

## Opinion

## Epicormic Resprouting in Fire-Prone Ecosystems

Juli G. Pausas<sup>1,3,\*,@</sup> and Jon E. Keeley<sup>2</sup>

Many plants resprout from basal buds after disturbance, and this is common in shrublands subjected to high-intensity fires. However, resprouting after fire from epicormic (stem) buds is globally far less common. Unlike basal resprouting, post-fire epicormic resprouting is a key plant adaptation for retention of the arborescent skeleton after fire, allowing rapid recovery of the forest or woodland and leading to greater ecosystem resilience under recurrent high-intensity fires. Here we review the biogeography of epicormic resprouting, the mechanisms of protection, the fire regimes where it occurs, and the evolutionary drivers that shaped this trait. We propose that epicormic resprouting is adaptive in ecosystems with high fire frequency and relatively high productivity, at moderate–high fire intensities.

## Post-Fire Epicormic Resprouting

Many plant species from a wide range of ecosystems are able to recover their green biomass after disturbance by resprouting new shoots [1]. It is often assumed that the higher the intensity of the disturbance, the lower the height at which buds resprout new shoots [2–4]. The consequence is that after a severe disturbance, such as an intense fire, most resprouting species resprout from buds buried beneath the bark of structures at the base of the plant or belowground. Thus, many plants living in fire-prone ecosystems have evolved structures to concentrate buds belowground (e.g., lignotubers, xylopodia, woody rhizomes [5–8]). This has significant implications for growth form as most of these are multistemmed shrubs.

However, a number of arborescent species stand out from this pattern and resprout from the trunk or branches in the crown canopy even after a high-intensity fire, a phenomenon termed post-fire epicormic resprouting. Many plants can generate epicormic shoots after light disturbances, but here we refer to those species that resprout epicormically after fire, and especially after **crown fires** (see [Glossary](#)). Particularly striking is the fact that forests subjected to similar fire intensities often exhibit striking differences with respect to epicormic resprouting. For example, the vigorous epicormic resprouting in the native eucalypt forests in Australia contrast with the total lack of resprouting in the dead *Pinus radiata* plantation right next to the forest despite them experiencing similar fire intensity (personal observations). Similarly, eucalypt plantations in southern Europe show vigorous epicormic resprouting after crown fires compared with the native broad-leaved trees (basal resprouting) and pines (fire killed) [9,10]. Because epicormic resprouters maintain their structure after fire, the ability to resprout epicormically has strong implications for the speed of vegetation recovery and carbon balance and in general on ecosystem functioning. Despite the importance of this unique fire adaptation, it has not been globally well documented and is poorly represented in plant trait databases [11]. In this Opinion article we address the question of why some tree lineages have evolved epicormic resprouting and others have not. To do so, we examine the distribution of epicormic resprouting among plants, the **fire regimes** where they live, and the evolutionary drivers that shaped epicormic resprouting.

## Trends

Whether a tree resprouts from the base or from stem (epicormic) buds has strong implications for forest structure and carbon balance in post-fire conditions.

Epicormic resprouting is a key plant trait that allows quick regeneration of the tree and of ecosystem functioning.

Epicormic resprouting is especially adaptive in ecosystems with high fire frequency and relatively high productivity, at moderate–high fire intensities.

Epicormic resprouters are the trees most resilient to high-intensity crown fires.

<sup>1</sup>CIDE-CSIC, Carretera CV-315, Km 10.7, Montcada, Valencia, Spain

<sup>2</sup>US Geological Survey, Western Ecological Research Center, Sequoia-Kings Canyon Field Station, Three Rivers, CA 93271, USA

<sup>3</sup><http://www.uv.es/jgpausas/>

@Twitter: @jgpausas

\*Correspondence: [juli.g.pausas@uv.es](mailto:juli.g.pausas@uv.es) (J.G. Pausas).

## Biogeography

Perhaps one of the most thoroughly studied cases of epicormic resprouting is in the Australian genus *Eucalyptus* and the closely related genera *Corymbia* and *Angophora* [12,13]. Following **high-intensity crown fires** in these *Eucalyptus* forests, the vast majority of trees, regardless of size, resprout epicormically (Figure 1). Within less than 1 year these forests are well on their way to recovering their full canopy. However, resprouting is of variable importance in



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**Figure 1. Examples of Post-Fire Epicormic Resprouting after a Crown Fire.** (A) *Eucalyptus diversicolor* 18 months after fire in Western Australia. (B) *Quercus suber* woodland 1.5 years post-fire in southern Portugal. (C) *Pinus canariensis* woodland a few years after fire; (D) epicormic resprouts of *P. canariensis* 3 months post-fire. Photographs by G. Wardell-Johnson (A), F.X. Catry (B), and J.G. Pausas (C,D).

## Glossary

**Crown fires:** fires in woody-dominated vegetation that affect most of the crown of the dominant plants; fire might spread through the crowns (active crown fire) or through surface fuels but torching individual tree crowns (passive crown fires).

The frequency is often lower than in surface fire regimes and thus available fuels are often greater, contributing to more intense fires.

We distinguish two types; see below.

**Fire regime:** wildfire characteristics that prevail in a given area; it may vary through time. It is typically defined by frequency, intensity, seasonality, and types of fuels consumed. Spatial variability leading to differing levels of patchiness may also characterize the fire regime. Two common and contrasted fire regimes are surface fire regimes and crown fire regimes; mixed fire regimes also occur.

**High-intensity crown fires:** crown fires that burn a major fraction of the twigs and branches (woody-fueled fires); typical of Mediterranean and boreal ecosystems. Their frequency is typically lower than that of low-intensity crown fires.

**Low-intensity crown fires:** crown fires that burn (or only scorch) the foliage of the crowns but most woody parts (twigs and branches) are not consumed. They are often passive crown fires and are typical of some tropical and subtropical forests and woodlands. Because they do not consume woody fuels, they can be more frequent than high-intensity crown fires. A regime of frequent low-intensity crown fires is likely to select for epicormic resprouting.

**Mixed surface-crown fires:** surface fires in forests or woodlands with frequent torching to the crowns generating a mosaic of surface and crown fires. The proportions of surface versus crown fires vary markedly in both time and space. In many coniferous forests, they are typically called mixed-severity fires, but for the sake of generality the term should be independent of the effects of fire on the tree (severity).

**Surface fires:** fires that affect surface fuels only; they spread through fine fuels in the herbaceous and litter layer (grass-fueled fires, litter-fueled fires). They are typical of grasslands, savannas, and woodlands. In forest ecosystems

*Eucalyptus* and some have limited capacity for resprouting and are considered post-fire obligate seeders [14,15]. There are other trees with post-fire epicormic resprouting in Australia as well as in South Africa (Table 1), including examples that exhibit within-species (among-population) variability in epicormic and basal resprouting [16,17].

In the northern hemisphere, the genus *Quercus* also exhibits widespread occurrence of epicormic resprouting after fire (Table 1 and Figure 1). This is true only in the arborescent species; all shrubby oaks resprout from the base. Thick-barked arborescent oaks that resprout epicormically resprout from the base when in a juvenile state (i.e., the bark is still too thin to allow stem survival) or when debarked, as is the case in cork oak (*Quercus suber*, debarked due to otherwise non-lethal commercial cork extraction [18,19]).

Conifers are distinct in that resprouting is relatively rare compared with woody angiosperms. A few species do resprout [20–23]; however, they generally do not resprout epicormically after an intense fire, with a few exceptions. For instance, *Pseudotsuga macrocarpa* in the Californian chaparral resprouts vigorously after fire from upper branches but only when growing on steep slopes where fire intensities are lower; otherwise it dies [24]. Another exception is in the genus *Pinus*, where the majority of more than 125 species have evolved in close association with fire [20,25–27]. Of the few resprouting pines, some are able to produce a few epicormic short branches especially at the lower part of the bole or when young (e.g., *Pinus rigida*, *Pinus serotina*, *Pinus patula*, *Pinus montezumae*; [28,29]), although they are often completely killed by crown fires. In some cases, however, they can generate epicormic resprouts after fires that defoliate the tree (e.g., *P. rigida*). *Pinus canariensis* stands out as a strong post-fire epicormic resprouter after high-intensity crown fires (Figure 1 and Table 1), with a magnitude of resprouting equivalent to that of the eucalypts and cork oak. Resprouting of this species is successful in all trees of any size, from saplings (with basal resprouting) to mature trees (with strong epicormic resprouting). Indeed, *Pinus canariensis* was used in the past in some reforestation projects in Spain intermixed with *Pinus halepensis*; when it burns in the typical high-intensity crown fires of *P. halepensis*, *P. canariensis* shows quick full crown recovery by epicormic resprouting (and *P. halepensis* dies and recruits post-fire from seeds [30]).

surface fires are often called understory fires and there is a vertical discontinuity of the fuels in such a way that tree crowns are not affected by the fire. Surface fires are often frequent but of low intensity, but can be of high severity for trees with thin bark (e.g., rainforests).

Table 1. Selected Species with Field Evidence of Epicormic Resprouting after High-Intensity Fires, with a Rough Indication of the Outer Bark Thickness in Adult Plants<sup>a</sup>

Species	Region	Outer bark <sup>b</sup>	Refs
<i>Allocasuarina decussata</i>	Australia	Thick	[47]
<i>Banksia attenuata</i>	Australia	Thin	[17]
<i>Banksia menziesii</i>	Australia	Thick	[16]
<i>Corymbia calophylla</i>	Australia	Thick	[47]
<i>Eucalyptus diversicolor</i>	Australia	Thin	[47,48]
<i>Eucalyptus guilfoylei</i>	Australia	Thick	[47]
<i>Eucalyptus marginata</i>	Australia	Thin	[47]
<i>Pinus canariensis</i>	Canary Is.	Thick	[49]
<i>Protea nitida</i>	South Africa	Thick	[22]
<i>Quercus agrifolia</i>	California	Very thick	[50]
<i>Quercus kelloggii</i>	California	Thick	[51]
<i>Quercus suber</i>	Med. Basin	Very thick	[18,19]

<sup>a</sup>This is not an exhaustive list but includes some illustrative examples documented in the literature.

<sup>b</sup>Thin, 1–2 cm; thick, 2–4 cm; very thick, >4 cm).



## Fire Regime

Many plants can generate epicormic shoots after light disturbances (e.g., browsing, drought, stand thinning, low-intensity fires, insect defoliation, strong winds [31]) but this does not mean they generally resprout epicormically after fire, as the heat of a fire may kill epicormic buds if they are not well protected (Box 1). Post-fire epicormic resprouting occurs in some ecosystems subject to frequent crown fires (forests) as well as those under frequent **surface fires** (savannas and open woodlands; Figure 2).

Post-fire epicormic resprouting is widespread in savannas [32–34], where grass-fuelled fires are frequent and of low intensity. For instance, of the 63 species studied in an African savanna [34], 18 species (in eight families) showed stem buds strongly covered by bark, 13 species (ten families) showed no protection, and 32 species (17 families) showed intermediate values of bud protection. In many of these savannas, epicormic resprouting is especially important for juveniles, where the plant canopy is lower than the flame height of surface fires. Depending on its bud protection, species resprout epicormically or from basal buds. In Brazilian savannas (*cerrado*) with low soil fertility and high rainfall, trees grow slowly, but grasses are tall and juveniles are unable to surpass flame height during the inter-fire interval; thus, a thick corky bark coupled with leaves that have weak flammability allows young trees to resist fires [33,35,36]. In this system the flame height in relation to the tree height is high, making thick bark at the top of the branches adaptive [37]. Recurrent fires consume only the terminal twigs and plants resprout epicormically lower on the stem, generating the typical appearance of tortuous *cerrado* trees [36].

In ecosystems under high-intensity crown fires, epicormic resprouting is globally rare. For instance, associated with Californian chaparral is *Pseudostuga macrocarpa*, a tall tree that resprouts vigorously after fire from upper branches. This species commonly grows in association with chaparral and is often burned by high-intensity crown fires. Following fire it is typically killed where it has colonized into dense chaparral and fuel loads are high but it survives in refugia on steep slopes where fire intensities are lower and epicormic resprouting allows populations to recover rapidly [24]. Another illustrative example is the case of *Q. suber* and *Quercus ilex*, which often coexist in forests with a crown-fire regime in the western Mediterranean Basin; in such

### Box 1. Mechanisms for Bud Protection

Epicormic resprouting arises from protected buds (or bud-forming cells) in the stem and branches [12,13,44]. These latent or dormant buds, typically of axillary origin, can be activated at any time in response to defoliation (e.g., drought, insects), but if they are properly protected they can be massively activated after defoliation by fire. There are at least two mechanisms by which species may protect these stem buds and bud-forming tissues from the high temperatures of the fire: one is to develop a thick, protective outer bark [37,38]; the other is to sink the buds deeply into the inner bark or even the outer wood [12,44]. In both cases buds are, to some extent, protected by the bark, but in the latter case the outer bark may be relatively thin, as in the case of some *Eucalyptus* (Table 1). Eucalypts have multiple strands of cells that can form buds at various depths when they receive the appropriate hormonal signal [13]. A thick, corky bark in the twigs and branches not only protects the buds but also reduces flammability [35] and thus reduces fire intensity and severity. Extremely thick outer bark can engulf buds and reduce resprouting [45], but in some species furrows in the bark and narrow tubes connecting the bud to the outside of the stem seem to prevent obstruction [46].

In many tropical savannas, where fires are of low intensity (surface fires), there is a range of intermediate situations with high variability in the degree of protection; for example, northern Australia [32] and southern Africa [34], although in South American savannas having a thick, corky outer bark seems to be the dominant mechanism allowing bud survival and subsequent epicormic resprouting [33,36].

In some species, despite having bud-forming tissues and showing an ability to generate some epicormic shoots, post-fire epicormic resprouting is weak or nil, especially after high-intensity fires; this is the case for the obligate post-fire seeder *Eucalyptus regnans* [15]. That is, the presence of bud traces in the wood or epicormic shoots in the trunk does not ensure post-fire epicormic resprouting, even for trees from fire-prone ecosystems.

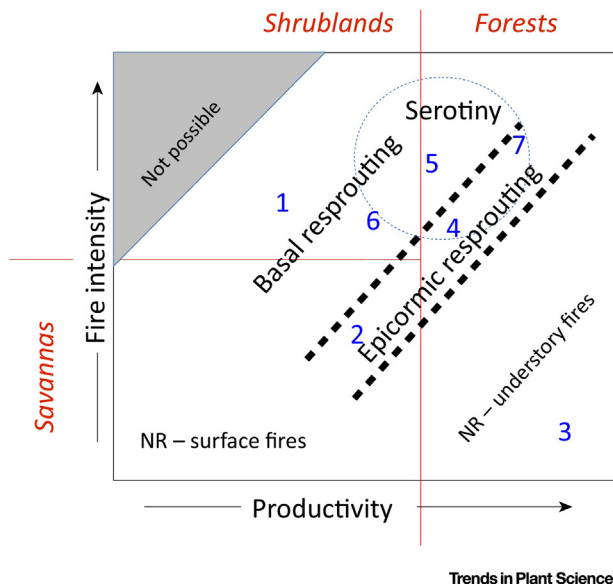


Figure 2. Schematic Representation of the Occurrence of Post-Fire Epicormic Resprouting, Basal Resprouting, and Serotiny in Relation to Fire Intensity and Site Productivity. In any ecosystem there are often a variety of strategies coexisting; here we highlight the main strategy for the dominant woody species. This refers to ecosystems with high natural ignitions (high fire frequency). In this space, serotiny (in the circle) and epicormic resprouting (between thick broken lines) often overlap, but they disaggregate in a third dimension (not shown): fire frequency. Serotiny is unlikely when fire intervals are shorter than the maturity age. Note that low-productivity environments cannot support high-intensity fires (grey area). Red lines are rough limits between forests, shrublands, and savannas, although in fact they can overlap along the productivity gradient. Woodlands (not indicated for simplicity) would be located under high-productivity savannas and low-productivity forests. 'NR' means conditions where resprouting is of little relevance (weak or absent) for the dominant growth form; for example, where flame height to plant height is low [37], like in forest with frequent understory fires protected by thick basal bark (right) or in some savannas and grasslands (left). Numbers are the approximate locations of some ecosystems: 1, chaparral-type shrublands; 2, Brazilian savannas; 3, *Pinus ponderosa*, *Pinus palustris*; 4, *Pinus rigida*, *Pinus serotina*; 5, *Pinus halepensis*; 6, mallee-type *Eucalyptus*; 7, tall *Eucalyptus*, *Pinus canariensis*.

high-intensity fires, *Q. suber* (with thicker bark) resprouts epicormically while *Q. ilex* resprouts from the base. However, they also coexist in open woodlands (savannas and *dehesas* [19]), and if they burn in a crown fire the fire intensity is lower than in the forests (low-intensity passive crown fires) and both show epicormic resprouting. Of the species that do resprout epicormically after high-intensity (woody fuelled) fire (Table 1), only a few (e.g., *Eucalyptus* spp., *P. canariensis*, *Quercus* spp.) are dominant in forest and woodlands of Mediterranean and warm temperate ecosystems, making these ecosystems strongly resilient to most fire regimes. In such ecosystems, crown fires are not stand-replacing as in the case of crown fires in the majority of Northern Hemisphere conifer forests.

### Evolutionary Drivers

Epicormic resprouting is adaptive in fire-prone ecosystems because the plant does not lose the bulk of woody biomass after fire, thus enabling the canopy crown to recover quickly. Retention of the tree skeleton after a crown fire has decided advantages (e.g., in terms of plant biomass and height as well as in seed production after fire) over species that resprout from the base or regenerate from seeds. So, one could ask why epicormic resprouting is not more frequent. Allocating some carbon to a thick bark would save a large amount of carbon lost in the dead stems.

We propose that epicormic resprouting is adaptive in certain conditions defined mainly by site productivity, fire frequency, and fire intensity (Figure 2). One of the prerequisites for this strategy is site productivity sufficient to sustain an arborescent growth form. In open savanna habitats where herbaceous fuels promote frequent low-intensity fires, epicormic resprouting has clear advantages by rapidly reestablishing the canopy crown on the original structure. In these low-intensity fires, small increases in bud protection are adaptive. This is especially evident in ecosystems where small plants persist within the flame zone of grass-fueled fires for long, as in the Brazilian savannas (cerrado); in such cases, fire acts in a manner similar to **low-intensity crown fires** [38] and selects for epicormic resprouting. A more difficult question, however, is why some forest species have evolved epicormic resprouting and others have not. On low-to-moderate-productivity sites, shrubland species have developed the ability to resprout basally after fire and regenerate in entirety their shrub canopy crown (Figure 2). On more productive sites, trees predominate and their response to fire is rather more variable. On highly productive sites some species can escape fire by maintaining the tree canopy high above surface fuels (e.g., *Pinus ponderosa* or *Pinus palustris* woodlands; Figure 2); the evolution of thick bark around the base of the tree, sometimes coupled with self-pruning of the lower branches, is sufficient to survive these frequent understory fires [20,27,38]. However, where productivity is more limited trees cannot outgrow surface fires; rather, they are connected by ladder fuels that extend into the canopy, and thus trees are subjected to crown fires. Some such species have adapted to periodic high-intensity crown fires by evolving serotinous cones that maintain an aerial seed bank that responds to fire by releasing seeds for abundant post-fire seedling recruitment [39]. However, serotiny would be favored only if the mean fire interval were longer than the time required for seedlings to reach maturity. That is, epicormic resprouting is adaptive under frequent fires that affect the crown: (i) if fires are so frequent (in relation to tree maturity) and homogeneous that serotiny fails (immaturity risk; see Box 3 in ref [23]); and (ii) in lineages that lack structures suitable for becoming serotinous (e.g., oaks). So, epicormic resprouting is likely to be selected for in forests or woodlands with moderate productivity and high fire frequency where the upper canopies are scorched from surface fires that feed on lower branches and adjacent mid-level fuels (passive crown fires). The foliage and small branches from abundant post-fire resprouting along the stem (e.g., in pines and eucalypts) could act as a ladder fuel to carry the fire to the crown, further enhancing crown fires. The fact that some post-fire epicormic resprouters also have some level of serotiny (some *Eucalyptus*, *P. canariensis*, and a few American pines like *Pinus leiophylla* [21]) emphasizes the existence of some similarities between the fire regimes selecting for these two traits (Figure 2) and suggests that fire regimes with fire intervals varying around a value similar to the maturity age could make both traits adaptive.

In *Eucalyptus* epicormic resprouting is an ancient trait dating back to about 60 Ma [40], when climatic conditions in Australia were less arid and, coupled with low-nutrient substrates, crown fires were possibly less intense than contemporary fires. Such low-intensity crown fires could give the appropriate selective environment for the evolution of bud-protection mechanisms in the stem (Box 1). Then, with increased aridification and seasonality during the Cenozoic [41], fire would have increased in intensity and thus further selected for stronger bud protection. This quantitative increase in bud protection is not depicted in phylogenetic analyses based on binary data (epicormic resprouter: yes/no [40]). It is also interesting to note that some eucalypt species, despite having some bud traces in the outermost wood (i.e., bud-forming potential), do not resprout epicormically after fire or do so only weakly (e.g., *Eucalyptus regnans* [15]); this is because the bud-forming cells are the only ones remaining alive and thus the vascular cambium in that area is dead. These species are in a phylogenetic clade of epicormic resprouters and thus seem to be a case of loss of resprouting capacity in favor of the post-fire seeding species [23].

## Concluding Remarks

Many plant lineages in environments subjected to predictable fires have evolved the capacity for resprouting after such disturbance [22,42]. Most emphasis has been placed on whether a species resprouts or not; however, whether a plant resprouts from basal or from upper epicormic buds has important implications for the speed of regeneration and ecosystem functioning in general. Yet epicormic resprouting is poorly recorded in the literature and is absent in most plant trait databases (see Outstanding Questions). Epicormic resprouting can be achieved through various mechanisms (Box 1) and has appeared in different lineages and on different continents; thus, it is an example of convergent evolution in fire-prone ecosystems. It is likely to be an adaptation to fire and especially to a regime of frequent fires that affect tree crowns. It has probably been favored where productivity is sufficient to maintain an arborescent growth form, fire intensity is sufficient to defoliate the tree canopy crown, and fire frequency is high (in conifers, too high for serotiny to be reliable). Given the high resilience of forest and woodlands dominated by epicormic resprouters, these species are good candidates for reforestation in fire-prone ecosystems [19]. Understanding post-fire epicormic resprouting may allow us to better predict ecosystem responses to fire regime changes under scenarios of global change and especially to better predict carbon budgets [43], as these differ drastically between basal and epicormic resprouters (see Outstanding Questions). Overall, more attention should be given to key traits related to disturbance responses, as they have implications for our understanding of the future of many of our ecosystems.

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## Outstanding Questions

Can we test the proposed model (Figure 2) with global data? This requires compiling information on epicormic resprouting at the global scale in a standardized form and making it available in global plant trait databases.

How did epicormic resprouting evolve in relation to other resprouting mechanisms? A phylogenetic approach would be desirable.

Can we quantify the advantage of epicormic resprouting, for instance using closely related species or populations with different resprouting types?

What is the fire intensity threshold for switching between epicormic and basal resprouting?

How do predictions of carbon balance and ecosystem function improve when epicormic resprouting is included in vegetation dynamics models?

To what extent are epicormic resprouters resilient to any fire regime change?

Can we relate among-population (intraspecific) variability in epicormic resprouting to fire regime variability?

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