside the fire season to which species are adapted. For example, Werner [12] argues that variation in the recovery of juvenile trees in response to season of fire in an Australian tropical savanna is influenced by seasonally varying belowground carbohydrate reserves; juvenile trees burned while their reserves are at their minimum are less likely to retain their competitive position in the canopy. As many species persist through a combination of traits, their response to altered fire seasonality may be complex and potentially influenced by a range of mechanisms.

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In this review, we propose specific mechanisms that drive plant population shifts as a consequence of varying season of fire. These mechanisms are tied to seasonally varying physical seed attributes and plant phenology, including periods of growth and dormancy, energy storage, flowering, seed production, germination, and seedling establishment [6,13].

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**Box 1. Changing Fire Seasons**

In fire-prone ecosystems, fires are historically most likely to occur during hot and/or dry seasons, when suitable fuel moisture conditions and natural ignition sources coincide [93,94]. However, global environmental changes have increased the occurrence of planned and unplanned fires outside this historically high fire danger season [1,95–98].

Long-term warming and drying associated with climate change can bring forward the timing of snowmelt, increase evaporative demand, dries fuel more quickly, and truncates the moderating influence of rainfall or overnight recovery of humidity [96,99,100]. In many regions, the combination of chronic warming with discrete weather events (e.g., heatwaves) has extended the occurrence of hazardous fire weather into unprecedented times of the year [3,101]. Fire weather season length has increased by nearly 20% across the Earth's vegetated surface (Figure I; [3]). Parts of western North America, Brazil, and East Africa now have fire seasons over 1 month longer than they were 35 years ago [3,102]. The most significant increases occur where not only temperature but also changes in humidity, length of rain-free intervals, and wind speeds are most pronounced [3].

Increased anthropogenic ignitions also drive changing fire seasons [1,97]. Humans and their infrastructure are major sources of ignitions, which can be distributed throughout the year, unlike lightning-ignited fires which normally have a distinct seasonality (Figure II; [97,103]). Unplanned anthropogenic fires (i.e., arson, accidental) may account for a large proportion of area burned from anthropogenic ignitions, especially in fire-prone landscapes with sizeable human populations. In addition, the planned use of fire by land managers (i.e., **prescribed burning**) is often conducted outside the peak fire danger season, with safety advantages gained by avoiding high fire danger periods. Managed burns are implemented to reduce the risk of uncontrollable wildfires during times of high fire danger, to restore fire-dependent ecosystems, and sometimes to manage individual threatened species [104,105]. However, conducting burns during periods of lower fire danger often extends the occurrence of fire to seasons when it would otherwise be rare. Climate change-driven expansion of the fire season also impacts the window for safe managed burning, with the likely consequence of prescribed burns being extended even further into unprecedented times of the year [106].

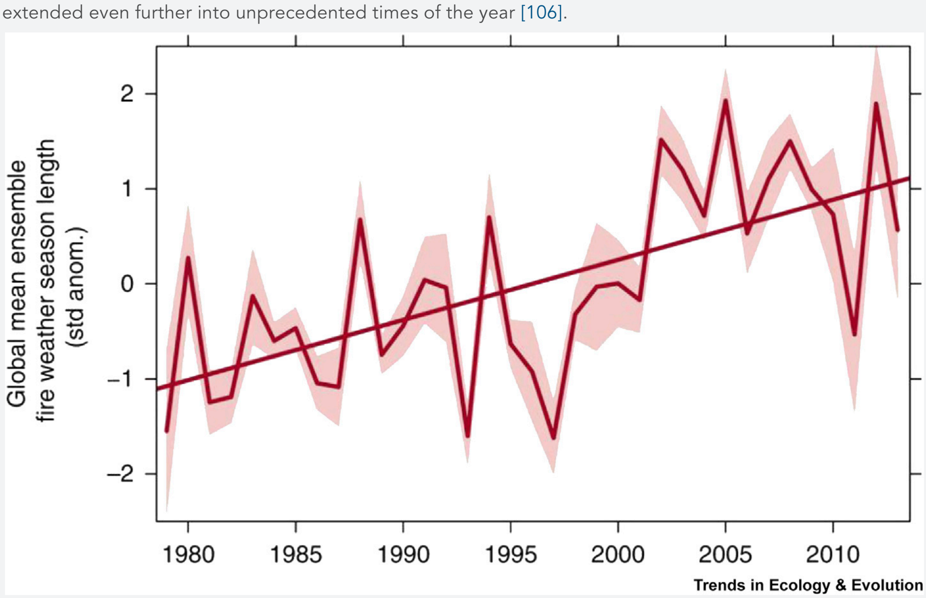


**Figure I. Changes in Global Mean Fire Weather Season Length from 1979 to 2013 with 95% Confidence Limits (Shaded Area).**

The y-axis refers to deviations from the average over this time period. Globally, the fire weather season has lengthened by nearly 20%. Reproduced from [3].

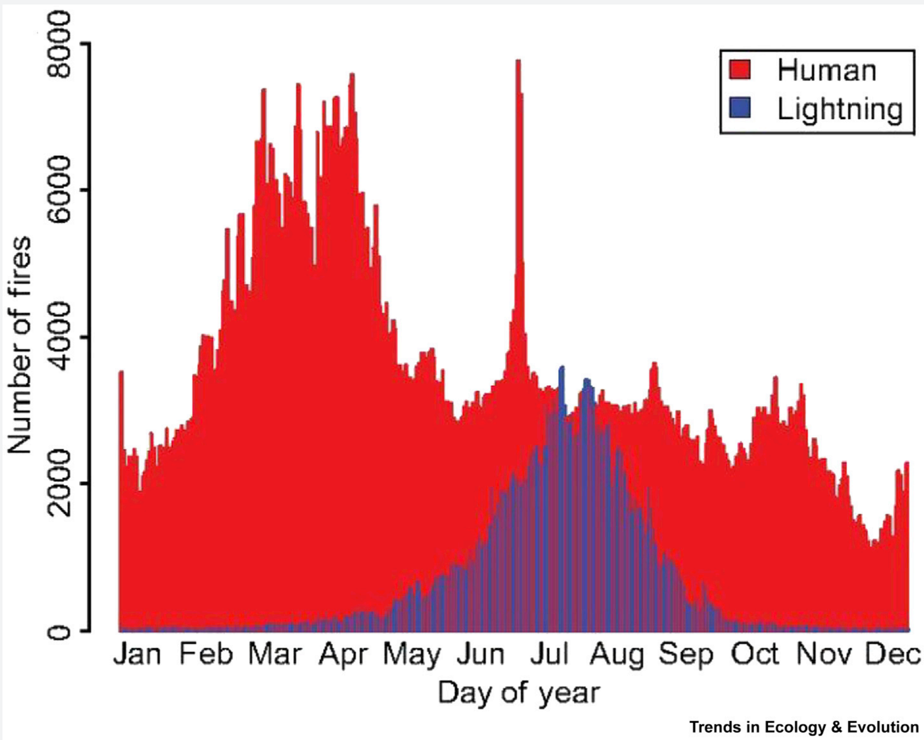


**Figure II. Frequency Distribution of Wildfires Across the Contiguous USA from 1992 to 2012, Separated by Ignition Source.**

The number of wildfires in the dataset is 1.5 million. Reproduced from [97].

## Glossary

**Anthropogenic ignition sources**: ignitions derived from human activities, deliberate and planned (from a land-management perspective), deliberate and unplanned (arson), or accidental (e.g., sparks from vehicles or infrastructure).

**Dormancy**: refers to seed dormancy – seeds that do not initiate germination despite suitable environmental cues.

**Fire intensity**: the fuel consumed or energy released during a fire (often expressed as W $m^{-1}$ $s^{-1}$ of fire front). Fire intensity and severity are not always correlated.

**Fire regime**: the long-term pattern of fire interval, intensity or severity, seasonality, size, and type (ground, understory, or canopy), traditionally defined for a point location to include mean and variance around these components; sometimes also considered to include spatial attributes such as fire extent and patchiness.

**Fire-prone ecosystems**: ecosystems that regularly experience fire (on short or long timeframes) and are broadly resilient to its occurrence as part of a long-term fire regime.

**Fire season**: the period of the year with weather and fuel moisture conditions suitable for fire spread.

**Fire seasonality**: the timing of fire throughout the year.

**Fire severity**: the impact of fire on vegetation (e.g., percentage crown scorch) measured directly or via remotely sensed data. Fire intensity and severity are not always correlated.

**Geophytes**: plants that retain one or more buds in a subterranean storage organ (e.g., bulbs, tubers) and that grow vegetatively, and often flower, and then die back annually.

**Physical dormancy**: a trait in which seeds possess a water-impermeable seed or fruit coat, also sometimes called 'hard seededness'.

**Plant functional types**: groups of species classed by their functional responses corresponding to combinations of relevant functional traits.

**Prescribed burning**: fire deliberately implemented under controlled conditions by land managers, often with the aim of

## Mechanisms of Fire Seasonality Effects

A predictive understanding of the key mechanisms driving fire seasonality effects can be developed by focusing on the processes of demographic change in plant populations. Here we employ a conceptual demographic framework based on the rationale that plant populations are able to persist in fire-prone environments when rates of recruitment plus survival are comparable with rates of mortality [14–16]. Fire often directly affects mortality, with individuals of obligate seeding species killed by complete canopy scorch. To persist, their populations must compensate through equal or higher rates of post-fire seedling recruitment, which is enabled by traits such as **serotiny**, and various forms of seed dormancy. By contrast, adult populations of **resprouter** species can survive and regrow after fire at high rates but rely on periodic seedling recruitment to offset occasional adult mortality owing to fire or inter-fire mortality (including senescence) [17]. Fire seasonality can influence the demographic processes of recruitment, survival, mortality, and fecundity by affecting one or more of seven key mechanisms across three critical life history stages and the transitions between them (Figure 1):

- Adult survival
  - o Mechanism 1: adult survival and growth.
- Propagule availability
  - o Mechanism 2: post-fire flowering and seed production.
  - o Mechanism 3: pre-fire seed bank availability.
  - o Mechanism 4: juvenile growth and maturity.

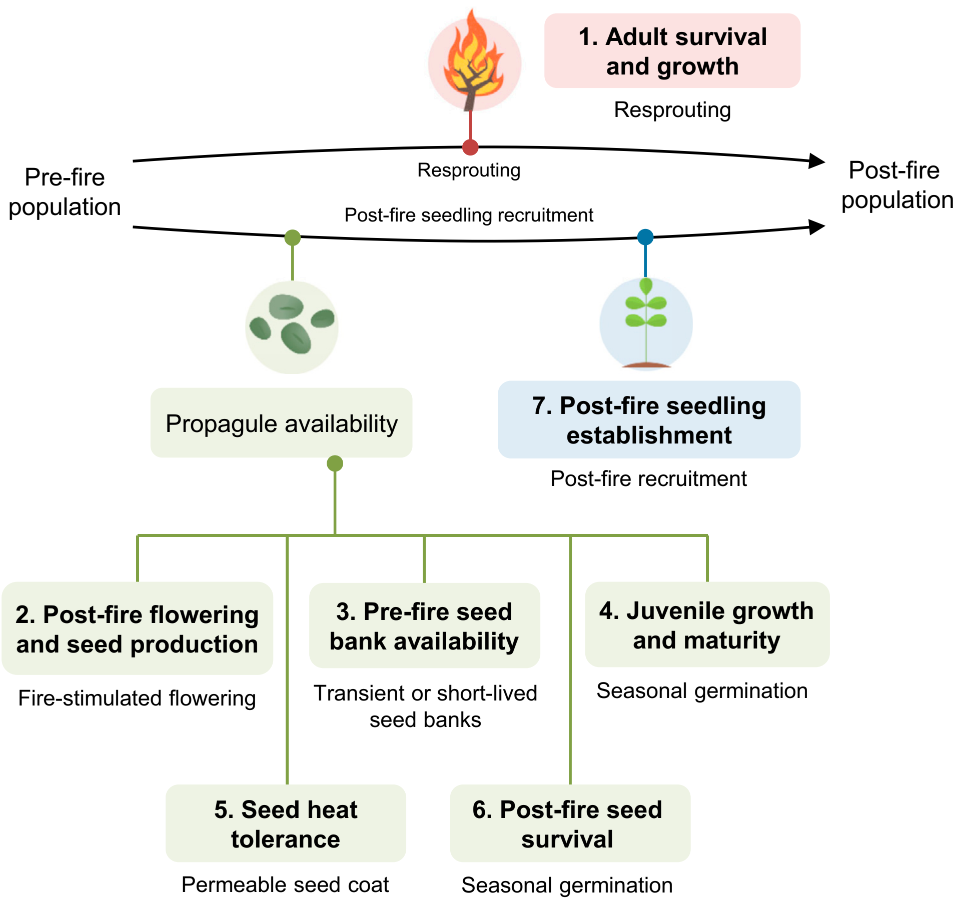


**Figure 1. Conceptual Demographic Framework Identifying Seven Key Mechanisms Driving Fire Seasonality Effects on Plant Populations.**
Fire seasonality can alter population dynamics via impacts on adult survival (red box), propagule availability (green boxes), and post-fire seedling establishment (blue box). The two pathways reflect the two major strategies for population persistence in fire-prone environments (i.e., resprouting and post-fire seedling recruitment). Some species persist through a combination of both. The text under each mechanism identifies the plant or seed traits that make species vulnerable to decline, explained in the section 'An Explanation of the Mechanisms'. Graphics provided by www.vecteezy.com/.

reducing future fire hazard through the combustion of surface and near-surface fuels (also 'controlled', 'fuel reduction', or 'hazard reduction' burning).
**Resprouter**: plants with the capacity to survive and regrow vegetatively after fire from buds protected from the heat of the fire.
**Seed bank**: a reserve of viable seeds in the soil or in woody fruits in the plant canopy. Transient seed banks comprise seeds that do not live beyond the first germination season following maturation. Persistent seed banks comprise overlapping generations of seeds, with at least some seeds surviving until the second germination season. Persistent seed banks may range from short lived (2–5 years) to long lived (5 to >10 years).
**Serotiny**: the storage of mature seeds in closed woody cones or fruits in the plant canopy for longer than 1 year, so that a persistent seed bank develops.

  - Mechanism 5: seed heat tolerance.
  - Mechanism 6: post-fire seed survival.
- Post-fire seedling establishment
  - Mechanism 7: post-fire seedling establishment.

These mechanisms are detailed below. By focusing on the mechanisms that drive demographic responses to fire, we can disentangle the effects of fire seasonality from covarying fire regime effects (especially the effects of fire intensity and severity), unify existing hypotheses of the causes of fire seasonality effects, and proffer the use of a conceptual demographic framework to shape future research examining fire seasonality effects and their interactions with other fire regime components.

## Evidence from the Literature

To gather evidence for these mechanisms from the literature, we systematically searched the Scopus database on 12 July 2019 for papers using the terms (fire OR burn) AND (season*) AND (effect* OR impact*) AND (recruit* OR resprout* OR surviv* OR regenerat* OR germinat*).

This search returned 926 papers, of which 143 considered relevant fire seasonality effects on plant populations (see Table S1 in the supplemental information online for a full list of reviewed papers). The number of papers published on this topic peaked in 2018 ($n$ = 11), highlighting increasing interest and underscoring the need to summarize available evidence on fire seasonality effects. Included in this literature are eight review papers that address fire seasonality effects on plants in some capacity. While the most comprehensive of these, a review of prescribed fire seasonality effects in the continental USA, alludes to the role of plant phenology in plant responses to season of fire, much of the evidence cited is confounded by strong interactions between fire seasonality and fire intensity and severity [6]. Other reviews had a regional focus (e.g., the Sydney region of southeastern Australia [18,19], the Cape Floristic Region of South Africa [20–22], southwestern Western Australia [23]), while others focused more on other fire regime effects (especially fire frequency [24]), and generally cover only a particular species group (e.g., banksias [25], oaks [26]). By contrast, we present a global review focused on the demographic mechanisms of fire seasonality effects independent of covarying fire intensity and severity applicable across a range of climate, vegetation, and **plant functional types**.

We considered that 74 of these 143 papers (52%) did not report explicit demographic effects or were unable to isolate fire seasonality from other fire regime components due to declared or obvious interactions with fire intensity, fire severity, or other environmental factors. Such confounded findings mean that observed responses cannot be attributed to fire seasonality alone, a point often acknowledged by authors – the most frequent case being where studies reported changes in density or vegetation cover in relation to fires in different seasons but where fire intensity covaried with season.

Besides the eight review papers, the remaining 61 papers (43%) provide direct evidence for demographic effects (or noneffects) of altered fire seasonality or quantified phenological cycles with strong implications for fire response, providing nonconfounded evidence of the mechanisms proposed. The authors of these studies controlled for fire intensity and severity by, for example, experimentally clipping individual adult plants at different times of the year aligned with seasonal growth patterns, emulating the effect of varying timing of fire. We focus on these 61 papers in our explanation of the identified mechanisms below.

Of the identified mechanisms, adult survival and growth (mechanism 1) has been the most commonly studied in relation to fire seasonality, largely driven by research from the southeastern USA (Figure 2A). Reporting of fire seasonality effects is strongly geographically biased, with 59 (41%) of the 143 papers returned in the literature search (confounded or otherwise) originating from the USA, followed by Australia with 41 papers (29%; Figure 2A). Tests for the presence or absence of demographic effects of altered fire seasonality come from six different climate types and six different vegetation types, highlighting their global relevance (Figure 2B). Nonetheless, there are key evidence gaps in various climate and vegetation types as well as for different mechanisms (Figure 2B). These gaps may simply be explained by a lack of research or may indicate that a certain mechanism is unimportant for the persistence of populations in these climate or vegetation types, possibly because particular plant functional types (with their specific vulnerabilities) are poorly represented there.

## An Explanation of the Mechanisms

Below we provide an explanation of the identified mechanisms, how they interact with plant and seed traits to affect the persistence of plant populations, and the evidence for these in the reviewed literature.

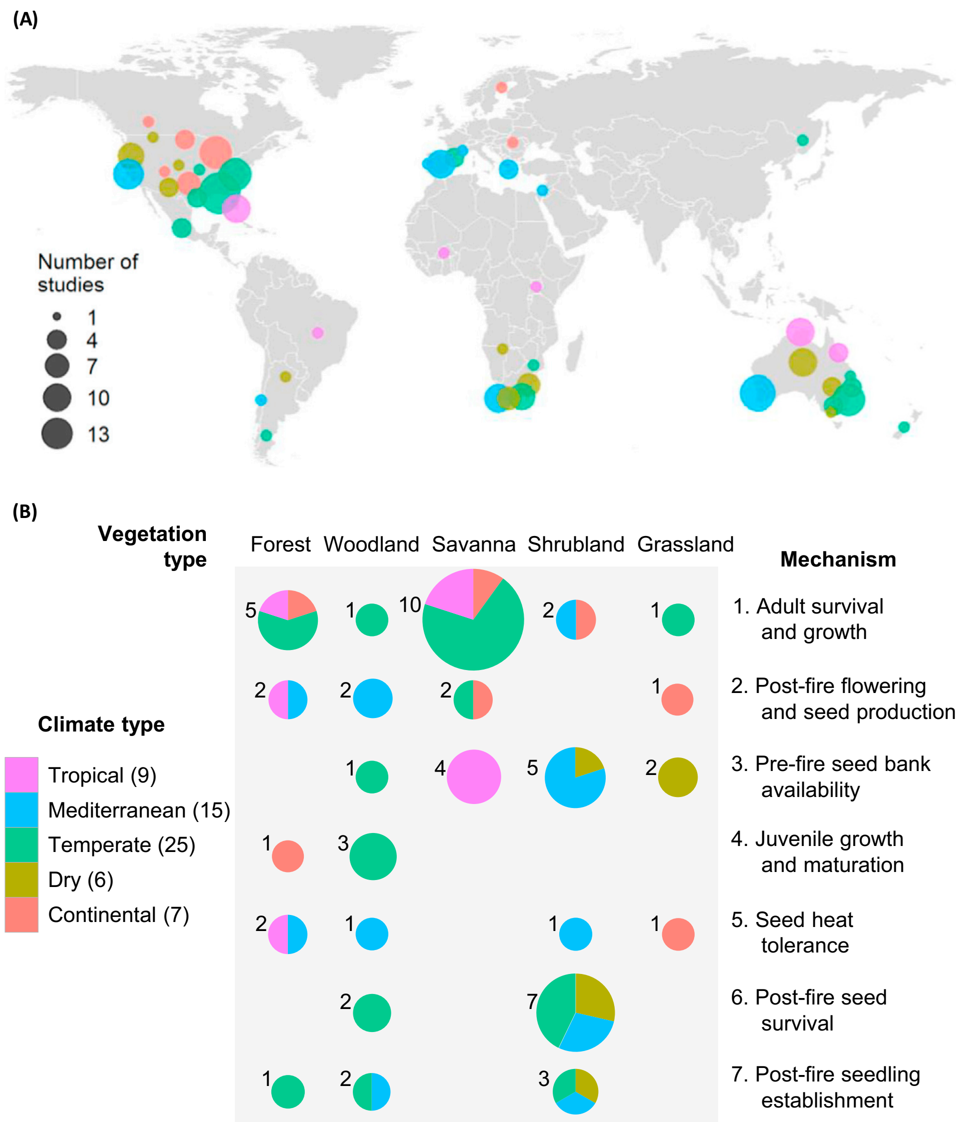


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**Figure 2. Results of Fire Seasonality Literature Review.**
(A) Global distribution of all reviewed studies (confounded or otherwise) on effects of altered fire seasonality on plant population persistence. Colors of circles correspond to the climate types described in (B). Confounded studies refer to papers that reported population responses to season of fire but were unable to isolate fire seasonality from other fire regime components due to declared or obvious interactions with fire intensity, fire severity, or other environmental factors. (B) The number of studies from different climate and vegetation types that provide direct evidence for each demographic mechanism. Sizes of circles depict the total number of studies reviewed for each mechanism in different vegetation types (number given). Colors indicate the number of studies reviewed in different climate types within each vegetation type, with the total number of studies reviewed from each climate type across all mechanisms given in parentheses in the figure legend 'Climate type'. Two papers cover two different mechanisms each and one paper from marshland vegetation relevant to mechanism 1 is not shown here for clarity. Regions lacking numbers indicate evidence gaps. Climate types are based on the Köppen climate classification: Tropical, savanna climate (Aw); Mediterranean (Csa and Csb), that is, temperate climates with strongly seasonal rainfall; Temperate, humid subtropical (Cfa) and oceanic (Cfb), that is, temperate climates with weakly seasonal rainfall; Dry, arid (BW) and semiarid (BS); Continental, hot (Dfa) or warm (Dfb) summer humid continental. See Table S1 in the supplemental information online for a full list of reviewed papers.

## Mechanism 1: Adult Survival and Growth

Plants with the ability to survive fire and regrow afterwards (i.e., resprouters) require adequate protection and energy reserves to do so [27]. If resprouters experience fire at times of the year when their energy reserves (e.g., nonstructural carbohydrates) are low, they may be less likely to survive or resprout with vigor [10,28,29]. In many species, especially **geophytes** and resprouters with deciduous leaves, energy reserves are at their lowest after the initiation of seasonal growth and/or reproduction and before the assimilation of carbohydrates from growing season photosynthesis [28,30–32]. Resprouters can also be affected by the timing of fire in the growing season, such that plants burned later in the growing season will have little time to grow and regain energy reserves before the dormant season and therefore are at risk of reduced growth or increased mortality in the following years [28,33,34]. By contrast, plants burned early in the growing season generally have a longer period to resprout, grow, and reassimilate energy into storage organs before the next dormant season [34].

The 20 studies reviewed for this mechanism come from four different climate types and five different vegetation types (Figure 2B). Two of these studies quantified seasonal fluctuations in carbohydrate reserves in a lignotuberous shrub from a Mediterranean-climate shrubland [30] and in a rhizomatous sedge from a temperate grassland [31], indicating potential population responses to fire seasonality. The remaining 18 studies reported the direct fire response of resprouter populations to altered fire seasonality. Fourteen of these, from three different climate regions and five different vegetation types, reported reduced survival and regrowth of resprouting shrubs, trees, orchids, and a vine after growing season fires compared with dormant season fires [9,10,12,29,35–41] or for resprouting shrubs after fires later in the growing season compared with fires early in the growing season [28,33,34], irrespective of fire intensity and severity. Resprouter survival and post-fire growth was reduced, on average, by 67% owing to altered fire seasonality (Figure 3). The remaining four studies reported inconclusive or nonsignificant results for resprouting shrubs and trees and a resprouting grass from savannas, forests, and marshlands with weakly seasonal rainfall temperate climates [32,42–44].

Differences in the sensitivity of plant tissues to the heat of fire at different times of the year may also reduce resprouter survival and regrowth. Resprouting species protect buds under insulating woody growth, bark, leaf sheaths, and/or soil, the protective properties of which may change with seasonal growth phenology, including bark shedding, leaf flush, and soil and tissue moisture content [27]. In such cases, fire at times when plant tissues are most sensitive may result in tissue death, reduced future growth potential (by killing buds), and exposure of surviving tissues to pathogen attack. Nonetheless, we found no evidence for this subsidiary hypothesis in the literature.

## Mechanism 2: Post-fire Flowering and Seed Production

Facultative and obligate fire-stimulated flowering species flower and produce seeds abundantly or solely, respectively, in response to fire [45]. Fire seasonality can affect these species when fires occur during or shortly before the season in which peak flowering usually occurs. Such fires may substantially delay, or fail to stimulate, prolific post-fire flowering and therefore reduce seed production and the availability of propagules for seedling recruitment [13,36,46–50]. For example, Bowen and Pate [46] found that inflorescence production in a common facultative post-fire flowering shrub in southwestern Australia was as much as halved following spring fires (i.e., prior to peak flowering) compared with flowering after summer and autumn fires (after peak flowering). For plants with fire-stimulated flowering, it has been hypothesized that fires that occur during, or shortly before, the peak flowering period reduce the time available for plants to recover and accumulate resources prior to flowering, leading to the production of fewer flowers and fewer seeds available for post-fire recruitment [47,48,51]. Reduced seed production lowers the probability of post-fire seedling recruitment and delayed seed production diminishes the competitive advantage of the post-fire flowering strategy, making populations much more dependent on the survival of resprouting individuals [45,49]. All seven studies reviewed for this mechanism reported evidence for clear negative effects of altered fire seasonality for post-fire flowering shrubs, grasses, and other herbaceous species (Figure 3) from all but dry climate types and all but shrubland vegetation (Figure 2B). In these cases, flowering was

| | | Plant phenology or state | | Demographic fire seasonality effect | |
|---|---|---|---|---|---|
| Mechanism | Vulnerable trait | Resistant | Sensitive | Reviewed papers that reported negative effect | Magnitude of negative effect (middle line is mean) |
| 1. Adult survival and growth | Resprouting | Dormant | Growing | 14 / 18 | Density, survival, or biomass |
| 2. Post-fire flowering and seed production | Fire-stimulated flowering | Longer time before flowering | Shortly before flowering | 7 / 7 | Flowering, no. of flowering plants |
| 3. Pre-fire seed bank availability | Transient or short-lived seed bank | Large viable seed bank | Small viable seed bank | 11 / 11 | Seed bank size from peak |
| 4. Juvenile growth and maturity | Seasonal germination | Immediate germination | Delayed germination | 2 / 2 | Plant size or maturity |
| 5. Seed heat tolerance | Permeable seed coat | 'Dry' seeds | 'Wet' seeds | 5 / 5 | Germination after heat exposure |
| 6. Post-fire seed survival | Seasonal germination | Immediate germination | Delayed germination | 4 / 9 | Seed survival or seedling recruitment |
| 7. Post-fire seedling establishment | Post-fire recruitment | Longer establishment period | Shortened establishment period | 3 / 5 | Seedling density or survival |

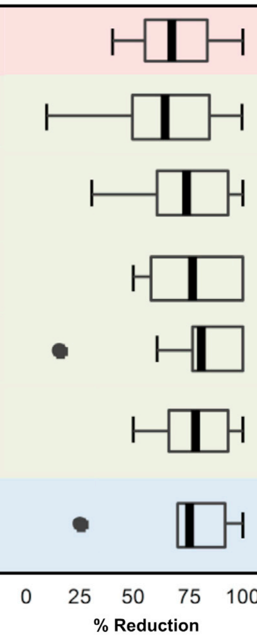


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**Figure 3. Summary of Vulnerabilities of Selected Plant Functional Traits to Altered Fire Seasonality for Each Proposed Mechanism.** Fire seasonality can interact with plant phenological and physical attributes that vary seasonally between resistant and sensitive states ('Plant phenology or state'), to produce demographic change. Studies considered to provide nonconfounded evidence suggest that populations that experience fire when individuals are in a sensitive state are overwhelmingly likely to suffer negative demographic effects. 'Reviewed papers that reported negative effect' presents the fraction of the total number of papers that reported a negative effect of altered fire seasonality; the remaining papers reported no demographic effect. No studies reported a positive demographic effect of altered fire seasonality. Only reviewed studies that reported or had strong evidence for (e.g., through changes in seed bank size) direct population responses to altered fire seasonality are included here; others that quantified phenology but not fire responses are not included. 'Magnitude of negative effect' is the distribution of reported percentage reduction (boxplot) in specified demographic measures ('Density, survival, or biomass' etc.) owing to altered fire seasonality from reviewed papers that reported a negative effect only. Row colors reflect impacts on adult survival (red), propagule availability (green), and post-fire seedling establishment (blue), as per Figure 1. See Table S1 in the supplemental information online for a full list of reviewed papers classified as 'Demographic'.

reduced, on average, by 62% when plants were burned during, or shortly before, their peak flowering season (Figure 3).

## Mechanism 3: Pre-fire Seed Bank Availability

Species with transient or short-lived seed banks experience fluctuations in seed bank size throughout the year as new seeds are produced and others germinate, lose viability, or die [52–56]. Transient seed banks depend on annual seed production to replenish seed banks, while short-lived seeds banks (i.e., seed persistence of 2–5 years) have a distribution of seed ages where the majority of seeds are likely to be those produced in the past year [57]. Fire seasonality can affect post-fire seedling recruitment for species with these seed bank types through interactions with seasonal seed bank dynamics [8,52,54,56,58–60]. The greatest period of risk for species with transient or short-lived seed banks from this mechanism is from fire immediately prior to seed ripening and dispersal [8,52–54,56,58,60–63]. For example, Figueroa *et al.* [53] found that mean soil seed bank density for grasses, forbs, and shrubs in a Mediterranean-climate shrubland of central Chile was 20 times lower in late winter (before seed ripening) than late spring (after seed ripening). Low soil seed bank density in late winter was attributed to germination, seed decay, and granivory prior to this period. Fire in winter in this ecosystem would coincide with the lowest number of propagules available for post-fire regeneration, in contrast to summer fires when propagule abundance is near its maximum. Species with long-lived seed banks are less impacted by this mechanism as the current year's seed crop represents a smaller portion of the total seed bank [64]. All 11 studies reviewed that quantified seasonal fluctuations in seed bank size reported, on average, a 74% reduction in seed bank size at certain times of the year for trees, shrubs, grasses, and forbs with transient or short-lived seed banks (Figure 3). The authors of these studies suggested potential negative consequences for post-fire seedling recruitment if populations were burned during periods of reduced seed bank size. These studies came from all but continental climate types and all but forest vegetation (Figure 2B).

## Mechanism 4: Juvenile Growth and Maturity

Fire seasonality can affect how rapidly seedlings emerge after fire in species with seasonal germination requirements [65]. A large delay in seedling emergence may result from a large mismatch between the timing of fire and the occurrence of suitable germination conditions. This delay can cause juveniles to grow and mature more slowly and potentially produce fewer propagules as a result of competition from earlier-establishing seedlings and resprouters [66–68]. For an obligate seeding shrub with seasonal germination cues from temperate southeastern Australia, Ooi [68] found that 90% of seedlings that emerged rapidly after summer fires had flowered by 3 years of age, whereas no seedlings that had delayed emergence after winter fires flowered by the same age. Seedlings that grow and mature more slowly may miss any benefit from the increased availability of resources and reduced competition soon after fire, leading to reduced future reproductive potential [66]. Studies reviewed for this mechanism that quantified the fire response of populations reported negative effects of altered fire seasonality on shrubs and herbs with seasonal germination requirements (Figure 3). These came from woodlands and forests of temperate and continental climates (Figure 2B). They reported that plants grew and matured, on average, 77% more slowly when germination was delayed due to altered fire seasonality (Figure 3).

## Mechanism 5: Seed Heat Tolerance

Many plants that inhabit fire-prone ecosystems produce seeds that are tolerant of relatively high temperatures [69–71]. Timing of fire can directly affect seed heat tolerance for species with permeable seed coats (i.e., all species except those with **physical dormancy**) if fire occurs when seeds are hydrated [69,70,72–74]. These seeds gain or lose moisture according to the water potential gradient between their internal tissues and the surrounding soil [75–77]. As seed tissues imbibe and seed moisture content increases in these species, seeds become increasingly sensitive to the elevated temperatures associated with fire. The increased risk of mortality from fires that occur when seeds are hydrated results in fewer propagules available for post-fire seedling recruitment [69,70,72–74]. For example, Tangney *et al*. [70] demonstrated that lethal temperatures of 'wet' seeds (preconditioned at 95% relative humidity) were, on average, 34°C lower than 'dry' seeds (preconditioned at 15% relative humidity). This mechanism is unique in the sense that it is not related to plant phenology but rather to environmentally driven variation in seed physical state. While seed hydration conditions may be highly variable within a short period of time (days or weeks), we argue that they are strongly associated with rainfall patterns and therefore are seasonally predictable in highly seasonal rainfall environments. Seeds are more likely to be hydrated during the wet season than during the dry season and therefore fires during the wet season may result in higher seed mortality. All five studies reviewed for this mechanism provide evidence for negative effects of altered fire seasonality, on trees, shrubs, grasses, and herbaceous species with seeds with permeable seed coats (Figure 3). These studies came from forests, woodlands, shrublands, and grasslands across three different climate types (Figure 2B). In these studies, germination was reduced, on average, by 81% when seeds were exposed to elevated temperatures while hydrated compared with seeds that were not hydrated (Figure 3).

## Mechanism 6: Post-fire Seed Survival

Seeds that survive the heat of fire must also survive until the next germination season. During this time, seeds released from serotinous fruits after fire may suffer losses from predation [78,79] and exposure to high temperatures on the soil surface, which may kill or shorten the lifespan of seeds [79,80]. In ecosystems that are seasonally dry, seeds can be exposed to such conditions for extended periods of time if released following fire at the end of the wet season or shortly after, but do not germinate until the next wet season, leading to increased seed mortality and reduced post-fire recruitment [78–81]. For example, Bond [78] studied the survival of *Protea* spp. (Proteaceae) seeds buried in soil for 15 weeks over the dry season (simulating conditions following a fire in spring; i.e., the end of the wet season) in South Africa's southern Cape region and found that nine times fewer seeds survived when exposed to seed predators compared with those inside rodent and bird exclosures. By contrast, in ecosystems with less-seasonal rainfall patterns, seeds are unlikely to be exposed to decay and predation for extended periods of time due to the greater frequency of suitable germination conditions. Evidence from these less-seasonal rainfall environments shows that season of fire shows little correlation with post-fire seedling recruitment success [82–86]. Four of the nine studies reviewed for this mechanism provide evidence of negative fire seasonality effects on resprouting and obligate seeding shrubs with seasonal germination (Figure 3), from seasonally dry Mediterranean and dry climate shrublands (Figure 2B). In these studies, post-fire seed survival was reduced, on average, by 79% when seeds were exposed to decay and predation for extended periods of time owing to season of fire (Figure 3). The other five studies reviewed showed little effect of fire seasonality in weakly seasonal rainfall woodlands and shrublands (Figure 2B), with variation in recruitment success attributed to unpredictable differences in post-fire soil moisture conditions.

Evidence for a heightened risk of seed loss with prolonged post-fire seed exposure is available only for serotinous species; however, species with soil-stored seed banks that have germination cued by fire may also be influenced by this mechanism. Seeds of soil-stored species are exposed to predators and high temperatures throughout their life in the soil (irrespective of fire), but a fire that occurs well before the germination season may increase this exposure. The removal of vegetation and leaf litter by fire would reduce their insulating effect and the resulting higher diurnal temperatures could increase seed mortality. Previously impermeable seeds that have had their physical dormancy broken by fire may be at increased risk of predation due to the release of volatiles that are perceived by seed predators on resumption of seed metabolism [87]. However, we found no test of these subsidiary hypotheses in the literature.

## Mechanism 7: Post-fire Seedling Establishment

In ecosystems with predictable seasonal drought, fire seasonality can affect the success of post-fire seedling establishment by altering the period of seedling establishment prior to the onset of the dry season [88–90]. Where seasons of drought and rainfall are predictable, seedling emergence early in the wet season (i.e., the normal pattern of germination and emergence following a dry-season fire) allows a longer period of growth prior to the onset of the next dry season compared with seedlings that emerge late in the wet season (e.g., after a wet-season fire). Seedlings emerging later in the wet season are known to suffer greater rates of mortality once seasonal drought begins [89,90]. Potts *et al.* [89] demonstrated that seedlings emerging after spring (late wet season) burns in northern California chaparral suffered mortality over the first summer at a rate 30–50% higher than in seedlings emerging after autumn (late dry season) burns. While ecosystems with weakly seasonal rainfall patterns may not experience regular drought, similar hydrological stress could be experienced during hot summer periods because of greater evaporation rates [91,92]. Three studies reviewed for this mechanism provide evidence of negative fire seasonality effects for shrubs, grasses, and herbaceous species (Figure 3) from forests, woodlands, and shrublands across three different climate types, including weakly seasonal rainfall climates (Figure 2B). In these cases, post-fire seedling survival or density was reduced, on average, by 75% (Figure 3). Two other studies reviewed showed little effect of altered fire seasonality on seedling survival in temperate and dry climates, with seasonally unpredictable rainfall.

## Concluding Remarks and Future Perspectives

Fire seasons are changing across the globe as climate continues to warm and ignitions associated with human activities continue to increase. While the drivers of plant population response to some components of the fire regime (e.g., frequency) are well understood and well researched, there remains a limited understanding of the consequences of altered fire seasonality for plant populations and communities. We employ a demographic framework to identify and describe seven mechanisms of fire seasonality effects independent of other fire regime components and post-fire environmental factors. These mechanisms are based on the timing of fire relative to seasonal plant phenological and seed physical attribute states and their impacts on key plant demographic rates. Collectively, these mechanisms indicate distinct trait-based responses and broad demographic effects of fire seasonality.

Plant communities that inhabit strongly seasonal rainfall environments (e.g., Mediterranean-climate or seasonal tropical savanna regions) may be highly sensitive to fire seasonality, given the close ties between plant phenology and environmental conditions. It is likely that these communities have an optimal season of fire for species persistence. Thus, considering fire seasonality in the management of these plant communities may help to avoid consequent shifts in composition and dominance hierarchies. In weakly seasonal rainfall environments (i.e., where rainfall is relatively evenly spread throughout the year), variation in season of fire may have less effect on plant communities, providing land managers with greater freedom to vary fire seasonality for other benefits with less risk of damaging biodiversity values. However, particular species inhabiting less-seasonal rainfall environments may exhibit sensitivity to altered fire seasonality depending on their traits.

Across the 57 reviewed studies that reported or had strong evidence for (e.g., through changes in seed bank size) nonconfounded demographic effects of fire seasonality, the vast majority (81%) identified negative impacts of altered fire seasonality (Figure 3). Despite this consistency of responses, there remain evidence gaps for each mechanism across most climate and vegetation types (Figure 2B). By distinguishing confounded and nonconfounded fire seasonality effects, and detailing and assessing mechanisms, this review fills a gap in ecological understanding that is critical for conservation, land management, and fire management policy development in fire-affected ecosystems.

A combination of empirical (i.e., field-based) and experimental (field and laboratory) research is needed to further develop and test our knowledge of fire seasonality effects across a range of ecosystems and plant functional types (see Outstanding Questions). Such understanding will inform land managers on how to mitigate species decline or loss and maintain key ecological processes as fire regimes continue to change in response to ongoing global environmental change.

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## Supplemental Information

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### Outstanding Questions

How common and significant are the impacts of altered fire seasonality? We found evidence for demographic fire seasonality effects from scores of species in over 50 studies globally. Each mechanism is likely to be relevant only for species with a subset of traits. The contributions of these species to communities, the number of such species that are impacted, the extent of the impact, and the consequences for ecosystem change and biodiversity conservation need further study.

What are the possible interactions between fire seasonality and fire intensity/severity at coarse scales? Fires outside of the historically high fire danger season may be of lower intensity and therefore more patchy, leaving unburned areas. How this patchiness affects species or population persistence merits further attention.

How plastic are key phenological traits that are sensitive to altered fire seasonality? Traits such as flowering time, seed production, and seed dormancy could change over time in response to changing climate. It is likely that substantial variation across traits and taxa exist with regard to plasticity and further work documenting this will point the way towards identifying the most vulnerable traits, taxa, and ecosystems globally.

What is the balance between planned versus unplanned fire in shifting fire seasonality? If planned fire (i.e., prescribed burning) were a large contributor to altered fire seasonality, there would be a direct opportunity to limit negative impacts. In some regions, the area burned by prescribed fires is relatively small. However, further work comparing areas burned by fire type may be merited in many other regions.

Will a future of altered fire seasonality 'squeeze' plants out of existence? Conceptual models, such as the 'fire interval squeeze' model, examine consequences for altered

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fire frequency with evidence and frameworks suggesting serious extirpation risk. Seasonality is another dimension of the fire regime and the mechanisms presented here deserve consideration in a similar framework.

Can we define periods of sensitivity for each mechanism? Further research and evidence to quantify the magnitude and temporal window of sensitivity to fires outside the historically high fire danger season would be an important contribution. This is particularly important given that a sizeable portion of fires in some regions are intentionally carried out by land managers.

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