Keith, D. A., Dunker, B. Driscoll, D.A. (2020). Dispersal: The Eighth Fire Seasonality Effect on Plants. *Trends in Ecology & Evolution* Vol. 35, Issue 4: 305-307.

DOI: https://doi.org/10.1016/j.tree.2019.12.001

Dispersal: the eighth fire seasonality effect on plants

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Keywords: population viability, fire regime, plant demography, wind dispersal, dust devils

Miller et al. [1] provide a much-needed review of the mechanisms of plant population response to variations in fire season. They identify seven population processes in plant life cycles for which there is evidence of sensitivity to fire season. These include effects of fire season on adult survival and growth, post-fire seedling establishment and five mechanisms related to propagule availability (post-fire flowering and seed production, pre-fire seed bank availability, juvenile growth and maturity, seed heat tolerance and post-fire seed survival). We suggest an eighth mechanism of fire seasonality effects involving propagule dispersal.

Post-fire dispersal is particularly important for species with seeds released after fire from serotinous seed banks and dispersed by wind and gravity. Unlike six of the other seven mechanisms of fire seasonality effects, the wind dispersal mechanism is driven by physical environmental processes, rather than seasonally varying seed attributes and plant phenology. The exception involves seasonal variation in soil moisture that drives seed hydration and reduced heat tolerance [1]. Fire seasonality could influence plant propagule dispersal by animals through changes in seasonal behaviour or movement (e.g. greater removal of seeds to safe sites by ants in warm temperatures after fire [2]), but we found no studies on post-fire zoochory that address seasonality directly.

For wind-dispersed propagules, dispersal distances depend on frictional resistance, measured by terminal falling velocity (a seed trait), release height (a plant trait) and air turbulence (an environmental characteristic) [3]. Dispersal distance is more sensitive to vertical updraft components than horizontal components of air turbulence [3]. Updraft, and consequently dispersal distance, is influenced by several seasonal factors including fire (Box 1).

Dunker et al. [6] showed that after summer fires, ambient updraft was marginally greater, and dispersal distances for *Callitris verrucosa* (mallee pine) seeds were significantly longer than updraft and seed dispersal distances after autumn and spring fires. *Calltiris verrucosa* has winged seeds (2 - 6 mm wide, 2 - 30 mg) that are released *en masse* after fire from serotinous seed banks that retain seeds within heat-insulated woody fruits in the plant canopy. Serotiny is linked to fire seasonality effects because it ensures immediate release of propagules into the post-fire environment when albedo is lowest and surface heating and updraft are greatest. Fire seasonality effects on dispersal may also occur in species that flower and release their seeds within a year after fire (Box 1), or occur within fire mosaics where non-serotinous propagules are dispersed by updraft generated in adjacent burnt patches.

As well as ambient updraft, heating may initiate non-linear near-surface meteorological processes that result in local vortices known as willy willies or dust devils [7]. Vortices are associated with very strong heating of flat, low-albedo surfaces, large temperature lapse rates within 2 m of the surface and horizontal wind shear caused by surface irregularities. These conditions generate very strong rotational updrafts that may extend hundreds of metres into the atmosphere [3, 7]. Vortices are very common in arid and semi-arid climates worldwide [8], but also occur in more humid regions after fire [4, pers. obs.]. In arid zones, tracking surveys suggest that most of the land surface of bare areas could be exposed to the vortex updraft over periods of a few days [3].

Local vortices were implicated in dispersal of *Banksia* seeds from serotinous fruits after fire in a Mediterranean-type climate [9]. Genetic analyses of a post-fire population of *Banksia hookeriana* (Hooker's Banksia) suggest that 7% of seedlings established more than 1.5 km distant from putative parent plants, far beyond dispersal distances in the order of 10s of metres measured in seed release and track experiments on a similar species [10]. Enhancement of post-fire wind dispersal by vortices could explain this discrepancy and may be a mechanism for continental-scale dispersal events identified in historical biogeographic studies.

Depending on other demographic parameters such as mortality, we hypothesise that warm or dry season fires will result in lower extinction risks because they promote stronger post-fire updraft than fires in other seasons, leading to greater seed dispersal, rescue effects (whereby small populations avoid extinction through immigration), recolonization [11] and gene flow, enhancing genetic diversity, fitness and resilience to environmental change [12]. Contemporary shifts in fire season due to climate forcing and human ignitions therefore have similar implication for plant extinction risks due to dispersal limitation as other mechanisms of fire seasonality effects [1].

Dispersal is poorly understood, yet critical to species persistence in a changing climate. We are unaware of any empirical or modelling studies of post-fire plant propagule dispersal by local vortices. Several important questions await research answers: how sensitive is dispersal distance to fire season and severity; how often do post-fire vortices occur in different climate and landscape settings and how does this influence dispersal kernels; how do propagule traits influence dispersal distances; and how do vortex characteristics (and dispersal outcomes) change with time since fire? These questions provide fertile ground for future cross-disciplinary research in ecology, genetics and physics.

Acknowledgements

DAK is supported by Australian Research Council Linkage Grant LP180100741, the NSW Bushfire Research Hub and the National Environmental Science Program Threatened Species Hub.

Box 1. Factors influencing updraft

Updraft is more frequent and stronger when heating of the land surface generates large temperature lapse rates (i.e. change with altitude) and convectional air movement [4]. Greater insolation in summer generates more surface heating and updraft than in other seasons. Surface heating should also be greater in post-fire conditions due to reduced albedo effects associated with black coloration of charcoal and ash. Quintana et al. [5] found that moderate and high severity forest fires that consumed all foliage and deposited a black surface charcoal layer reduced land surface albedo by 21% (wavelengths 0.4 - 14.4 μm as detected by MODIS satellite). The effect was even larger (30% decrease) for near-infrared wavelengths, which have the greatest effect on surface heating. Within a year, albedo had increased above pre-fire levels due to absorption of energy by photosynthesis in the young regrowth, diverting energy that would otherwise heat the land surface. The albedo effect of low-severity fires was weaker, but still significant. In addition to enhanced updraft, fire may be expected to promote plant propagule dispersal by reducing vegetation obstacles to horizontal and vertical movement of propagules through the air column, and this effect should increase with fire severity.

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