

*Research review***Towards understanding resprouting at the global scale**

Juli G. Pausas¹, R. Brandon Pratt², Jon E. Keeley^{3,4}, Anna L. Jacobsen², Aaron R. Ramirez⁵, Alberto Vilagrosa⁶, Susana Paula⁷, Iolana N. Kanekua-Pia⁸, Stephen D. Davis⁸

1) CIDE-CSIC, Ctra.Naquera Km 4.5 (IVIA), 46113 Montcada, Valencia, Spain

2) California State University, 9001 Stockdale Highway, Bakersfield, CA 93311, USA

3) U.S. Geological Survey, Sequoia-Kings Canyon Field Station, Three Rivers, CA 93271, USA

4) Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, 90095, USA

5) University of California, Berkeley, CA 94720, USA

6) CEAM-Universitat d'Alacant, PO Box 99, 03080 Alacant, Spain

7) ICAE, Universidad Austral de Chile, Campus Isla Teja, Casilla 567, Valdivia, Chile

8) Pepperdine University, 24255 Pacific Coast Highway, Malibu, CA 90263, USA

Author for correspondence: Juli G. Pausas, Tel: +34 963 424124, Email: juli.g.pausas@uv.es

Word count: 4285 (from Introduction to Acknowledgements, included)

Number of figures: 5

Number of boxes: 2

Number of appendices: 5

Summary

Understanding and predicting plant response to disturbance is of paramount importance in our changing world. Resprouting ability is often considered a simple qualitative trait and used in many ecological studies. Our aim is to show some of the complexities of resprouting while highlighting cautions that need be taken in using resprouting ability to predict vegetation responses across disturbance types and biomes. There are marked differences in resprouting depending on the disturbance type, and fire is often the most severe disturbance because it includes both defoliation and lethal temperatures. In the mediterranean biome, there are differences in functional strategies to cope with water deficit between reproters (dehydration avoiders) and non-resprouters (dehydration tolerators); however, there is little research to unambiguously extrapolate these results to other biomes. Furthermore, predictions of vegetation responses to changes in disturbance regimes require consideration of not only resprouting but also other relevant traits (e.g., seeding, bark thickness) and the different correlations among traits observed in different biomes; models lacking these details would behave poorly at the global scale. Overall, the lessons learned from a given disturbance regime and biome (e.g., crown-fire mediterranean ecosystems) can guide research in other ecosystems but should not be extrapolated at the global scale.

Key words: cavitation, disturbance, drought regime, drought strategies, postfire strategies, resprouting, xylem.

Introduction

Resprouting refers to the ability of some plants to form new shoots after destruction of living tissues from disturbance. It is common in many plants worldwide and thought to be common in ancient floras (Pausas & Keeley 2014). Because resprouting enables the survival of individuals after disturbance, it is a key plant functional trait in many ecosystems and has been reviewed elsewhere (Bellingham & Sparrow 2000, Clarke et al. 2013, Pausas & Keeley 2014). Given the important shifts in disturbance regimes in our changing world, understanding resprouting and predicting post-disturbance responses is of paramount importance.

Resprouting is often considered a species-specific binary trait (Pausas et al. 2004), with some species able to resprout and others lacking this ability (but see Vesik & Westoby 2004). However, this is an overly simplistic view; resprouting is a mode of regeneration and therefore it is better considered in the context of other modes such as seeding (Box 1). Classification of species as resprouters vs non-resprouters coupled with seeding response, has been successfully used in specific contexts (i.e., mediterranean ecosystems with crown-fire regimes, Pausas et al. 2004, Ackerly 2004, Pausas & Keeley 2014), but it is uncertain that this would provide significant explanatory power at the global scale. This is because resprouting is a trait that increases fitness under many different disturbance types, occurs in a wide range of environments, is widespread in many lineages, and is morphologically very diverse (Keeley et al. 2012). Below we review important considerations in understanding resprouting at the global scale and using this trait for accurate predictions in a changing world. Specifically we address the following questions: (1) Since global change includes regime changes in many disturbances (e.g., drought, fire, herbivory and wind), to what extent does a single qualitative trait, like resprouting ability, is useful for predicting global change responses? (2) One of the main global change drivers is the increased frequency and intensity of droughts; the higher resources allocated to the root system by resprouters allows them not only to accumulate reserves for resprouting, but also to access more stable water sources. Thus, we ask to what extent does the differences between resprouters and non-resprouters affect their resistance to drought? And (3) Can we use resprouting to improve our prediction of vegetation response to global change in global vegetation models? By answering these questions, we highlight some pitfalls in understanding plant resprouting at the global scale.

Does disturbance-type matter?

Resprouting has been studied as a response to many disturbances, including wind, freezing, drought, and large animals; however, much focus has been on fire. Consequently, there is considerable information on postfire resprouting ability in trait databases (e.g., FEIS-USDA Forest Service, Paula et al. 2009). This information is mostly binary at the species level. If the ability to resprout was intrinsic to the species and independent of the type of disturbance (e.g., Zeppel et al. 2015) then the cumulative information in the databases could be used for predicting vegetation responses to any disturbance. The basis of this hypothesis is that resprouting species have dormant buds (or bud-forming tissues) and accumulate reserves (nonstructural carbohydrates) that are mobilised in response to a biomass removal from any disturbance or stress factor. In this framework, it has been suggested that the ability to resprout after fire could be an indicator of the capacity to recover after drought, and thus be a useful proxy for predicting vegetation dynamics in a warming world (Zeppel et al. 2015).

However, there are major differences between fire and other disturbances that may influence resprouting and limit generalizations. Although disturbance typically leads to defoliation, fire, due to high temperatures, causes additional impacts and some species with an innate capacity for

resprouting may not resprout after fire due to the lethal effects of the fire. Some plants have resprouting buds with very little protection that are killed by the heat of a fire but not by other disturbances. Even for fire survivors, the heat from fire may nucleate cavitation and deform xylem conduits leading to postfire water stress (Michaletz et al. 2012). Consequently, most plants that resprout after fire are also likely to resprout after many other types of disturbances, but the opposite is not necessarily true. Supporting this, there is evidence for lower resprouting ability after fire than after clipping (see compilation by Vesk & Westoby 2004 and Vesk et al. 2004). There are also cases in which plants resprout after fire but may fail to regenerate after drought. For instance, root systems are often protected from fires by the soil, but they are vulnerable to drought disturbance (cavitation, Pratt et al. 2007); thus, in the case of a very intense drought, extensive embolism formation in the shoot and root may preclude resprouting, even for a species that commonly resprout after a fire (see next section).

Additionally, fire not only defoliates a plant and has lethal effects on meristemic tissues (buds, cambium), it also depletes the litter layer, changes nutrient dynamics and kills interacting species (antagonistic, mutualistic and pathogen species). In addition, there is a flush of new resource after fire, but not after other disturbances. Consequently, many disturbances produce different community and ecosystem dynamics compared with fire (e.g., Nguyen-Xuan et al. 2000, Te Beest et al. 2015).

When determining whether or not a species is a postfire resprouter, it is important to consider that on a landscape scale fires are heterogeneous. There may be some plants that experience low fire intensity and are only partially defoliated; these plants may successfully recover by resprouting new leaves and shoots. However, this resprouting is not indicative of the postfire resprouting ability of the species. Postfire resprouters are defined as those species that generate new shoots following full scorching of the plant (Box 1; Gill 1981, Pausas et al. 2004; Pausas & Keeley 2014). Many postfire non-resprouters can also produce new shoots and survive when they are only partially scorched (eg. Hanson & North 2006, Fernandes et al. 2008).

Even in the case of fire, different fire regimes can generate different pressures that select for different traits (Pausas 2015). Fire affects plants very differently in ecosystems under crown fire regimes (e.g., shrublands) and those under understory fire regimes (e.g., some conifer forest and open woodlands), and these two fire regimes can coexist at the landscape scale. The sharp boundary between them represents a tipping point in which the selective factors for life history characteristics change state abruptly (Keeley *et al.* 2012). Despite radical differences in fire intensity and frequency, both systems have resprouting and non-resprouting species, but for very different reasons that are tied to the different selective environments. For example, crown fires select for non-resprouters that recruit seedlings after fire from *in situ* seed banks whereas forest ecosystems with understory fire regimes often comprise trees that are non-resprouters but persist due to their tall stature, clear boles due to self-pruning of dead branches and thick bark (Pausas 2015a,b).

Overall it seems that not all disturbances act with the same mechanism and produce the same plant and ecosystem responses, and equating the recovery from postfire resprouting with recovery from any other disturbance is an over-simplification. To what extent this simplification may be useful would depend on the specific question addressed, but the differences need to be kept in mind. Specifically, in the context of global change, predicting the response of plants to the disturbance by frequent droughts is of paramount importance. A clear example of the dissimilarity between resprouting and post-drought recovery includes species that survive drought periods by initially dropping their leaves and recover them after the drought; among these species there are a number of non-resprouters (e.g., *Cistus* species, Werner et al. 1999). Given that postfire resprouting is not

equivalent to drought response, we now ask what is the relation between these two processes.

Resprouting and drought resistance

Resprouters vs non-resprouters

Resprouting carries a cost of storing resources below-ground to maintain and protect a bud bank and support rapid post-disturbance regrowth (Pate et al. 1990; Schwil & Ackerly 2005; Moreira et al., 2012). In contrast, non-resprouters allocate the corresponding resources to other functions such as rapid growth and reproduction. In addition, resprouters survive and accumulate additional below ground biomass through multiple disturbances, thus their roots are frequently older and larger (i.e., they can explore a larger soil volume) than those of non-resprouters, even though shoots may be equal in height. All this implies that resprouters tend to have a higher root-to-shoot ratio that could provide greater access to water resources than non-resprouters. However, non-resprouters often coexist with resprouters in the same environment, and even tend to dominate in dry environments (see below). Thus we hypothesize that non-resprouters have developed physiological mechanisms for higher dehydration tolerance than resprouters (Keeley et al. 2012, Vilagrosa et al. 2014). Our global analysis suggests that the xylem of non-resprouting species is more resistant to dehydration-induced cavitation (P50) than that of resprouters (Fig. 1a, Notes S1 and S2). This result contrasts with the conclusions of Zeppel et al. (2015) and is likely attributable to their smaller dataset with some errors in assignment of resprouting (see Notes S1 for details).

Our observation that non-resprouters are more resistant to cavitation (Fig. 1a) is driven mainly by species in the mediterranean biome (Fig. 1b, Table 1). Comparisons between resprouting and non-resprouting species have been most extensively examined in this biome, and thus it is instructive to focus on it as a model. Numerous studies of cavitation resistance in California chaparral (Jacobsen et al., 2007; Pratt et al., 2007), and the Mediterranean basin (Hernández et al. 2011; Vilagrosa et al., 2014) support the pattern of greater tolerance in non-resprouters. Some support has also been found in the mediterranean-climate regions of South Africa (Pratt et al., 2012). Additionally, there are other traits that segregate out according to resprouting ability that also support this pattern. For example, mediterranean-climate non-resprouters generally have more structurally robust leaves (i.e. lower specific leaf area), greater xylem tissue density with lower water storage capacity, lower leaf area to xylem area of shoots (particularly for evergreen taxa), and higher vessel implosion resistance (Notes S3). All of this suggests that, in these ecosystems, there is a stronger environmental pressure for developing dehydration tolerance mechanisms in non-resprouters than in resprouters. In this sense, it has been hypothesized that these mechanism are due to the different regeneration niche of the two resprouting life histories (Pausas & Keeley 2014): many species recruit seedlings just after fire (i.e., postfire seeders, many of them are non-resprouters, Box 1), and thus the seasonally dry open-canopy environment has selected for dehydration tolerance; in contrast, obligate resprouters tend to successfully recruit seedlings in more shaded conditions. In support of this, seedlings of mediterranean non-resprouters typically have much greater survival in post-fire open canopy conditions than seedlings of co-occurring resprouter species (e.g. Thomas & Davis, 1989).

To fully understand species response to drought it is useful to frame the response in the context of different drought regimes (McDowell et al. 2008). In this framework, non-resprouters generally fit into a classification of tissue-dehydration tolerators (Box 2); i.e., they are more likely to resist droughts of low to moderate intensity and may be able to do so for a long time frame, particularly if their shallow roots allow them to respond to small pulses of rain. In fact, non-resprouters generally

have traits associated with greater levels of productivity when water is available (Notes S3), which is an important part of the suite of traits defining the functional strategy of this life history type. In mediterranean-climate landscapes worldwide, there is field evidence suggesting that non-resprouters tend to dominate in sites that stay dry for longer (e.g., equator-facing slopes), while resprouters in sites with more reliable water throughout the year (Keeley et al. 2012). Examples of this pattern can be found in California (Meentemeyer & Moody, 2002), in the Mediterranean Basin (Pausas et al., 1999) or in Australia (Clarke & Knox 2002, Pausas & Bradstock 2007).

In contrast, for droughts of the highest intensity, non-resprouters are predicted to succumb to catastrophic hydraulic failure and suffer the greatest mortality because their shallow roots do not allow to maintain tissue hydration and they frequently reach negative water potentials that exceed cavitation thresholds (Fig. Box 2). A recent study conducted during an intense record drought in California, found that it was the non-resprouters that suffered the greatest mortality among established adult plants. In addition, the species with the greatest cavitation resistance (i.e. most negative P50) were the ones that had the greatest mortality (Paddock et al., 2013; Fig. 2). Other than the lack of resprouting ability, the characteristics shared by the species most vulnerable to short-term, high intensity drought was their shallow rooting habit and an inability to minimize tissue dehydration, presumably due to lack of stomatal control, leaf shedding, or low levels of capacitance. Combined, these data illustrate the susceptibility of non-resprouters relative to resprouters in mature stands during high intensity droughts, and points out that resistance to cavitation (e.g., P50) is not necessarily a good indicator of drought survival.

Overall there is a clear pattern in mediterranean-type environments suggesting that resprouters and non-resprouters have different mechanisms to deal with water deficit. To say that non-resprouters are more vulnerable to drought as recently suggested (Zeppel et al. 2015) is incomplete because it ignores the existence of different drought resistance mechanisms and the differential responses of non-resprouters and resprouters to different drought regimes. It would be useful to test for physiological differences between resprouting abilities in other ecosystems to evaluate the generality beyond mediterranean-type climate regions. This effort could provide a robust niche-based framework for predicting drought response at a broad scale.

Vulnerability to drought during resprouting

During post-disturbance resprouting, plants mobilize stored resources to grow new shoots (Moreira et al. 2012), and this could jeopardize their tolerance to drought stress (O'Brien et al. 2014), especially if rapidly expanding tissues are ontogenetically sensitive to dehydration (Saruwatari & Davis 1989). Thus, resprouts are likely to be more susceptible to drought injury than non-disturbed adults. This has been shown for chaparral resprouting species subject to an extreme drought during the postfire recovery period, where resprouts of burned plants had higher water-stress induced cavitation, higher depletion of carbohydrate reserves, and higher mortality than unburned plants of the same species (Pratt et al. 2014). A manipulative experiment with a common resprouting chaparral shrub, *Adenostoma fasciculatum* (chamise; R+S+; Fig. 3), also demonstrates the impact that drought conditions can have on resprouting: watering treatment increased post-fire survival during the first dry season while an experimental drought treatment resulted in a 2-fold increase in post-fire mortality (i.e., ~75% mortality) compared to watered plants (Fig. 3B).

There are at least two reasons why resprouting individuals are more sensitive to drought. First, resprouting shoots generally have higher stomatal conductance and a xylem that is more vulnerable to cavitation, compared to undisturbed plants (Fig. 4; Ramirez et al., 2012; Pratt et al., 2014). And second, if substantial aboveground biomass is lost during the disturbance, then considerable

carbohydrates have to be mobilized from underground stores to grow new shoots (Moreira et al. 2012). At the same time, root function must be sustained by mobilizing carbohydrates until significant shoot growth generates a surplus of photosynthate. If during this process CO₂ uptake is limited by stomatal restriction due to drought, then carbohydrates could be depleted leading to mortality (McDowell et al., 2008; Pratt et al., 2014).

Functional syndromes and modelling vegetation dynamics

The use of a single disturbance-related trait, such as resprouting, to generalise the response to disturbance at the global scale may be too simplistic. One of the reasons is that in different environments, resprouting is associated with a different set of traits (including other disturbance-related traits), and thus resprouters and non-resprouters may not respond in the same way in all biomes (Pausas 2001). For instance, in Mediterranean fire-prone ecosystems, non-resprouters tend to form a persistent seedbank in the soil or in the canopy (seeder species, R-S+, Box 1; Pausas et al. 2004, Keeley et al. 2012). Species of these types regenerate very well after fire by recruiting new individuals, and the number of individuals in these species often increases abruptly after fire, even under a drought (Pratt et al. 2014). Non-resprouting seeders recruit in open conditions postfire (Pausas & Keeley 2014) and are the most resistant to cavitation (see R-S+; Fig 1c); they are those that conform most clearly to the dehydration tolerant strategy (Box 2).

These trait correlations are contingent on biogeographic history and thus are ecosystem-dependent. For instance, in many savanna woodlands, non-resprouting species do not tend to form a seedbank but are often associated with having a very thick protective bark; in such ecosystems the bark protects the vital tissues of the plant (Pausas 2015a) and trees are not damaged by fire (understorey-fire ecosystems). In other cases, some non-resprouters have widely dispersed seeds, and even though local populations may not regenerate well after fire there may recruitment postfire from neighbour populations (metapopulation dynamics; e.g., some Asteraceae). Yet other non-resprouters may lack the ability to accumulate a seedbank and to disperse efficiently, and thus they recover slowly and they may experience local extinction after recurrent fires (e.g. Bowman et al. 2014). Consequently, to estimate post-disturbance regeneration at the global scale, a multi-trait approach (i.e. functional types or syndromes) is more appropriate (Pausas 2001). Predicting the dominance of resprouting along disturbance gradients (e.g., Bellingham & Sparrow 2000) may have predictive value at relatively small scales (e.g., within a biome), but will necessarily lack generality (e.g., among biomes) if the correlated traits are not considered. Even within the same biome there may be biogeographic and physical differences that explain divergences in trait correlations and syndromes. Examples of this within biome trait divergence can be found in multi-continental biomes like the mediterranean (Pausas et al., 2006), the tropical savanna (Dantas & Pausas 2013) and the boreal biome (Roger et al. 2015), or when there is a strong shift in community structure that acts as a tipping point in the selective regime (as in the savanna-forest mosaics, Dantas et al. 2013, or the mediterranean chaparral-coniferous forest boundaries, Keeley et al. 2012). Consequently, trait combinations need to be considered for predicting vegetation responses at large scale.

Many of the traits and trait combinations relevant for post-disturbance dynamics were included in early vegetation dynamic models working at small scale (e.g., Shugart & Noble 1981, Pausas 1999) and only recently have these traits been included in some global vegetation dynamic models. A step forward in global modelling was recently presented by Kelley et al. (2014) who included resprouting, together with bark thickness, for predicting vegetation and carbon dynamics in Australia. However, there are several reasons to expect that their model would behave poorly at the global scale. This includes their overestimation of resprouting capacity (they considered some non-

resprouting species to be resprouters; Notes S1) and their assumption that resprouters have a thicker bark than non-resprouters (Fig. 4 in Kelley et al. 2014). This assumption is only valid for trees with epicormic (stem) resprouting; there are many species with basal resprouting and thin bark (Pausas 2015a), and also many eucalypts with epicormic resprouting have a relatively thin bark because their protection mechanism is based on sinking their buds deeply into the trunk wood (Burrows 2002). Finally, they also included in their recruitment module of the model that the recruitment of resprouters was 10% that of the non-resprouters, which is unlikely to be general. For instance, in mediterranean ecosystems, recruitment of non-resprouting seeders is much higher than resprouters in the postfire year, but much lower in the years between fires. In non-mediterranean ecosystems, the difference in recruitment between resprouters and non-resprouters is probably quite different as postfire seeders are a unique syndrome of the mediterranean biome.

In summary, recent incorporations of disturbance-related traits such as resprouting in global vegetation models is a significant innovation; however, there is still need for improvement. Given the different carbon allocation patterns in resprouters and non-resprouters, the incorporation of these traits may have implications in the predicted carbon budget. Global models typically include climate-based functional types as their aim is to predict climatic-related changes. However, given the overwhelming evidence that disturbance regimes are also changing, the incorporation of disturbance-based functional types (e.g., Pausas 2015) is urgently needed. Developing models that accurately include plant disturbance responses at the global scale is certainly a challenge for the next-generation global dynamic models.

Concluding remarks: beyond binary responses

Postfire resprouting of species is often considered as a binary trait in many species, especially in mediterranean species where the frequency distribution of postfire resprouting tends to follow a binomial pattern (Pausas et al. 2004, Vesk et al. 2004). This is because in mediterranean climates, fires tend to be of very high intensity, and intermediate responses may be evolutionarily unstable (Pausas & Keeley 2014). However, in many ecosystems fires are typically less intense because they are more frequent (savannas), because the environment is wetter (tropical or montain forests), or because fuels are low (arid systems). In such ecosystems, the proportion of resprouted individuals may range widely without showing a clear binomial distribution (e.g., Vesk & Westoby 2004, Fig. 5). The causes of such variation are difficult to generalise and there is a clear need to improve our knowledge of resprouting behaviour outside the mediterranean biome. For instance, of the ca 500 species for which P50 values were compiled in Notes S1, we were able to assign the resprouting ability to 90% of the mediterranean species but to less than 50% of the non-mediterranean ones. Understanding resprouting in other biomes means going beyond binary responses and trying to understand resprouting variability. The dichotomy of resprouting vs non-resprouting species may explain a high proportion of variance in mediterranean ecosystems but probably little variance at the global scale. In addition, because fire intensities vary with vegetation type and climate, it may be difficult to compare resprouting across biomes. That is, a plant that resprouts after a fire in a tropical ecosystem could fail to resprout if subjected to a mediterranean high intensity fire. Consequently, the effect of disturbance on resprouting requires standardisation (e.g., by disturbance severity) in order to successfully compile a global resprouting database.

An additional layer of complexity is that resprouting, as a functional trait, is a very complex and morphologically and anatomically diverse trait. Plants may resprout from buds located in a variety of organs such as stems, roots, root crown, rhizomes, lignotubers, or bulbs (Clarke et al. 2013) and these may be related to a variety of evolutionary pressures. Given that resprouting is an ancestral trait in plants (Pausas & Keeley 2014), it is also likely that the adaptive importance of resprouting has changed over evolutionary time. For instance, resprouting from a lignotuber is a trait tightly

linked to fire-prone ecosystems and likely to evolve as response to fire (Keeley *et al.* 2011); however, resprouting from rhizomes, despite conferring fitness benefits to plants living in fire-prone ecosystems, is also common in many plants from non-fire prone ecosystems, and thus could be a response to a range of disturbance pressures. In addition, disentangling among disturbance is not always easy; for instance, the contention that resprouting of Hawaiian trees reflects an adaptation to drought because it increases along a gradient of increasing aridity (e.g., Busby *et al.* 2010) is confounded by the fact that fires in the Hawaiian Islands likewise increase along the same gradient during ENSO events (Chu *et al.* 2002). Disaggregating resprouting in the context of multiple types of resprouting, and disentangling the proportion of trait variance that is explained by each selective pressure (disturbance) is not an easy task, but the compilation of global databases together with time-calibrated phylogenies may provide a fruitful pathway.

In conclusion, there is a number of issues and cautions that need to be considered before using resprouting ability to predict vegetation responses across disturbance types and biomes. There are marked differences in resprouting, depending on the disturbance type, and fire is often the most severe disturbance. The relationship between postfire resprouting and drought resistance is well established for the mediterranean biome (Box 2, Fig. 1), although more work is needed in mediterranean ecosystems of the Southern Hemisphere. Preliminary results in other biomes are not yet conclusive (Table S1), and classifying the resprouting ability in those biomes becomes more complex (Fig. 5). There is a lack of physiological studies on resprouting outside of the mediterranean biome to unambiguously use this trait as a surrogate for drought response and mortality at the global scale. Modelling exercises need to consider the different response of the species depending on the drought regime (specifically, duration and intensity; Box 2); they also need to consider that correlations between resprouting and other disturbance response traits vary with biome and continent, and thus the success of a species in response to a disturbance most likely results from a related set of traits. Studies of longer term droughts aimed at different resprouting types are generally lacking, but recent protracted droughts in California are facilitating ongoing natural experiments.

Acknowledgements

This work has been performed under the framework of the TREVOL projects (CGL2012-39938-C02-01 to JGP) from the Spanish government. ALJ, RBP, AV and SP were supported by the following grants: IOS-1252232 (NSF), IOS-0845125 (NSF), CGL-2011-30531-CO2-02 (SURVIVE project, Spain), ID-1120458 (FONDECYT Regular 2012, Chile), respectively. Michael F. Tobin is thanked for his work on resprouter vulnerability curves. *Centro de Investigaciones sobre Desertificación* (CIDE; Desertification Research Center) is a joint research institute of the Spanish National Research Council (CSIC), the University of Valencia and Generalitat Valenciana. *Fundación Centro de Estudios Ambientales del Mediterráneo* (CEAM) is supported by *Generalitat Valenciana*. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. government.

References

- Ackerly DD. 2004. Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecological Monographs* **74**: 25-44.
- Bellingham PJ, Sparrow AD. 2000. Resprouting as a life history strategy in woody plant communities. *Oikos* **89**: 409-416.
- Bowman DMJS, MacDermott HJ, Nichols SC, Murphy BP. 2014. A grass–fire cycle eliminates an obligate-seeding tree in a tropical savanna. *Ecology and Evolution* **4**: 4185–4194.
- Brodrribb TJ, McAdam SAM, Jordan GJ, Martins SCV. 2014. Conifer species adapt to low-rainfall

climates by following one of two divergent pathways. *Proceedings of the National Academy of Sciences* **111**: 14489-14493.

- Burrows GE. 2002.** Epicormic strand structure in *Angophora*, *Eucalyptus* and *Lophostemon* (Myrtaceae) - implications for fire resistance and recovery. *New Phytologist* **153**: 111-131.
- Busby PE, Vitousek P, Dirzo R. 2010.** Prevalence of tree regeneration by sprouting and seeding along a rainfall gradient in Hawai'i. *Biotropica* **42**: 80-86.
- Chu P-S, Yan W, Fujioka F. 2002.** Fire-climate relationships and long-lead seasonal wildfire prediction for Hawaii. *International Journal of Wildland Fire* **11**: 25-31.
- Clarke PJ, Knox JE. 2002.** Post-fire response of shrubs in the tablelands of eastern Australia: Do existing models explain habitat differences? *Australian Journal of Botany* **50**: 53-62.
- Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, Enright NJ, Knox KJE. 2013.** Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist* **197**: 19-35.
- Dantas VL, Batalha MA, Pausas JG. 2013.** Fire drives functional thresholds on the savanna-forest transition. *Ecology* **94**: 2454-2463.
- Dantas VL, Pausas JG. 2013.** The lanky and the corky: fire-escape strategies in savanna woody species. *Journal of Ecology* **101**: 1265-1272.
- Davis SD, Ewers FW, Sperry JS, Portwood KA, Crocker MC, Adams GC. 2002.** Shoot dieback during prolonged drought in *Ceanothus* (Rhamnaceae) chaparral of California: a possible case of hydraulic failure. *American Journal of Botany* **89**: 820-828.
- Fernandes PM, Vega JA, Jimenez E, Rigolot E. 2008.** Fire resistance of European pines. *Forest Ecology and Management* **256**: 246-255.
- Gill AM 1981.** Adaptive response of Australian vascular plant species to fires. In: R. H. Groves I. R. Noble eds. *Fire and the Australian biota*. Canberra: Australian Academy of Sciences, 243-271.
- Hanson CT, North MP. 2006.** Post-fire epicormic branching in Sierra Nevada *Abies concolor* (white fir). *International Journal of Wildland Fire* **15**: 31-35.
- Hernández EI, Pausas JG, Vilagrosa A. 2011.** Leaf physiological traits in relation to resprouter ability in the Mediterranean Basin. *Plant Ecology* **212**: 1959-1966.
- Hoffmann, W. A., R. M. Marchin, P. Abit, and O. L. Lau. 2011.** Hydraulic failure and tree dieback are associated with high wood density in a temperate forest under extreme drought. *Global Change Biology* **17**: 2731-2742.
- Jacobsen AL, Pratt RB, Ewers FW, Davis SD. 2007.** Cavitation resistance among 26 chaparral species of southern California. *Ecological Monographs* **77**: 99-115.
- Kaneakua IN. 2011.** *Comparison between stem hydraulic properties and mechanical strength of pre-fire adults to post-fire resprouts of the chaparral shrub Heteromeles arbutifolia*. Pepperdine University Malibu, California.
- Keeley JE, Bond WJ, Bradstock RA, Pausas JG, Rundel PW. 2012.** *Fire in Mediterranean ecosystems: ecology, evolution and management*: Cambridge University Press.
- Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA. 2011.** Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science* **16**: 406-411.
- Kelley DI, Harrison SP, Prentice IC. 2014.** Improved simulation of fire-vegetation interactions in the Land surface Processes and eXchanges dynamic global vegetation model (LPX-Mv1). *Geosci. Model Dev. Discuss.* **7**: 931-1000.
- McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG, Yepez EA. 2008.** Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* **178**: 719-739.
- Meentemeyer RK, Moody A. 2002.** Distribution of plant life history types in California chaparral: the role of topographically-determined drought severity. *Journal of Vegetation Science* **13**: 67-78.
- Michaletz ST, Johnson EA, Tyree MT. 2012.** Moving beyond the cambium necrosis hypothesis of post-fire tree mortality: cavitation and deformation of xylem in forest fires. *New Phytologist* **194**: 254-263.
- Moreira B, Tormo J, Pausas JG. 2012.** To resprout or not to resprout: factors driving intraspecific variability in resprouting. *Oikos* **121**: 1577-1584.
- Nguyen-Xuan T, Bergeron Y, Simard D, Fyles JW, Paré D. 2000.** The importance of forest floor disturbance in the early regeneration patterns of the boreal forest of western and central Quebec: a wildfire versus logging comparison. *Canadian Journal of Forest Research* **30**: 1353-1364.

- O'Brien MJ, Leuzinger S, Philipson CD, Tay J, Hector A. 2014.** Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. *Nature Climate Change* **4**: 710-714.
- Paddock W, Davis SD, Pratt RB, Jacobsen A, Tobin MF, López-Portillo J, Ewers FW. 2013.** Factors determining mortality of adult chaparral shrubs in an extreme drought year in California. *Aliso* **31**: 49-57.
- Pate JS, Froend RH, Bowen BJ, Hansen A, Kuo J. 1990.** Seedling growth and storage characteristics of seeder and resprouter species of Mediterranean-type ecosystems of SW Australia. *Annals of Botany* **65**: 585-601.
- Paula S, Arianoutsou M, Kazanis D, Tavsanoglu Ç, Lloret F, Buhk C, Ojeda F, Luna B, Moreno JM, Rodrigo A, Espelta JM, Palacio S, Fernández-Santos B, Fernandes PM, Pausas JG. 2009.** Fire-related traits for plant species of the Mediterranean Basin. *Ecology* **90**: 1420-1420.
- Pausas JG, Bradstock RA, Keith DA, Keeley JE. 2004.** Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology* **85**: 1085-1100.
- Pausas JG, Bradstock RA. 2007.** Fire persistence traits of plants along a productivity and disturbance gradient in Mediterranean shrublands of SE Australia. *Global Ecology and Biogeography* **16**: 330-340.
- Pausas JG, Carbó E, Caturla RN, Gil JM, Vallejo R. 1999.** Post-fire regeneration patterns in the eastern Iberian Peninsula. *Acta Oecologica* **20**: 499-508.
- Pausas JG, Keeley JE, Verdú M. 2006.** Inferring differential evolutionary processes of plant persistence traits in Northern Hemisphere Mediterranean fire-prone ecosystems. *Journal of Ecology* **94**: 31-39.
- Pausas JG, Keeley JE. 2014.** Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist* **204**: 55-65.
- Pausas JG. 1999.** Response of plant functional types to changes in the fire regime in Mediterranean ecosystems: A simulation approach. *Journal of Vegetation Science* **10**: 717-722.
- Pausas JG. 2001.** Resprouting vs seeding - a Mediterranean perspective. *Oikos* **94**: 193-194.
- Pausas JG. 2015a.** Bark thickness and fire regime. *Functional Ecology* **29**: 315-327.
- Pausas JG. 2015b.** Evolutionary fire ecology: lessons learned from pines. *Trends in Plant Science* **20**: 318-324.
- Plaut JA, Yopez EA, Hill J, Pangle R, Sperry JS, Pockman WT, McDowell NG. 2012.** Hydraulic limits preceding mortality in a piñon–juniper woodland under experimental drought. *Plant, Cell & Environment* **35**: 1601-1617.
- Pratt RB, Jacobsen AL, Ewers FW, Davis SD. 2007.** Relationships among xylem transport, biomechanics and storage in stems and roots of nine Rhamnaceae species of the California chaparral. *New Phytologist* **174**: 787-798.
- Pratt RB, Jacobsen AL, Golgotiu KA, Sperry JS, Ewers FW, Davis SD. 2007.** Life history type and water stress tolerance in nine California chaparral species (Rhamnaceae). *Ecological Monographs* **77**: 239-253.
- Pratt RB, Jacobsen AL, Jacobs SM, Esler KJ. 2012.** Xylem transport safety and efficiency differ among fynbos shrub life history types and between two sites differing in mean rainfall. *International Journal of Plant Sciences* **173**: 474-483.
- Pratt RB, Jacobsen AL, Ramirez AR, Helms AM, Traugh CA, Tobin MF, Heffner MS, Davis SD. 2014.** Mortality of resprouting chaparral shrubs after a fire and during a record drought: physiological mechanisms and demographic consequences. *Global Change Biology* **20**: 893-907.
- Ramirez AR, Pratt RB, Jacobsen AL, Davis SD. 2012.** Exotic deer diminish post-fire resilience of native shrub communities on Santa Catalina Island, southern California. *Plant Ecology* **213**: 1037-1047.
- Rogers BM, Soja AJ, Goulden ML, Randerson JT. 2015.** Influence of tree species on continental differences in boreal fires and climate feedbacks. *Nature Geosci* **8**: 228-234.
- Saruwatari MW, Davis SD. 1989.** Tissue water relations of three chaparral shrub species after wildfire. *Oecologia* **80**: 303-308.
- Schwilk DW, Ackerly DD. 2005.** Is there a cost to resprouting? Seedling growth rate and drought tolerance in sprouting and nonsprouting *Ceanothus* (Rhamnaceae). *American Journal of Botany* **92**: 404-410.
- Shugart HH, Noble IR. 1981.** A computer model of succession and fire response of the high- altitude Eucalyptus forest of the Brindabella Range, Australian Capital Territory. *Australian Journal of Ecology* **6**: 149-164.
- Te Beast M, Mpandza NJ, Olf H. 2015.** Fire and simulated herbivory have antagonistic effects on

- resistance of savanna grasslands to alien shrub invasion. *Journal of Vegetation Science* **26**: 114-122.
- Thomas CM, Davis SD. 1989.** Recovery patterns of three chaparral shrub species after wildfire. *Oecologia* **80**: 309-320.
- Vesk P, Westoby M. 2004.** Sprouting ability across diverse disturbances and vegetation types worldwide. *Journal of Ecology* **92**: 310-320.
- Vesk PA, Warton DI, Westoby M. 2004.** Sprouting by semi-arid plants: testing a dichotomy and predictive traits. *Oikos* **107**: 72-89.
- Vilagrosa A, Hernández EI, Luis VC, Cochard H, Pausas JG. 2014.** Physiological differences explain the co-existence of different regeneration strategies in Mediterranean ecosystems. *New Phytologist* **201**: 1277-1288.
- Werner C, Correia O, Beyschlag W. 1999.** Two different strategies of Mediterranean macchia plants to avoid photoinhibitory damage by excessive radiation levels during summer drought. *Acta Oecologica* **20**: 15-23.
- West AG, Dawson TE, February EC, Midgley GF, Bond WJ, Aston TL. 2012.** Diverse functional responses to drought in a Mediterranean-type shrubland in South Africa. *New Phytologist* **195**(2): 396-407.
- Zeppel MJB, Harrison SP, Adams HD, Kelley DI, Li G, Tissue DT, Dawson TE, Fensham R, Medlyn BE, Palmer A, West AG, McDowell NG. 2015.** Drought and resprouting plants. *New Phytologist*: **206**: 583-589.

Supplementary Material

Table S1. Global P50-resprouting database

Notes S1. Reanalysis of the global P50 in relation to resprouting ability

Notes S2. Statistical comparison of P50 values between resprouting life histories

Notes S3. Functional differences between between resprouting life histories

Notes S4. References for Figure 5.

BOXES

BOX 1. Basic concepts

Postfire traits and strategies

Postfire resprouting (R): the ability to generate new shoots from dormant buds after stems have been fully scorched by fire. This term is preferable to sprouting, which refers to initiation of new shoots throughout the life cycle of a plant. Species are typically classified as resprouters (R+) or nonresprouters (R-) depending on resprouting ability.

Postfire seeding (S): the ability to generate a fire-resistant seed bank with seeds that germinate profusely after fires (fire-cued germination). Typically, such species restrict recruitment to a single pulse after a fire. Seeds may be stored in the soil or in the canopy. Species are typically classified as seeders (S+) or nonseeders (S-) depending on whether seeds display fire-cued germination and recruitment in post-fire pulses. Note that the term 'seeders' refers strictly to postfire conditions, and cannot be attributed to plants that regenerate by seeds in other conditions.

Obligate resprouters (R+S-): plants that solely rely on resprouting to regenerate after fire (resprouters without postfire seeding ability). These plants do not germinate after fire because they lack a fire-resistant seed bank. Note that obligate resprouters might reproduce by seeds during the fire-free interval, but the terminology of seeders and resprouters refers to the postfire conditions.

Facultative seeders (R+S+): plants that have both mechanisms for regenerating after fire, that is, they are able to resprout and to germinate after fire.

Obligate seeders (R-S+): plants that do not resprout and rely on seeding to regenerate their population after fire (nonresprouters with postfire seeding ability).

Postfire colonizers (R-S-): plants that lack a mechanism for local post fire persistence, but they can recruit after fire by seeds dispersed from unburned patches or from populations outside the fire perimeter (metapopulation dynamics).

Drought-related strategies

Water stress, drought stress, dehydration stress: the stress due to a water deficit.

Drought regime: different aspects of a drought that can have different effects on plants. Two key aspects are intensity and duration of water deficits (Box 2); two additional factors are temperature and vapour pressure deficits.

Drought resistance: the ability to survive a drought. This can be achieved by tolerating or avoiding tissue dehydration.

Dehydration (Drought) avoidance: the strict meaning of "drought," as a meteorological term, is a prolonged absence of precipitation, extending over geographical space, and thus cannot be "avoided" by plants per se. However, plants can avoid tissue dehydration caused by drought through deep roots, stomatal closure, growth near a water source, tissue water storage, and shedding of leaves (in the case of drought deciduous species).

Dehydration (Drought) tolerance: a drought resistance mode whereby tissues experience significant dehydration but avoid injury. In some cases injurious strain may be sustained, but plants are able to either tolerate it or repair it.

Anisohydric: a form of stomatal regulation that leads to tissue water deficits, measured at midday, when the available water in the environment declines.

Isohydric: a form of stomatal regulation that leads to stable water status, typically measured at midday, in response to fluctuating water availability.

BOX 2. Drought resistance strategies

Plants with different regulatory strategies with respect to water status are hypothesized to be differentially affected by drought regime, which include drought intensity and duration (McDowell et al. 2008). At one end of a continuum are species that dehydrate as the available moisture declines (**dehydration tolerators**). These species generally have shallow roots, they often suffer important water potential oscillations (weak stomatal control, i.e., anisohydric regulation; Box 1), and they lack sufficient water stores to avoid dehydration. The anisohydric regulation allows continued gas exchange during drought; and a shallow rooting habit enables a rapid response to pulses of moisture, but at the expense of greater tissue dehydration (Brodribb et al., 2014). Thus, these species maintain dehydration tolerance mechanisms such as high resistance to xylem cavitation and mechanically strong lignified tissues (high wood density and low specific leaf area) with low water storage capacity. At the opposite end of the spectrum are species that tightly regulate their water status within a narrow range (**dehydration avoiders**). This is accomplished by strict stomatal control and low water potential oscillations (isohydric regulation, Box 1) or leaf shedding as available moisture declines, and these species typically access stable water reservoirs with extensive roots or have increased tissue water storage capacity. Studies in both adults and seedlings suggest that mediterranean resprouters tend to correspond to dehydration avoiders while mediterranean non-resprouters to dehydration tolerators (Notes S3). Note that there are non-resprouters with a strong dehydration tolerance that also have mechanisms to partially avoid tissue dehydration, such as *Cistus* species that drop their leaves under extreme drought conditions (Werner et al. 1999).

Short-term droughts of the highest intensity are hypothesized to be most lethal to dehydration tolerant species over short time-scales (Fig. Box 2). This is because shallow soil moisture may reach low levels causing tissues to dehydrate below a critical threshold that leads to catastrophic xylem dysfunction (Davis et al., 2002, Hoffmann et al. 2011, Paddock et al. 2013). In contrast, longer term and lower intensity droughts that do not deplete shallow soil water may be resisted by dehydration tolerant species. For dehydration avoiding species, a protracted drought of a sufficient intensity could lead to mortality due to carbon/energy deficits that may arise due to protracted stomatal closure (isohydric regulation), reduced canopy photosynthesis due to leaf shedding and ultimately the inability to maintain immune responses or meet respiratory demands of an extensive root system (Plaut et al., 2012) (Fig. Box 2). During the resprouting process, resprouters may be vulnerable to drought mortality caused either by carbohydrate depletion and/or hydraulic failure (Fig. Box 2 right); this is because stored carbohydrate reserves must maintain heterotrophic root function as well as rapid shoot elongation, and postfire shoot recovery is also associated with greater susceptibility to hydraulic failure (Fig. 4; See section “Vulnerability to drought during resprouting”).

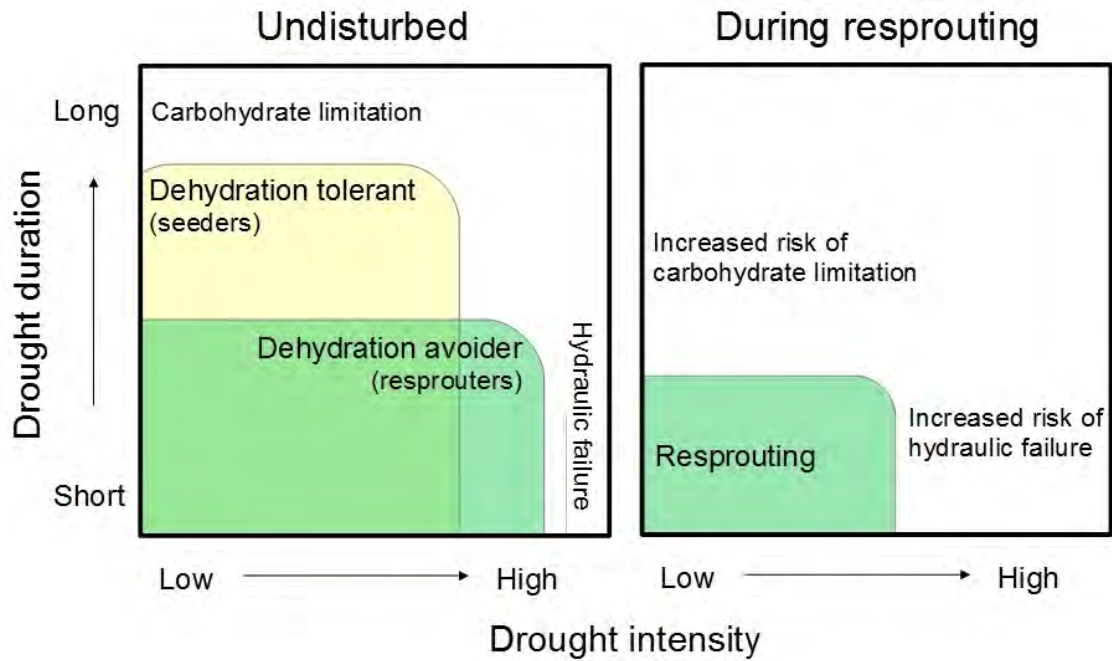


Figure in Box 2. Conceptual model depicting two key aspects of drought, the duration and intensity, and how they link with species that tolerate dehydration and those that avoid dehydration. Coloured areas are the safety zone for each type of species; blank regions correspond to the risky drought conditions: the risk of carbohydrate limitation (under a long drought) and the risk of hydraulic failure (under an intense droughts). In Mediterranean conditions, non-resprouters (seeders) are generally dehydration tolerant, whereas obligate resprouters are dehydration avoiders (left panel). During the process of resprouting, plants are more vulnerable to drought mortality caused by both carbohydrate depletion and/or hydraulic failure (smaller safe zone; right panel).

Figures

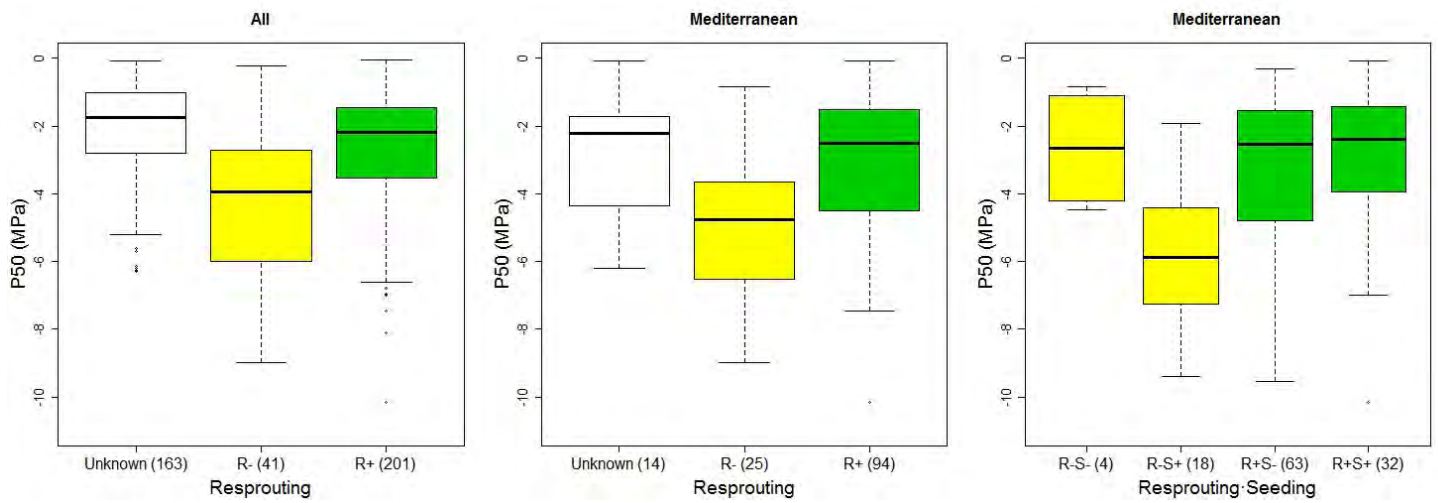


Fig. 1. Relationship between resistance to xylem cavitation (P50, MPa) and resprouting ability in angiosperm species from different biomes (left) and for a subset of mediterranean species (center). The third figure (right) shows the combination of two traits for the mediterranean species: resprouting (R+/R-, i.e. yes/no) and postfire seeding (S+/S-, i.e. yes/no); number of species considered in each case are in brackets (from bibliographic references see Table S1 for details). Resistance to xylem cavitation is expressed as the water potential (MPa) at which a plant loses 50% of hydraulic conductivity (see Notes S1 for more details and Notes S2 for statistics).

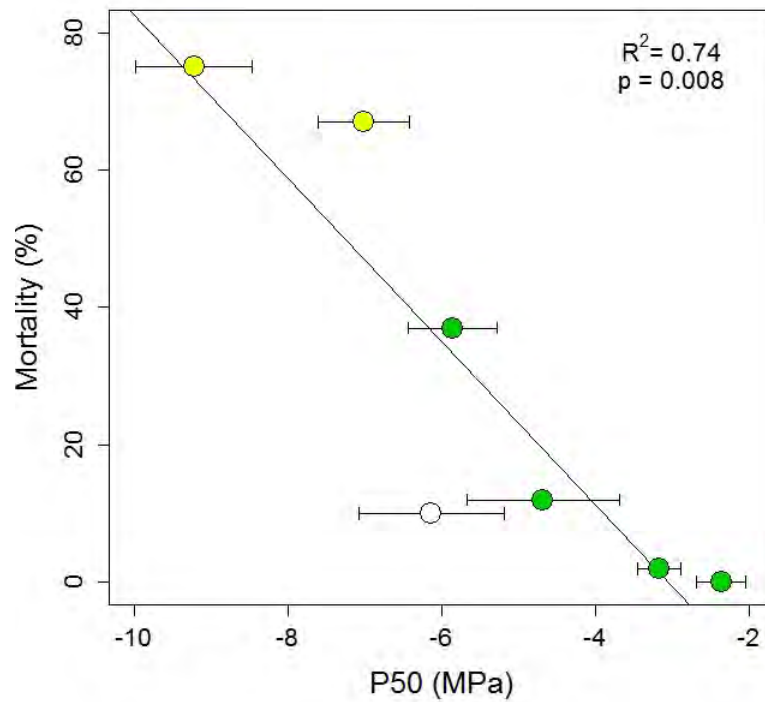


Fig. 2. Mortality during an intense drought is related to cavitation resistance (P50) in seven mediterranean species of the Californian chaparral. P50 is the water potential at 50% loss of hydraulic conductivity (more negative values correspond to greater levels of cavitation resistance). The figure shows that species with greater cavitation resistance exhibited greater mortality during an intense drought. Green symbols are for evergreen resprouters; yellow symbol are evergreen nonresprouters; the white symbol refers to a drought-deciduous species. The line indicates the linear regression; adjusted R^2 and the p-value of this regression are also shown (Data from Paddock et al., 2013).

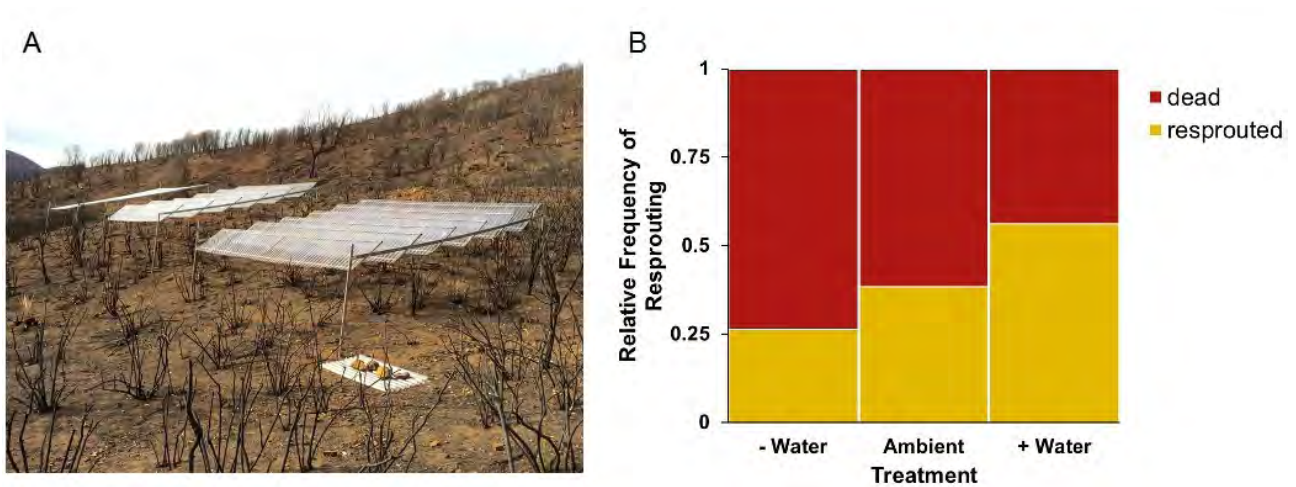


Fig. 3. (A) Postfire rainout shelter experiment in Santa Monica Mountains, southern California. Flat roofed shelters (- water treatment, far left) excluded 100% of wet season precipitation. Shelters with angled roof panels (ambient and + water treatments; center & right) allowed ambient rainfall to fall on the plots. In addition, water was added to one of the treatments (+water treatment; right) in simulated rainfall events that mimicked an extension of the rainy season. A total of 9-5x5 m plots and $n = 294$ chamise shrubs (*Adenostoma fasciculatum*) were included in the experiment. (B) Results of the watering treatment effect on post-fire resprouting of chamise expressed as the relative frequency of shrubs that resprouted (yellow) and died (red) after fire. The amount of water available during the first dry season after a fire significantly affected the number of plants that survived and resprouted ($\text{Chisq} = 18.43$, $\text{df} = 2$, $p < 0.001$). Note that the ambient treatment likely has lower than usual resprouting survival because the study was conducted during a natural drought.

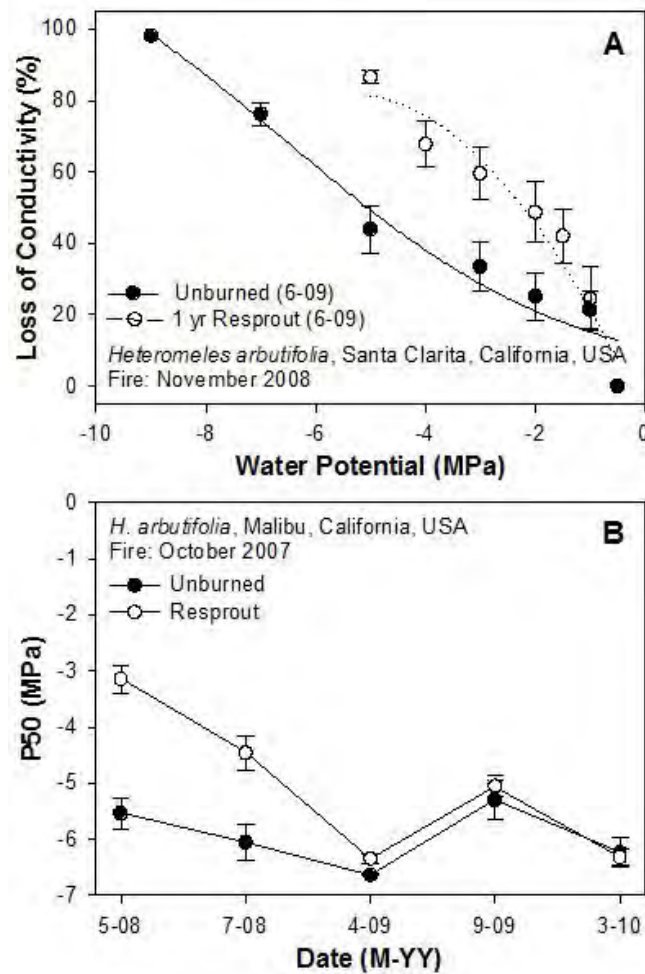


Fig. 4. The vulnerability to water-stress induced cavitation of plants during resprouting may vary compared to the vulnerability of plants that are not currently recovering from disturbance. (A) The chaparral shrub species *Heteromeles arbutifolia* (Rosaceae) displays a significant shift in the cavitation resistance of resprouting stems one-year post-fire compared to adjacent unburned plants measured at the same time and same site (Jacobsen et al., unpublished data; same pattern described for this species at a different site in Ramirez et al. 2012). (B) Data for this species collected over a longer period of time suggest that this shift in vulnerability may persist until two years post-fire (data from Kaneakua, 2011). Each point represents a mean of samples from ≥ 6 individuals ± 1 SE.

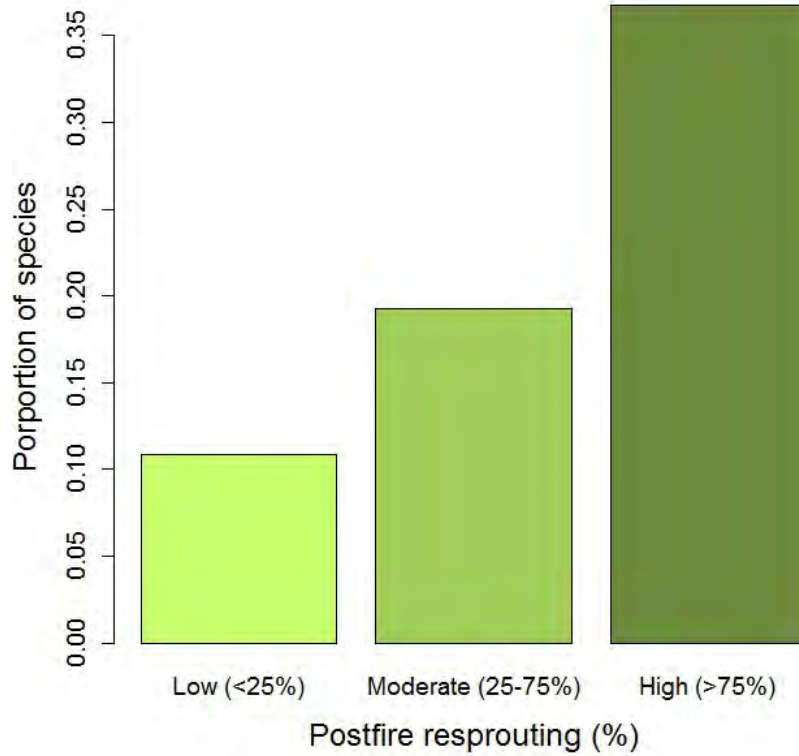


Fig. 5. Proportion of species with low (<25% of the individuals), moderate and high (> 75% of individuals) postfire resprouting in 111 tropical plant species from Latin America and Northern Australia (Notes S3). There is an important proportion of species with intermediate resprouting capacity.

***New Phytologist* Supporting Information**

Article title: Towards understanding resprouting at the global scale

Authors: Pausas JG, Pratt RB, Keeley JE, Jacobsen AL, Ramirez AR, Vilagrosa A, Paula S, Kanekua-Pia IN, Davis SD.

Article acceptance date: 26 July 2015

The following Supporting Information is available for this article:

Table S1 Global P50-resprouting database

Notes S1 Reanalysis of the global P50 in relation to resprouting ability

Notes S2 Statistical comparison of P50 between resprouting life histories

Notes S3 Functional differences between resprouters and nonresprouters

Notes S4 References for Figure 5

Table S1 Global P50-resprouting database

File: Table_S1_Global-P50-Resp-Data_2015.06.xls

Notes S1 Reanalysis of the global P50 in relation to resprouting ability

In a recent study, Zeppel et al. (2015) concluded that “trait differences between resprouting and nonresprouting species suggest that more intense and severe drought is required to induce mortality in resprouting species than in nonresprouting woody plants.” To support this conclusion, the authors used a dataset on species resistance to xylem cavitation (i.e., the water potential at which a plant loses 50% of xylem hydraulic conductivity; P50) compiled by Choat *et al.* (2012) and they searched for the postfire resprouting ability of species from different trait databases. From the 480 species in Choat *et al.* (2012) they were able to assign the resprouting ability (yes/no) to 269 species (56%; 172 angiosperms and 97 gymnosperms). Their analysis showed that angiosperm resprouters were more cavitation resistant than non-resprouters (they did not find differences for gymnosperms). Because the authors did not publish their resprouting classifications and declined a request to share their classification, their results are not easy to replicate. We performed a similar exercise with an improved P50 dataset and found a different result: the xylem of nonresprouter species was more resistant to cavitation (lower P50 values) than resprouters (figure below). Our results are consistent with numerous previous studies of cavitation resistance comparing resprouters to non-resprouters (Jacobsen et al., 2007b; Pratt et al., 2008; Pratt et al., 2012b; Vilagrosa et al., 2014). In addition, P50 is not always a good indicator of drought resistance, as extreme drought conditions can cause mortality to species with very low P50 (Fig 2 in main text; Hoffman et al. 2011; see Box 1 for the variety of responses depending on the drought regime).

The discrepancy in the results between the Zeppel et al. (2015) study and our new analysis could reflect some of the complexities in understanding resprouting. It is possible that we obtained the resprouting ability for a very different set of species, or that we found different resprouting responses for the same species, or both. Our approach was based on published references, and we assigned species as resprouter or non-resprouter only if there were clear evidences of postfire resprouting; we define postfire resprouters as those species that generate new shoots once the plant is fully scorched (Gill 1981, Pausas et al. 2004; Pausas & Keeley 2014). Observations of resprouting after light fires are not indicative of the resprouting ability of the plant because many typical non-resprouters, if they are only partially scorched (defoliated) can produce new shoots and survive. Different criteria on resprouting is a plausible explanation for the contrasted results, as illustrated in the genus *Abies*: most fire ecologist would suggest that *Abies* species are not postfire resprouters (e.g. FEIS database), while Zeppel et al. (2015) explicitly said that this genus contain several resprouting species (in

their words, “*Pinus*, *Juniperus* and *Abies* contain the most resprouting species within gymnosperms”). Their classification is probably based on the observation that under a light fire many non-resprouting species, including *Abies* (e.g., Hanson & North 2006), may survive and their crown recover from unaffected buds in branches. Deviations from the classification used in our analysis by the Zeppel et al. (2015) study could perhaps also be derived from their use of the Kelley et al. (2014) classifications; Kelley et al. (2014) classified some highly cavitation resistant Californian species as resprouters (*Ceanothus* spp. subgenus *Cerastes* and *Arctostaphylos glauca*) when they are unequivocally non-resprouters. Without the database used by Zeppel et al. (2015) for their analysis we cannot know the exact reason for the different results; nevertheless, our analysis suggests that the results by Zeppel et al. (2015) cannot not be supported (see Supplemental Table S1 for resprouting classification and references as analysed in the present study).

A second reason why the analysis by Zeppel et al. (2015) may potentially misrepresent the drought responses of resprouting versus non-resprouting species is that their analysis included studies which used different methods for constructing vulnerability curves and P50 values, which was confounded with resprouting type (Fig. S1, Table S1). This may especially influence the Choat et al. (2012) dataset because they reported only a single P50 value from a single study for a given species rather than an across study mean. Some researchers do not flush out emboli prior to generating a vulnerability curve, which generally has the effect to make P50 values more negative, i.e. more resistant to cavitation (Sperry et al., 2012; Hacke et al., 2015). It is currently debated as to whether it is best practice to flush or not flush stems prior to generation of a vulnerability curve (Wang et al., 2014; Hacke et al., 2015; Jansen et al., 2015), but that need not concern us here. The best practice to analyse resprouters and non-resprouters is to compare across data that are not confounded by errors introduced by differences in methods. Laboratories that consistently do not flush stems prior to analyses have primarily analysed resprouting species, thus in the Zeppel et al. (2015) analysis, the resprouter group contained a mix of flushed and unflushed curves. By contrast, the non-resprouters data were largely based on flushed curves.

Our preliminary analyses suggested that the P50 estimated using both flushed and unflushed studies tended to be more negative than the P50 estimated from studies that only included flushed studies; although the magnitude of the difference was not large. To address this confounding factor, we generated a new database that differed from that of Choat et al. (2012) in three ways: First, we included many more studies than the Choat et al. (2012) database. In many cases the newly included data were from species already in the database for which we took an average from across additional studies to arrive at a value for a particular species. Second, we specifically identified studies that reported data from flushed vulnerability curves, so that the present study and future studies can control for disparities in methods. Lastly, we added additional studies that have been conducted in the last three years, which added many new species to the database. Our results are consistent across analyses, but they are strengthened by the inclusion of only studies that are controlled for flushing (figure below; Table S1 for a complete list of species P50s, references for these values, and flushing identifications).

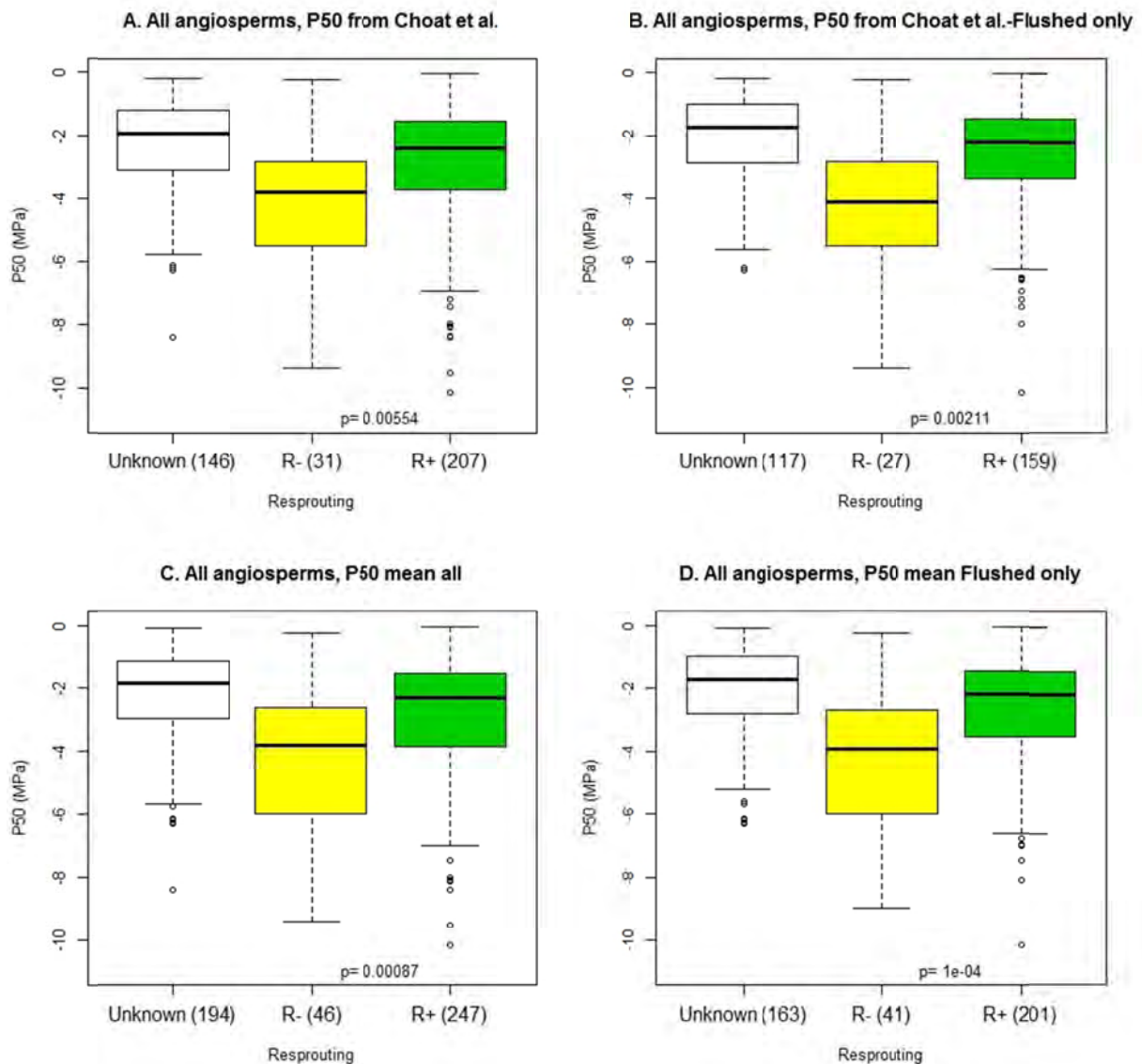


Figure Notes S1. Relationship between resistance to xylem cavitation (P50, MPa) and resprouting ability in angiosperms. Species are grouped in resprouters (R+), non-resprouters (R-), or 'Unknown' (with the number of species in brackets) from bibliographic references (see Table S1 for details). P-values refer to the difference in P50 between resprouters and nonresprouters. Different plots refer to different sets of P50 data as follows: (A) P50 from Choat et al. (2012); (B) Selected cases from Choat et al. (2012) that use flushed curves methods; (C) An enlarged dataset (more species and using means for species for which P50 have been reported across multiple studies); and (D) as C but only using values obtained using flushed methods (this is the dataset used in Figure 1 of the main text and in Notes S2). The data is available in Table S1 (file Table_S1_Global-P50-Resp-Data_2015.06.xls).

References (Notes S1)

- Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Feild TS, Gleason SM, Hacke UG, Jacobsen AL, Lens F, Maherali H, Martinez-Vilalta J, Mayr S, Mencuccini M, Mitchell PJ, Nardini A, Pittermann J, Pratt RB, Sperry JS, Westoby M, Wright IJ, Zanne AE. 2012.** Global convergence in the vulnerability of forests to drought. *Nature* **491**: 752-755.
- Fernandes PM, Vega JA, Jimenez E, Rigolot E. 2008.** Fire resistance of European pines. *Forest Ecology and Management* **256**: 246–255.
- Gill AM 1981.** Adaptive response of Australian vascular plant species to fires. In: R. H. Groves, R. Noble eds. *Fire and the Australian biota*. Canberra: Australian Academy of Sciences, 243-271.
- Hacke UG, Venturas MD, MacKinnon ED, Jacobsen AL, Sperry JS, Pratt RB. 2015.** The standard centrifuge method accurately measures vulnerability curves of long-vesselled olive stems. *New Phytologist* **205**: 116-127.
- Hanson CT, North MP. 2006.** Post-fire epicormic branching in Sierra Nevada *Abies concolor* (white fir). *International Journal of Wildland Fire* **15**: 31-35.
- Hoffmann WA, Marchin RM, Abit P, Lau OL. 2011.** Hydraulic failure and tree dieback are associated with high wood density in a temperate forest under extreme drought. *Global Change Biology* **17**: 2731-2742.
- Jacobsen AL, Pratt RB, Ewers FW, Davis SD. 2007.** Cavitation resistance among 26 chaparral species of southern California. *Ecological Monographs* **77**: 99-115.
- Jansen S, Schuldt B, Choat B. 2015.** Current controversies and challenges in applying plant hydraulic techniques. *New Phytologist* **205**: 961-964.
- Kelley DI, Harrison SP, Prentice IC. 2014.** Improved simulation of fire-vegetation interactions in the Land surface Processes and eXchanges dynamic global vegetation model (LPX-Mv1). *Geosci. Model Dev. Discuss.* **7**: 931-1000.
- Pausas JG, Bradstock RA, Keith DA, Keeley JE. 2004.** Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology* **85**: 1085-1100.
- Pausas JG, Keeley JE. 2014b.** Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist* **204**: 55-65.
- Pratt R, Jacobsen A, Mohla R, Ewers F, Davis S. 2008.** Linkage between water stress tolerance and life history type in seedlings of nine chaparral species (Rhamnaceae). *Journal of Ecology* **96**: 1252-1265.
- Pratt RB, Jacobsen AL, Jacobs SM, Esler KJ. 2012.** Xylem transport safety and efficiency differ among fynbos shrub life history types and between two sites differing in mean rainfall. *International Journal of Plant Sciences* **173**: 474-483.

- Sperry JS, Christman MA, Torres-Ruiz JM, Taneda H, Smith DD. 2012.** Vulnerability curves by centrifugation: is there an open vessel artefact, and are 'r' shaped curves necessarily invalid? *Plant, Cell & Environment* **35**: 601-610.
- Vilagrosa A, Hernández EI, Luis VC, Cochard H, Pausas JG. 2014.** Physiological differences explain the co-existence of different regeneration strategies in Mediterranean ecosystems. *New Phytologist* **201**: 1277-1288.
- Wang R, Zhang L, Zhang S, Cai J, Tyree MT. 2014.** Water relations of *Robinia pseudoacacia* L.: do vessels cavitate and refill diurnally or are R-shaped curves invalid in *Robinia*? *Plant, Cell & Environment* **37**: 2667-2678.
- Zeppel MJB, Harrison SP, Adams HD, Kelley DI, Li G, Tissue DT, Dawson TE, Fensham R, Medlyn BE, Palmer A, West AG, McDowell NG. 2015.** Drought and resprouting plants. *New Phytologist*: doi:10.1111/nph.13205.

Notes S2 Statistical comparison of P50 between resprouting life histories

Table: Mean P50 values (n: number of species considered) for resprouters (R+) and non-resprouters (R-) considering plants from all biomes, from the Mediterranean biome only, and from all biomes excluding the Mediterranean. The statistical tests refer to the comparison of P50 values (obtained using the flushed methods) between R+ and R- in standard cross-species analyses (ANOVA) and in phylogenetically-controlled analyses (phy). See Fig. 1 and Notes S1 for visualizing the variability.

	R+		R-		test	
	Mean	n	Mean	n	ANOVA (F, p)	phy
All biomes (Fig. 1a, S1d)	-2.71	201	-4.32	41	28.7, p <0.0001	p < 0.0001
Mediterranean (Fig. 1b)	-3.07	94	-4.89	25	8.75, p = 0.0003	p < 0.0001
Non-mediterranean	-2.40	107	-3.40	16	7.5, p = 0.0006	p = 0.26

Phylogenetically-controlled analysis: We first generated the topology of a phylogenetic tree for the species considered in each analysis using the Phylomatic software (Webb et al. 2008) on the basis of a magatree (APG III 2009). Then, nodes were dated based on Wikström et al. (2001) and Verdú & Pausas (2013); undated nodes were adjusted using the BLADJ algorithm available in Phylocom. We tested the differences between resprouting abilities by means of a generalized estimating equation (GEE), which is a procedure that uses a GLM approach incorporating the phylogenetic relatedness among species as a correlation matrix in the model (Paradis and Claude 2002).

References (Notes S2)

APG III. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* **161**: 105-121.

Paradis E, Claude J. 2002. Analysis of comparative data using generalized estimating equations. *Journal of Theoretical Biology* **218**: 175-185.

Verdú M, Pausas JG. 2013. Syndrome-driven diversification in a mediterranean ecosystem. *Evolution* **67**: 1756-1766.

Webb CO, Ackerly DD, Kembel SW. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* **24**: 2098-2100.

Wikström N, Savolainen V, Chase MW. 2001. Evolution of the angiosperms: calibrating the family tree. *Proceedings of the Royal Society B* **268**: 2211-222

Notes S3 Functional differences between resprouters and nonresprouters

Summary of functional differences between resprouters (R+) and non-resprouters (R-) in Mediterranean-type ecosystems.

Functional trait	R+	R-	References
Cavitation resistance	Lower	Higher	Jacobsen et al. 2007b, Pratt et al. 2007b, Hernández et al. 2011, Pratt et al., 2012, Vilagrosa et al. 2014
Vessel length	Shorter	Longer	Jacobsen et al. 2007b
Vessel density (number/area)	Lower	Higher	Vilagrosa et al., 2014
Specific leaf area (SLA)	Higher	Lower	Paula & Pausas 2006, Hernández et al. 2011, Pratt et al. 2012, Pratt et al., 2007b, Ramirez et al., 2012, Pugnaire et al., 2006
Leaf area to xylem area of shoots	Higher	Lower	Ackerly 2004
Carbon assimilation per area when water is available	Lower	Higher	Hernández et al. 2011, Galle et al. 2011; Pratt et al. 2012, Pugnaire et al., 2006
Stomatal conductance (g_s max)	Lower	Higher	Hernández et al. 2011; Galle et al. 2011; Vilagrosa et al., 2014; Ramírez et al., 2012b; Pratt et al., 2012, Pugnaire et al., 2006
Instantaneous water-use efficiency (WUE)	Higher	Lower	Hernández et al. 2011; Vilagrosa et al., 2014
Specific root length (SRL)	Lower	Higher	Paula & Pausas 2011
Seedling root/shoot ratio	Higher	Lower	Pratt et al., 2012; Pugnaire et al., 2006
Xylem water storage capacity	Higher	Lower	Pratt et al. 2007a
Minimum seasonal Ψ_w	Higher	Lower	Jacobsen et al., 2008; Pratt et al., 2007b; Paddock et al., 2013

References (Notes S3)

- Ackerly DD. 2004.** Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecological Monographs* **74**: 25-44.
- Davis S, Ewers F, Wood J, Reeves J, Kolb K. 1999.** Differential susceptibility to xylem cavitation among three pairs of *Ceanothus* species in the Transverse Mountain Ranges of southern California. *Écoscience* **6**: 180-186.
- Galle A, Florez-Sarasa I, Aououad HE, Flexas J. 2011.** The Mediterranean evergreen *Quercus ilex* and the semi-deciduous *Cistus albidus* differ in their leaf gas exchange regulation and acclimation to repeated drought and re-watering cycles. *Journal of Experimental Botany* **62**: 5207-5216.
- Hernández EI, Pausas JG, Vilagrosa A. 2011.** Leaf physiological traits in relation to resprouter ability in the Mediterranean Basin. *Plant Ecology* **212**: 1959-1966.
- Jacobsen AL, Pratt RB, Davis SD, Ewers FW. 2007a.** Cavitation resistance and seasonal hydraulics differ among three arid Californian plant communities. *Plant, Cell & Environment* **30**: 1599-1609.
- Jacobsen AL, Pratt RB, Ewers FW, Davis SD. 2007b.** Cavitation resistance among 26 chaparral species of southern California. *Ecological Monographs* **77**: 99-115.
- Jacobsen AL, Pratt RB, Davis SD, Ewers FW. 2008.** Comparative community physiology: nonconvergence in water relations among three semi-arid shrub communities. *New Phytologist* **180**: 100-113.
- Paula S, Pausas JG. 2006.** Leaf traits and resprouting ability in the Mediterranean basin. *Functional Ecology* **20**: 941-947.
- Paula S, Pausas JG. 2011.** Root traits explain different foraging strategies between resprouting life histories. *Oecologia* **165**: 321-331.
- Pratt RB, Jacobsen AL, Ewers FW, Davis SD. 2007a.** Relationships among xylem transport, biomechanics and storage in stems and roots of nine Rhamnaceae species of the California chaparral. *New Phytologist* **174**: 787-798.
- Pratt RB, Jacobsen AL, Golgotiu KA, Sperry JS, Ewers FW, Davis SD. 2007b.** Life history type and water stress tolerance in nine California chaparral species (Rhamnaceae). *Ecological Monographs* **77**: 239-253.
- Pratt RB, Jacobsen AL, Hernandez J, Ewers FW, North GB, Davis SD. 2012.** Allocation tradeoffs among chaparral shrub seedlings with different life history types (Rhamnaceae). *American Journal of Botany* **99**: 1464-1476.
- Pratt RB, North GB, Jacobsen AL, Ewers FW, Davis SD. 2010.** Xylem root and shoot hydraulics is linked to life history type in chaparral seedlings. *Functional Ecology* **24**: 70-81.

Pugnaire, F. I., Iii, F. S. C., & Hardig, T. M. 2006. Evolutionary changes in correlations among functional traits in *Ceanothus* in response to Mediterranean conditions. *Web Ecology* **6**: 17–26.

Ramírez, D. a., Parra, A., Resco de Dios, V., & Moreno, J. M. 2012. Differences in morpho-physiological leaf traits reflect the response of growth to drought in a seeder but not in a resprouter Mediterranean species. *Functional Plant Biology* **39**: 332-341.

Vilagrosa A, Hernández EI, Luis VC, Cochard H, Pausas JG. 2014. Physiological differences explain the co-existence of different regeneration strategies in Mediterranean ecosystems. *New Phytologist* **201**: 1277-1288.

Notes S4 References for Figure 5

Kauffman JB. 1991. Survival by sprouting following fire in tropical forests of the eastern Amazon. *Biotropica* **23**: 219-224.

Lloret F, Verdú M, Flores-Hernández N, Valiente-Banuet A. 1999. Fire and resprouting in Mediterranean ecosystems: insights from an external biogeographical region, the mexical shrubland. *American Journal of Botany* **86**: 1655-1661.

Medeiros MB, Miranda HS. 2008. Post-fire resprouting and mortality in cerrado woody plant species over a three-year period. *Edinburgh Journal of Botany* **65**: 53-68.

Pinard MA, Putz FE, Licona JC. 1999. Tree mortality and vine proliferation following a wildfire in a subhumid tropical forest in eastern Bolivia. *Forest Ecology and Management* **116**: 247-252.

Williams RJ, Cook GD, Gill AM, Moore PHR. 1999. Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Australian Journal of Ecology* **24**: 50-59.