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# Introduction

## Research questions

# Methods

## Study area

We surveyed aspen seedling regeneration across forests that burned in the Cameron Peak Fire located in northern central Colorado (Fig. ). Over the period from August to December 2020, the Cameron Peak Fire burned 845 square kilometers ([MTBS Project 2022](#ref-mtbsproject2022)). The fire burned across a wide gradient of elevation ranging from about 1616 to 3618 meters above sea level. Approximately 62% of the fire burned at moderate to high severity.

Typically, the study area experiences warm summers (1991-2020 mean July daily maximum temperature: 23.5°C), cold winters (1991-2020 mean January daily minimum temperature: -11.1°C), and moderate amounts of precipitation (1991-2020 mean total annual precipitation: 551.7 mm) ([PRISM Climate Group 2021](#ref-prismclimategroup2021)). Notably, the study area received about 10% more precipitation in the two years following fire then then 1991-2020 normal ([PRISM Climate Group 2021](#ref-prismclimategroup2021)).

Pre-fire forest composition and structure within the Cameron Peak burn scar varied with elevation. Lower elevation zones below 2800 m were characterized by dry and mesic montane forests, dominated by ponderosa pine (*Pinus ponderosa*), with lesser components of Douglas-fir (*Pseudotsuga menziesii*). Moderate and higher elevation stands between approximately 2800 – 3300 m were made up of subalpine forest, dominated by Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*). Only about 3% of the area burned was dominated by aspen prior to fire, most (~80%) of which occurred between 2252 and 2880 m in elevation (Fig. ). About 38% of the aspen forest burned at high severity.

## Study sites

We surveyed 34 sites in the summer of 2022 (Fig. ). All sites were selected so that the

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**Figure** **:** The study area

## Field data collection

At each site, we recorded the coordinates, elevation, slope, aspect, and pre-fire tree-species composition. We then established two perpendicular 2 x 50 m transects that intersected at the midpoint. We tallied the presence of all conifer seedlings, aspen seedlings, and aspen root suckers within each transect and recorded their location along the transect within 2 x 2m subplots. Aspen seedlings were differentiated from root suckers using methods outlined by Kreider et al. ([2020](#X44bfc23e7c771928f103170a5120f8dbe5a4826)), which have been demonstrated to be more than 95% accurate ([Kreider and Yocom 2021](#Xb37a08252af320b6a65b3f38a24c3f3726e41e1)) and were shown to be effective in our study area ([Carter et al. 2024](#X518c5e11f1226b7f0686c896ea7fda75925f525)). For aspen seedlings and suckers, we additionally measured height and recorded the presence or absence of any browsing damage.

To better understand how microsite conditions may influence aspen seedling establishment, we additionally recorded microsite characteristics for all aspen seedlings. We recorded information on susbtrate, microtopographic conditions (Flat, Slope, Concave, or Convex) within 2.5 cm of seedling (hereafter ‘small microtopography’) and within 50 cm of seedling (hereafter ‘large microtopography’), presence or absence of small (diameter = 2.5-10 cm) and large (diameter >10 cm) coarse woody debris (CWD) within 10 cm of seedling, and distance to the nearest aspen sucker when suckers were present within 50 m. To understand if seedlings preferentially established in certain microsite conditions, we also collected microsite conditions at 5 meter intervals along each transect.

## Post-fire establishment within the Cameron Peak Fire

## Environmental drivers of post-fire aspen seedling establishment

## Microsite drivers of aspen seedling establishment

To understand if aspen seedlings preferentially established in different microsite conditions, we followed the approach outlined by Kreider and Yocom ([2021](#Xb37a08252af320b6a65b3f38a24c3f3726e41e1)). Briefly, we first modeled the probability that aspen seedlings occur in each category of the predictor variable using a mixed effect multinomial logistic regression. We then modeled the probability that systematically surveyed points occurred in each category of the variable. We used these two models to quantify microsite preference following methods outlined by Krieder and Yocom (2021) .

Here, preference values greater than zero indicate seedlings established in that microsite condition more often than expected. Multinomial regression was performed in R (R Core Team 2024) using the mclogit package (Elff 2022).

## Leading indicators of recruitment

# Results

## Post-fire establishment within the Cameron Peak Fire

Despite the absence of mature aspen in the pre-fire stand, aspen seedlings were present at 62% of sites (n=21 sites; Fig. ). Across plots with aspen seedlings, density averaged 2310 seedlings per hectare, but was highly variable and ranged between 100 and 15700 seedlings per hectare. Within plots with aspen seedlings, on average only 12.1% of the fifty 2 x 2 m subplots contained seedlings (mean:6 subplots; range=1 - 30 subplots). Within subplots with aspen seedlings, we observed between 0.25 and 6.5 seedlings per square meter (mean=0.95 seedlings per square meter). While all sites lacked mature aspen prior to the fire, we observed aspen suckers at 1 site.

Post-fire conifer regeneration was limited two years following fire (Fig. ). Conifer seedlings were found at 59% of plots, with a mean density of 429 seedlings per hectare. Within plots with conifer seedlings, on average only 9.2%of the fifty 2 x 2 m subplots contained seedlings (mean=4.6 subplots; range=1 -21 subplots). Within subplots with conifer seedlings, we observed between 0.25 and 2 seedlings per square meter (mean=0.4 seedlings per square meter). Lodgepole pine seedlings were most common and were present at 47% of sites, nearly all of which had lodgepole pine in the pre-fire community. When lodgepole seedlings were present, density averaged 768.8 seedlings per hectare (range:100 -2700 seedlings per hectare). While subalpine fir and Engelmann spruce were common at our study sites prior to fire, we found very limited regeneration of either species. Subalpine fir regeneration occurred at one site with a density of 300 seedlings per hectare. Engelmann spruce regeneration occurred at 3 sites and when present averaged 400 seedlings per hectare (range=100 - 800 seedlings per hectare). Prior to the fire, ponderosa pine was present at 7 sites and of these sites we found ponderosa pine seedlings at 3 sites with an average density of 267 seedlings per hectare (range:100 - 500 seedlings per hectare). Finally, Douglas fir was present at 2 sites prior to the fire, but absent from all sites following fire (Fig. ).

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**Figure** **:** Patterns of post-fire establishment by pre-fire composition.

## Environmental drivers of post-fire aspen seedling establishment

Our model correctly predicted 81% of the sites where aspen seedlings were observed (17 of the 21 sites without aspen seedlings), but only 46 % of the absences (6 of the 13 sites without aspen seedlings).

Overall, our model explained about 72 % of the variation in seedling density across the plots.

**Table** **:** Summary of zero-inflated negative binomial model results for absence (zero model) and abundance (count model) of post fire aspen stems. Model results are standardized beta coefficients, standard errors (SE), z scores, and p values.

| Model | Predictor | Estimate | SE | z | p |
| --- | --- | --- | --- | --- | --- |
| Zero model | Intercept | -0.554 | 0.386 | -1.434 | 0.152 |
| Zero model | Elevation | -0.798 | 0.404 | -1.974 | 0.048 |
| Count model | Intercept | 7.261 | 0.261 | 27.848 | 0.000 |
| Count model | Conifer density | 0.615 | 0.236 | 2.603 | 0.009 |

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**Figure** **:** Patterns of post-fire establishment by pre-fire composition.

![](data:application/octet-stream;base64,)

**Figure** **:** Microsite preferences

## Leading indicators of potential recruitment

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**Figure** **:** Patterns of post-fire establishment by pre-fire composition.

## Browsing

Across our study sites, only 18% of seedlings had visible evidence of browsing (n= 86 seedlings). Nonetheless evidence of browsing was present at 57% of sites with aspen seedlings (n= 12 sites).

When browsing occurred within a site, on average 29% of seedlings were browsed (range: 5 - 58%). Within subplots with browsing, on average 46% of seedlings within a subplot were browsed (range: 5 - 100%). At both the site and subplot level, the proportion of seedlings browsed increased with aspen seedling density, however these effects were only significant at the subplot level.

# References

Carter, S., S. Hart, C. Rhoades, and M. Rocca. 2024. [Occurrence, distribution, and driving environmental factors of quaking aspen regeneration by seed in the cameron peak fire burn scar](https://api.mountainscholar.org/server/api/core/bitstreams/14cc73e5-8e74-42f2-b414-45e877ef91c0/content).

Kreider, M. R., K. E. Mock, and L. L. Yocom. 2020. [Methods for Distinguishing Aspen Seedlings from Suckers in the Field](https://doi.org/10.1093/jofore/fvaa030). Journal of Forestry:fvaa030.

Kreider, M. R., and L. L. Yocom. 2021. [Aspen seedling establishment, survival, and growth following a high-severity wildfire](https://doi.org/10.1016/j.foreco.2021.119248). Forest Ecology and Management 493:119248.

MTBS Project. 2022. [MTBS data access: Burned area boundaries dataset](https://mtbs.gov/direct-download).

PRISM Climate Group. 2021. [Monthly 30-year climate normals (1981-2010)](https://prism.oregonstate.edu/normals/).

# Supplementary Material

**Table** **:** Summary of zero-inflated negative binomial model selection results for the zero and count parts of the model.

| Predictor | Model | AIC | likelihood ratio Chi-squared statistic | p |
| --- | --- | --- | --- | --- |
| Full model | Zero model | 411.0 |  |  |
| Elevation | Zero model | 413.9 | 4.9 | 0.027 |
| Aspect | Zero model | 410.8 | 1.8 | 0.185 |
| Slope | Zero model | 409.5 | 0.5 | 0.470 |
| Herb | Zero model | 410.3 | 1.3 | 0.263 |
| Conifer | Zero model | 410.1 | 1.1 | 0.287 |
| Full model | Count model | 406.3 |  |  |
| Elevation | Count model | 405.0 | 0.7 | 0.410 |
| Aspect | Count model | 404.3 | 0.0 | 0.881 |
| Slope | Count model | 404.4 | 0.1 | 0.754 |
| Herb | Count model | 405.4 | 1.1 | 0.298 |
| Conifer | Count model | 408.6 | 4.3 | 0.037 |

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**Figure S****:**