CSIRO PUBLISHING

International Journal of Wildland Fire **2019**, *28*, 62–69
https://doi.org/10.1071/WF18133

Response of Arizona cypress (*Hesperocyparis arizonica*) to the Horseshoe Two Megafire in a south-eastern Arizona Sky Island mountain range

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Abstract. We examined the response of Arizona cypress (*Hesperocyparis arizonica*) to the 2011 Horseshoe Two Megafire in the Chiricahua Mountains, Arizona, USA. We documented cover type, fire severity, cypress mortality and seedling establishment in 60 plots. In plots subject to severe fire, most mature cypresses were killed, the canopy opened and seedlings established abundantly. These results were consistent across three canyons differing in topography and vegetation. Successful regeneration of Arizona cypress contrasts with low seedling establishment for pines in the same area after the Horseshoe Two Fire, a difference possibly explained by abundant serotinous seed production in cypress or its preference for riparian sites protected from extreme fire. Our results firmly establish Arizona cypress as a fire-sensitive but fire-embracing species that depends on stand-replacing fire for regeneration. Given the fire sensitivity of Arizona cypress, however, recent increases in the frequency of high-severity fires in the south-west USA could pose a threat to the long-term viability of this species by preventing individuals from reaching sexual maturity during fire intervals. This scenario, termed the 'interval squeeze', has been documented in tecate cypress (*H. forbesii*) in California. A drier future with more frequent wildfires could pose serious threats to all New World cypresses.

Additional keywords: Cupressaceae, interval squeeze, seedling establishment, serotiny; stand-replacing fire.

Received 10 August 2018, accepted 30 October 2018, published online 23 November 2018

Introduction

The New World cypresses (*Hesperocyparis*; Adams *et al.* 2009) are the rarest group of conifers in North America (Wolf 1948; Little 1971) and a focus of conservation concern (Royal Botanic Garden of Edinburgh 2018). These 16 species were more widespread in western North America during the cooler, moister late Pleistocene (Van Devender and Spaulding 1979; Betancourt *et al.* 1990; Thompson and Anderson 2000), but today they are largely confined to protected canyons in mountain ranges.

Hesperocyparis species exhibit strikingly similar traits indicative of a fire-embracing strategy adapted to stand-replacing wildfire (Schwilk and Ackerly 2001): thin bark, poor self-pruning, fire-sensitive trees, an aerial seed bank in the form of serotinous cones, germination largely restricted to bare soil, shade intolerance, and rapid juvenile growth (Wolf 1948; Armstrong 1966; Vogl *et al.* 1977; Parker 1980*a*; Moir 1982; Zedler 1986). Substantial fire ecology research has been carried out on some *Hesperocyparis* species (e.g. tecate cypress, *H. forbesii*; Rodriguez-Buritica *et al.* 2010), but is lacking in others, such as Arizona cypress (*H. arizonica*). This species is restricted to mountain canyons and uplands in the Sierra Madre of northern Mexico and from Trans-Pecos Texas to south-eastern Arizona (Fig. 1; Wolf 1948; Little 1971; Sullivan 1993; Poulos and Camp 2010). Lightning-ignited wildfire is a dominant force in these environments, and most of the resident woody plants evolved in this context (DeBano *et al.* 1995). The pre-Euro-American (before the late 1800s) fire regimes of these areas were complex. Fire histories reveal a frequent surface fire regime in Madrean pine–oak forests (e.g. Swetnam and Baisan 1996; Fulé *et al.* 1997; Swetnam et al. 2001), but mixed fire severity prevailed in more exposed chaparral and oak–juniper–pinyon woodlands (Baisan and Morino 2000).

Like most other *Hesperocyparis* species, Arizona cypress is a thin-barked, fire-sensitive and long-lived (up to at least 450 years) species that produces serotinous cones and requires mineral soil for germination and high light levels for growth to maturity, suggesting evolution in the context of infrequent, stand-replacing fire rather than frequent, low-severity fire (Wolf 1948; Vogl *et al.* 1977; Parker 1980*a*; Moir 1982; Wright and Bailey 1982; Sullivan 1993). These traits likely drive the dynamics of populations of this species in the context of both historic and contemporary fire regimes (and possibly other natural disturbances such as flooding).

Compared with more common tree species in the South-west (e.g. ponderosa pine, *Pinus ponderosa* Lawson & C. Lawson), few studies have examined the responses of Arizona cypress to fire (but see Parker 1980*a*; Moir 1982). The US Forest Service's Fire Effects Information System has a mere 43 words in the 'Plant response to fire' section for Arizona cypress (Sullivan 1993). Further research on the response of this species to fire is especially important given the ongoing changes in fire regimes in the American South-west and northern Mexico. The past three decades have seen a dramatic increase in wildfire severity and area burned across south-western North America, caused both by a build-up in fuels from more than a century of fire suppression and by hotter, drier conditions in the uplands on both sides of the US–Mexico border (Westerling *et al.* 2006; Dennison *et al.* 2014; Abatzoglou and Williams 2016; Kent *et al.* 2017). We know little about how Arizona cypress will respond to the changing fire regime, especially with respect to predicted regional increases in wildfire frequency and severity (Liu *et al.* 2013). Nor do we understand the response of Arizona cypress to fire in relation to topo-edaphic variation across landscapes. The species typically occurs in cool, protected canyons with higher soil moisture than surrounding areas (Sullivan 1993), but studies have documented populations on more exposed sites at higher elevations and on steep, north-facing slopes (Parker 1980*b*; Poulos and Camp 2010).

In the present paper, we examine the response of Arizona cypress to the 2011 Horseshoe Two Wildfire, 7 years post fire, in Chiricahua National Monument (CHIR) in the Sky Island archipelago of Arizona, USA. The Horseshoe Two Fire burned ~90 000 ha over 49 days, in a year in which megafires (wildfires >100 000 ha in size; Attiwill and Binkley 2013) burned throughout the region (Williams *et al.* 2014). The fire burned large portions of CHIR, at severities ranging from low to high. We investigated the response of Arizona cypress populations to the Horseshoe Two Wildfire across a range of fire severities in three different canyons in CHIR. We addressed three questions: (1) what were the mortality impacts of fire across the fire severity gradient? (2) What was the regeneration response where fire killed many mature cypresses and to what extent did seedling establishment vary across the fire severity gradient? And (3) to what extent did the response of cypress to fire vary across three different canyons that varied in topography and vegetation composition? We conclude by placing the results for Arizona cypress in the context of the past and future fire ecology of the New World cypresses.

Materials and methods

Chiricahua National Monument encompasses 4850 ha of the north-west part of the Chiricahua Mountains, in south-eastern Arizona (32°00′20″N, 109°21′24″W), part of the Sky Islands, an archipelago-like northern extension of the Sierra Madre Occidental in Mexico (DeBano *et al.* 1995). The mountains are oriented south-east to north-west, ~80 km in length, and ~1100 to 3000 m above sea level (asl). The terrain of CHIR ranges from largely flat desert grassland in the west to highly dissected, rocky uplands and steep-walled canyons over most of the park. The climate is semiarid (annual precipitation 490 mm), with a dry season that occurs typically from April to June (mean 43 mm) and a rainy season from July to September (mean 252 mm), driven by the North American Monsoon System (Adams and Comrie 1997). Near the CHIR visitor centre at ~1650 m asl, January average minimum and maximum temperatures are −1.2 and 13.4°C respectively; July average minimum and maximum temperatures are 15.5 and 31.8°C respectively. The elevational lapse rate of temperature in the mountains of south-eastern Arizona has been estimated at 7.5°C per 1000 m (Shreve 1915; see also Whittaker *et al.* 1968). The Sky Islands of the South-west support high levels of rare species and biodiversity, a region where major continental biomes mix in complex configurations (Whittaker and Niering 1975; Barton 1994; DeBano *et al.* 1995; Coblentz and Riitters 2004; Poulos *et al.* 2007; Poulos and Camp 2010).

The New World cypresses (now *Hesperocyparis*) were recently separated from the Old World cypresses (still *Cupressus*) at the generic level (Adams *et al.* 2009; Terry *et al.* 2012). The 16 species in *Hesperocyparis* occur in north-western Mexico and south-western and north-western USA. Previously *Cupressus arizonica* (Greene), Arizona cypress is now *H. arizonica* var. *arizonica* (Greene) Bartel, (Adams *et al.* 2009). Smooth-bark Arizona cypress has at times been considered a conspecific, but has now been elevated to species status (*H. glabra*; Adams *et al.* 2009).

We studied the post-fire response of Arizona cypress in 60 plots divided equally among three canyon watercourses that differed in topography, presence of permanent water and vegetation cover type (Fig. 1). In Echo Canyon, the narrowest, driest and highest-elevation canyon of the three, we sampled from just below the Echo Canyon trailhead to the canyon's intersection with Rhyolite Canyon. The most common woody plants were Arizona cypress, silverleaf oak (*Quercus hypoleucoides* A. Camus), Toumey oak (*Q. toumeyi* Sarg.), netleaf oak (*Q. rugosa* Née), and pointleaf manzanita (*Arctostaphylos pungens* Kunth). In Upper Bonita Canyon, which was intermediate among the three sites in canyon width and elevation, with running water in some places during the dry season, we sampled from its highest point along the Bonita Canyon Road to 100 m above the Bonita Canyon Campground. Typical vegetation included Arizona cypress, silverleaf oak, Toumey oak, netleaf oak, Arizona white oak (*Q. arizonica* Sarg.) and Arizona sycamore (*Platanus wrightii* S. Watson). In Lower Bonita Canyon, the widest and lowest-elevation canyon, also with aboveground water in some places during the dry season, we sampled from below the campground to the lower western boundary of CHIR. This canyon, as well as the upper Bonita Canyon (see above), likely offer groundwater for plants at all times of year. The most common woody plants were Arizona cypress, silverleaf oak, Arizona white oak, Emory oak (*Q. emoryi* Torr.), Arizona sycamore and alligator juniper (*Juniperus deppeana* Steud.).

At each of the three canyon sites, we established twenty 10-m-radius circular plots (0.03 ha), using a systematic sampling scheme, placing plots every 100 m along the linear, highly incised riparian–canyon habitat (Fig. 1). In cases where no cypresses occurred at a designated plot location or conditions were unsafe for sampling, we skipped to the next 100-m plot position. We recorded the location of each plot with a global positioning system unit. Using longitude and latitude, we derived raster environmental data from SRTM (Shuttle Radar Topography Mission) 1 arc-s (30-m resolution) digital elevation models (DEM) (https://earthexplorer.usgs.gov/, accessed

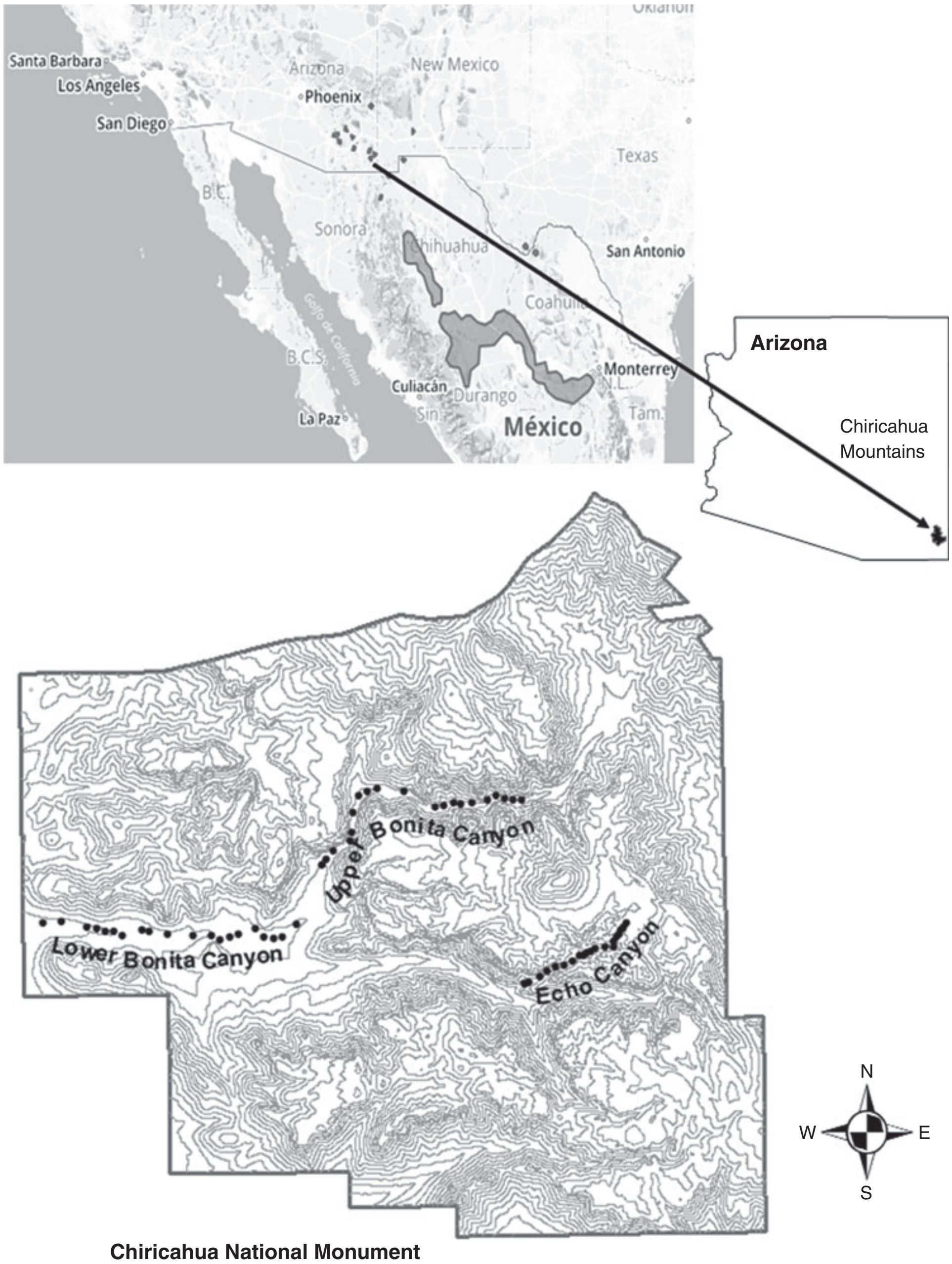

Fig. 1. Top: continental distribution of Arizona cypress (*Hesperocyparis arizonica*) (modified from Little 1971). Bottom: study area and plot locations in the three canyon study sites in Chiricahua National Monument, Chiricahua Mountains, Arizona, USA.

20 July 2018). To account for the difference in sample plot area and the 30-m resolution, we first smoothed raster data layers using a neighbourhood mean function with a 3×3 pixel neighbourhood size in the focal statistics operation in the spatial analyst toolbox of *ArcMap v10.3* (ArcGIS 2014). We then used the DEM data to generate (1) elevation (m), (2) slope (°), (3) incident solar radiation (W m^{-2}) over the entire year (at hourly intervals for the 15th day of each month of the year) using the ArcGIS solar radiation tool, and (4) a multiscalar terrain dissection index developed by Holden *et al.* (2011).

We determined fire severity for each plot, using the following categories: no fire – no evidence of char on trees; low severity – evidence of fire and mortality $<1/3$ of canopy trees of all species; moderate severity – evidence of fire and mortality 1/3–2/3 of canopy trees; and high severity – evidence of fire and mortality $>2/3$ of canopy trees. Remotely sensed fire severity data (e.g. differenced Normalized Burn Ratio (dNBR)) are available for CHIR, but the 30-m resolution is too coarse for the highly-incised creek locations of most of the plots. In a separate study on less-dissected terrain, we found a close

Table 1. Environmental differences among the three canyon areas

Differences in mean values (±1 s.e. in parentheses) among the three canyons for elevation (m), slope (degrees), multiscalar topographic dissection index (MSD), and annual solar radiation. Means that do not share a letter are significantly different ($P<0.01$, Tukey HSD test). ANOVA F values for differences among the three sites are shown (***, $P < 0.001$)

Values	Echo Canyon	Upper Bonita Canyon	Lower Bonita Canyon	ANOVA
Elevation	1952.1a (15.7)	1725.2b (11.7)	1593.6c (4.2)	246.6***
Slope	10.9a (1.1)	12.0a (0.8)	4.3b (1.5)	344.3***
MSD	5.2a (0.2)	3.9b (0.2)	3.9b (0.2)	15.8***
Solar radiation	1 764 159.5a (13893.8)	1 637 921.5b (18536.4)	1 672 514.0b (10420.8)	19.8***

correlation between the fire severity assessment used here and dNBR (Barton and Poulos 2018). Similar metrics to those used in the present paper have also been employed elsewhere (e.g. Chappell and Agee 1996; Larson and Franklin 2005).

At each plot, we determined the dominant vegetation cover type, using the following categories: open chaparral – shrub-sized woody plant cover ≤33%; closed chaparral – shrub-sized woody plants cover >33%; open woodland – tree-sized woody plants cover <33%; and closed woodland – tree-sized woody plants cover >33%. Based on living and dead mature trees, we also estimated the cover class for each plot for the pre-fire period before the Horseshoe Two Megafire.

For every cypress in the plot (live, standing dead, or dead and down with its former living base falling within the 10-m plot radius), we recorded whether it was alive or dead and measured its diameter at breast height (DBH) (for all stems ≥5 cm DBH). We used the number and basal area of dead Arizona cypress stems as a variable in some of the analyses, recognising that natural processes other than fire likely killed some of trees, especially in plots experiencing no and low-severity fire. The number of cypress seedlings was tallied within each plot, and we measured DBH for all post-fire seedlings ≥5 cm DBH.

Because 19 of the 60 plots had no Arizona cypress seedlings and 18 had no live cypress trees (i.e. strongly skewed data), we used non-parametric statistics (Wilcoxon signed-rank test, Kruskal–Wallis) for analyses using these variables as a dependent variable. We also used Kruskal–Wallis for the effect of fire severity on dead basal area and number of stems in order to use equivalent analyses for dead and live cypress as dependent variables. We used parametric statistics (one-way ANOVA, logistic regression) in cases where the data met the relevant assumptions of normality.

Results

The three canyons differed significantly in topography and annual incident solar radiation (Table 1). Echo Canyon, the highest-elevation location, and Upper Bonita Canyon, the next highest, did not differ in slope, but both were much steeper than Lower Bonita Canyon. Echo Canyon exhibited both higher terrain dissection and annual radiation than did the other two sites, which did not differ significantly for these two variables.

Of the 60 plots, 33 experienced high-severity fire, 6 moderate-severity fire, 10 low-severity fire and 11 did not burn. Compared with the other two sites, the Lower Bonita Canyon study area experienced a lower percentage of moderate- and high-severity fires (chi-square = 15.9, d.f. = 6, $P = 0.02$). For all 60 plots, the mean number of trees (≥5 cm DBH) killed by fire (or other causes) per plot was 6.1 (±1 s.e. = 0.7) or 194.2 per ha (±1 s.e. = 23.2); the number of cypresses surviving the fire was 3.1 (±1 s.e. = 0.5) per plot or 96.0 per ha (±1 s.e. = 15.4). We estimated that, on average, 65.9% (±1 s.e. = 4.9) of the pre-fire basal area was dead and 34.1% (±1 s.e. = 4.9) alive 7 years post fire. In plots that burned at moderate and high severity, the chance of survival in Arizona cypress increased with stem size (logistic regression: chi-square = 7.8, d.f. = 1, $P = 0.005$).

Tree basal area and the number of dead cypresses per plot were significantly higher in plots with higher rather than lower fire severity, whereas the opposite was true for live cypress basal area ($P < 0.01$; Fig. 2). The percentage of dead basal area corresponding to fire severity was as follows: high = 92.8% (±1 s.e.= 2.5), moderate = 60.2% (±1 s.e.= 9.5), low = 20.7 (±1 s.e.= 6.9), and none = 29.2% (±1 s.e.= 10.5). Plots subject to moderate- or high-severity fire were much more apt to transition from closed to open vegetation cover types (27 out of 29) compared with those that burned at low severity or not at all (0 out of 14 plots; chi-square = 31.2, d.f. = 1, $P = 0.0001$; Table 2).

Post-fire seedling establishment was variable: abundant in some plots but absent in others. For all plots, the mean number of cypress seedlings per plot was 9.2 (±1 s.e.= 2.0) or 292.8 per ha (±1 s.e.= 63.0). The number of cypress seedlings in a plot increased significantly with fire severity ($P < 0.05$; Figs 3, 4). Correspondingly, seedling establishment increased with dead cypress basal area and decreased with live basal area (Fig. 5*a* and b). This pattern also held for the number of dead and live cypress stems but was significant only for live trees (Fig. 5*c* and d). These relationships of seedling density with fire severity and dead and live Arizona cypress mature trees held for each of the canyons analysed separately. Seedling density was higher in plots with post-fire open vs closed cover types (Mann–Whitney U test, z = 3.32, $P = 0.0005$). As shown previously, open canopy plots were subject to higher fire severity and exhibited higher levels of dead cypress basal area.

Discussion

Our results confirm and extend past research suggesting that Arizona cypress regeneration is tied to wildfire, and especially to stand-replacing fire. We have shown that moderate- and

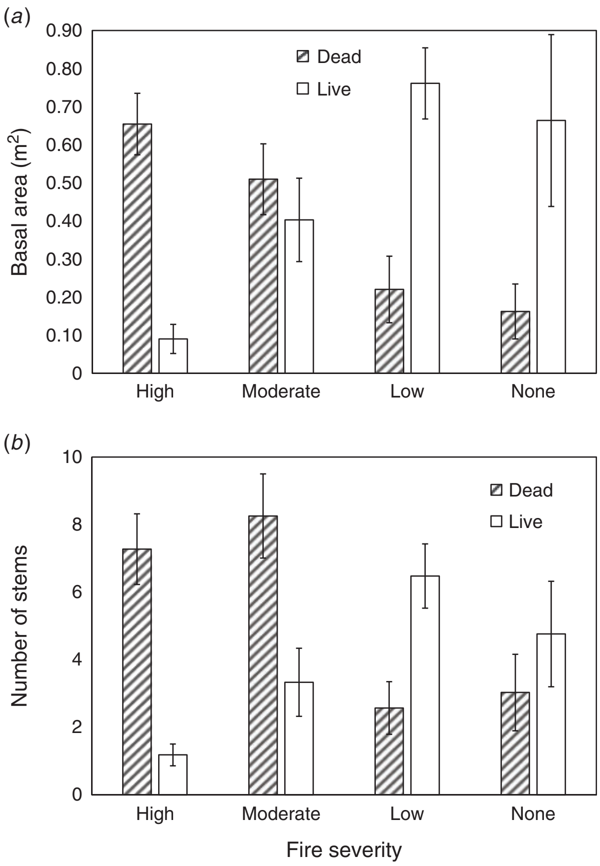

Fig. 2. Mean (±1 s.e.) for dead and live basal area (*a*) and number of stems (*b*) for Arizona cypress in relation to fire severity. Means within each combination (e.g. dead basal area) are statistically different (Kruskal–Wallis one-way analysis of variance, $P < 0.005$). Number of plots are as follows: 33 high-severity, 6 moderate-severity, 10 low-severity and 11 that did not burn.

Table 2. Cover types for plots before and after the fire

Number of plots for combinations of cover classes pre- and post fire (total = 60 plots). CW, closed woodland; OW, open woodland; OC, open chaparral; CC, closed chaparral

Pre-fire	Post fire	No fire	Low severity	Moderate severity	High severity
CW	CW	7	8	2	0
CW	OW	0	0	2	8
CW	OC	0	0	1	14
OW	OW	4	2	0	2
OW	OC	0	0	0	7
OW	CC	0	0	0	1
CC	OC	0	0	1	0

Fig. 3. Seedling establishment clustered around a fire-killed mature Arizona cypress. (Photo: Andrew M. Barton)

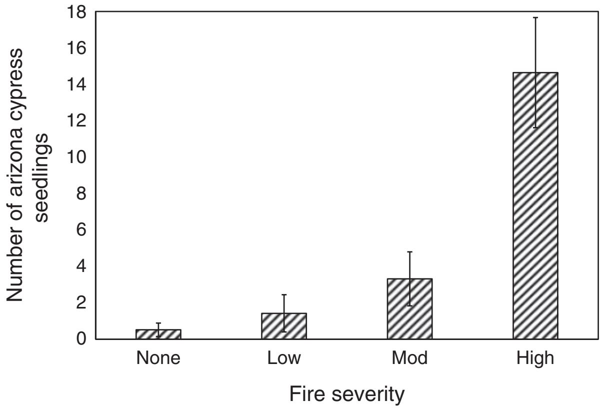

Fig. 4. Mean number (±1 s.e.) of Arizona cypress seedlings in relation to fire severity. Number of plots is given in the caption for Fig. 2. Means are significantly different across fire severity classes (Kruskal–Wallis one-way analysis of variance, $P < 0.0001$).

high-severity fire associated with the Horseshoe Two Megafire caused high levels of Arizona cypress morality, opened up the canopy and led to abundant seedling establishment, whereas post-fire tree regeneration was very low in sites that did not burn or experienced low-severity fire. Moderate- and high-severity fire very likely led to seedling establishment by releasing seeds from serotinous cones (Sullivan 1993), exposing mineral soil (Parker 1980*a*) and increasing incoming solar radiation for newly established seedlings (Vogl *et al.* 1977). The latter two environmental impacts have been documented in similar high-severity burn sites of the Horseshoe Two Fire in the Chiricahua Mountains (Barton and Poulos 2018). Our results, then, further

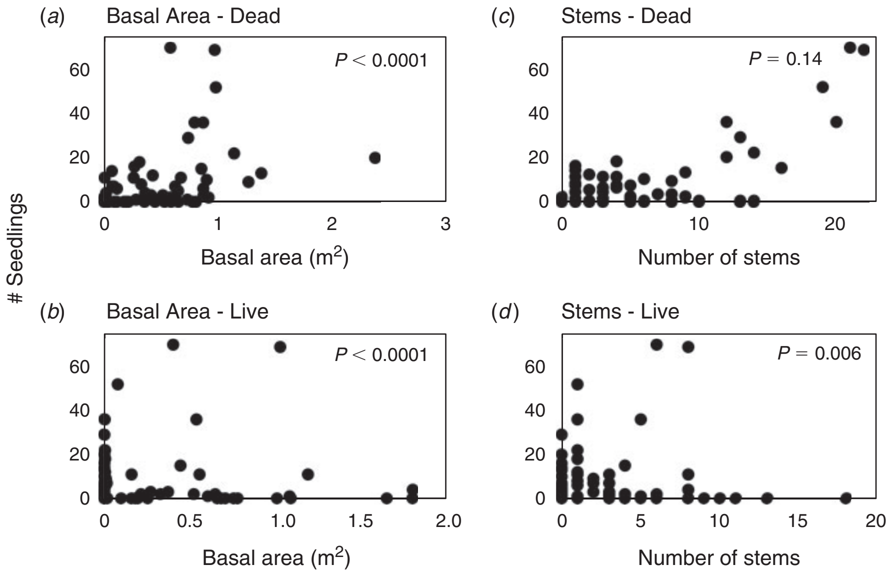

Fig. 5. Relationship of number of Arizona cypress seedlings to basal area and number of mature stems for dead and live cypress in 60 plots. *P* values are from Wilcoxon signed-rank test.

establish Arizona cypress as a long-lived, fire-sensitive but fire-embracing (Schwilk and Ackerly 2001) tree species dependent on high-severity fires or other disturbances for regeneration. The evidence presented here and elsewhere (e.g. Parker 1980*b*; Moir 1982) suggests strongly that Arizona cypress abundance would decline without fire.

Our results demonstrate that these population responses of Arizona cypress hold across a wide range of conditions, including in typical cypress habitat along permanent water courses in large, low-elevation canyons, but also in steep, drier, smaller, mid-elevation canyons. Although the three canyon study areas differed from one another with respect to topography, annual radiation, vegetation composition and likely the underlying availability of soil moisture resources, the effects of fire severity on seedling establishment, biomass of living and dead Arizona cypress, and canopy openness were consistent. The topographic distribution of Arizona cypress is broader than that encompassed by these three canyon sites both in the Chiricahua Mountains and elsewhere within its distribution range (e.g. Parker 1980*b*; Poulos *et al.* 2007; Poulos and Camp 2010), and it would be worthwhile for researchers to further examine variation in Arizona cypress stand dynamics in response to fire across this even wider continuum of conditions and geographical settings.

Successful regeneration of Arizona cypress after the Horseshoe Two Fire contrasts with that for pines at similar elevations in the Chiricahua Mountains. Barton and Poulos (2018; see also Barton 2002) found low levels of seedling establishment in Madrean pines (*Pinus discolor*, *P. leiophylla* and *P. engelmannii*) 5 years after the same fire event, especially in more xeric sites that burned at high severity. The lack of regeneration was attributed to the combined effects of severe fire and long-term drought. High levels of establishment of Arizona cypress compared with the pines probably does not stem from differences in drought tolerance. Like most Cupressaceae (e.g. Brodribb *et al.* 2010), Arizona cypress can be considered a xerophyte (Parker 1980*b*). The pines at similar elevations in the Chiricahua Mountains, however, exhibit high levels of drought tolerance (Barton and Teeri 1993), as well as distributions suggesting lower moisture demand compared with cypress (Wolf 1948; Little 1971; Parker 1980*b*).

Two alternative, non-mutually exclusive explanations for the difference in post-fire establishment between cypress and pines are worth further consideration. First, in five serotinous *Hesperocyparis* species in California, fire-related temperature treatments released enormous quantities of seeds (Milich *et al.* 2012), suggesting that seed pressure could be a possible post-fire regeneration advantage for Arizona cypress, although *P. leiophylla* exhibits semi-serotiny at the study site. Second, although their elevational ranges overlap, Arizona cypress typically occurs in more topographically sheltered sites with higher levels of moisture than do the pines, which may buffer juvenile cypress plants against the impacts of regional drought and extreme fire intensities. In fact, fire severity was generally lower and pine seedling establishment higher in such protected 'refugia' compared with more exposed sites (Barton and Poulos 2018).

The frequency of high-severity fires is increasing in the South-west USA (Westerling *et al.* 2006; Dennison *et al.* 2014; Abatzoglou and Williams 2016; Kent *et al.* 2017). Given the fire sensitivity of Arizona cypress, frequent, repeated high-severity fires could pose a threat to the long-term viability of these populations by preventing trees from reaching sexual maturity during inter-fire intervals, the positive effects of fire on establishment notwithstanding. This scenario has been verified for tecate cypress (*H. forbesii* Adams) in California by de Gouvenain and Ansary (2006), who found a positive growth rate for populations of this species only for more natural fire intervals of more than 40 years. Increased fire frequency, in fact, has been cited as one of the chief threats to the future of nearly all of the New World cypresses (Royal Botanic Garden of Edinburgh 2018). Terming it the 'interval squeeze,' Enright *et al.* (2015) argue that many woody plant species across the world may be confronted with the risk of slower growth rates combined with shorter fire-free intervals preventing regeneration in a drier, fiery world. The distributions of New World cypresses, like Arizona cypress, contracted significantly with the advent of drier, hotter conditions in the Holocene. A crucial conservation question today is the extent to which these relict species face further narrowing of refugia from increasing drought and fire frequency.

Conflicts of Interest

The authors declare no conflicts of interest.

Acknowledgements

We sincerely thank Michael Freiburger, Hunter Vannier and Isaiah Wilson–McFarlane for their dedication and good humour as field assistants. We are grateful to the staff of CHIR for logistical support, including resources managers Mike Holt and Hellen Fitting, and to the National Park Service (Task Agreement no. P17AC00940), Wesleyan University's College of the Environment, and the University of Maine at Farmington for funding. We appreciate the efforts of two reviewers, who provided excellent suggestions for improving the manuscript.

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