



ORIGINAL RESEARCH

Open Access



# Sexual and vegetative recruitment of trembling aspen following a high-severity boreal wildfire

Denyse A Dawe<sup>1\*</sup>, Ellen Whitman<sup>1</sup>, Michael Michaelian<sup>1</sup>, Alan J. Tepley<sup>2</sup> and Marc-André Parisien<sup>1</sup>

## Abstract

**Background** High-severity fire is rare in trembling aspen-dominated forests of the boreal region. The post-fire recruitment strategy of aspen, by either vegetative suckering or sexually (i.e., by seed), has considerable implications for subsequent forest structure, genetic diversity, and ecological resilience to shifting climatic and disturbance regimes. In this study, we take advantage of the unique opportunity provided by the Chuckegg Creek Wildfire (310,000 ha) in northern Alberta, Canada, which burned at high severity through aspen stands before and after spring green-up, to document how phenology, fire severity, and stand characteristics affect recruitment one year following the fire.

**Results** We found sites were dominated either by high-density patches of seedlings or a fairly uniform density of suckers, with few sites occupied by both. Sites dominated by seedlings burned predominantly after green-up. Using boosted regression trees, we found that surface fire severity best predicted both aspen seedling and sucker density at sites. Seedlings were favoured at sites that burned at high surface severity and after spring green-up, whereas suckering density was highest at sites that burned at moderate-high surface severity before green-up.

**Conclusion** Our research highlights the influence of surface fire severity and phenology on aspen recruitment. High fire severity, particularly after aspen green-up, reduced suckering while promoting seedling recruitment. Aspen seedlings filled the recruitment gap caused by this lowered, suckering response, providing an alternate route for aspen forest adaptive capacity after high-severity surface fire.

**Keywords** Boreal forest, *Populus tremuloides*, Post-fire recruitment, Seedlings, Suckering, Trembling aspen

## Resumen

**Antecedentes** Los fuegos de alta severidad son raros en bosques dominados por el álamo temblón (*aspen* en idioma inglés) en la región boreal de Canadá. La estrategia de reclutamiento post-fuego de este álamo, ya sea por rebrote vegetativo o por vía sexual (i.e. por semillas), tiene considerables implicancias para la futura estructura del bosque, la diversidad genética, y la resiliencia ecológica en regímenes climáticos y de disturbios cambiantes. En este estudio, aprovechamos la oportunidad única provista por el incendio de Chuckegg Creek (310.000 ha) en el norte de Alberta, Canadá, que quemó a alta severidad rodales de álamos antes y después del crecimiento y rebrote primaveral, para documentar cómo la fenología, la severidad del incendio, y las características de cada rodal afectaron el reclutamiento un año luego del incendio.

\*Correspondence:

Denyse A Dawe

denyse.dawe@nrcan-mnca.gc.ca

Full list of author information is available at the end of the article

**Resultados** Encontramos sitios que estaban dominados tanto por parches de alta densidad de plántulas o por una densidad uniforme de rebrotes, con muy pocos sitios ocupados por ambas formas de regeneración. Usando el algoritmo de árboles de predicción (i.e. *boosted regression trees*), encontramos que la severidad superficial fue el mejor predictor de la densidad tanto de plántulas como de rebrotes en los sitios. Las plántulas fueron favorecidas en los sitios que quemaron a alta severidad y luego del reverdecimiento de primavera, mientras que la densidad de los rebrotes fue mayor en los sitios que quemaron a moderada-alta severidad antes de ese reverdecimiento primaveral.

**Conclusión** Nuestra investigación subraya la influencia de los fuegos superficiales de alta severidad y de la fenología sobre el reclutamiento del álamo temblón. Los fuegos de alta severidad, particularmente luego del reverdecimiento primaveral, reducen el reclutamiento por rebrote, mientras que promueven el reclutamiento de plántulas nacidas de semillas. Las plántulas de álamo llenan los claros de regeneración causados por esta respuesta baja del rebrote, proveyendo de una ruta alternativa en la capacidad adaptativa del álamo temblón luego de fuegos superficiales de alta severidad.

## Background

Disturbance patterns in western Canada's trembling aspen (*Populus tremuloides* Michx.) forests are shifting, driven by a complex interplay of climatic and ecological factors (Worrall et al. 2013). In these forests, wildfires, droughts, and outbreaks of insects and other forest pathogens are responding to rapidly changing climate (Hogg et al. 2008, Michaelian et al. 2011, Nesbit et al. 2023). Warmer and drier conditions over western North America in the coming decades (Peng et al. 2011; Boulanger et al. 2014) are expected to amplify fire frequency, drought-induced dieback and mortality, and susceptibility to damage by insects and diseases in aspen-dominated areas (Volney and Hirsch 2005, Price et al. 2013). As the most widespread tree species in western North America, these changes to aspen health and productivity will influence the ecosystem services aspen forests provide, such as carbon sequestration and biodiversity, as well as affecting regional economies that depend on the timber industry (David et al. 2001; Kurz et al. 2013; McCullough et al. 2013).

The increasing occurrence of extreme fire weather driven by climatic shifts has led to intensified fire activity in aspen stands (Wang et al. 2015; Nesbit et al. 2023). Aspen-dominated stands are traditionally considered "firebreaks", as they either stop or slow down wildfires, thus making them easier to suppress (Fechner and Barrows 1976). Although aspen stands in the Canadian boreal forest are more flammable during the "spring window"—the period after snowmelt but before leaf flush—aspens forest flammability decreases drastically once leaves emerge in both the canopy and understory (hereafter, "green-up") (Parisien et al. 2023). This period is marked by an increase in stand foliar moisture, lower air temperature, higher relative humidity, and reduced drying of the duff and other understory fuels due to the shading of the leafy canopy, which limits insolation and wind exposure (Alexander 2010; Nesbit et al. 2023).

Extreme fire weather conditions do occasionally allow fire to burn in greened up aspen forests. This was exemplified by the 2019 Chuckegg Creek Fire, which ignited during the spring window and continued to burn into the post-green-up period, burning 310,000 ha of mostly aspen-dominated forest in northern Alberta.

Trembling aspen, a clonal species, responds to fires by recruiting either asexually, by vegetative regeneration from roots (hereafter, "suckering"), or sexually, by seed. Typically, a wildfire that causes the mortality of mature aspen stems will trigger a considerable suckering response from the aspen clone (Frey et al. 2003). Suckering allows aspen to use energy reserves within the root system to quickly recolonize a site (Perala 1990), providing a distinct competitive advantage following a disturbance (Greene et al. 1999). As a result, aspen clones can be remarkably long-lived, with documented clones in western Canada having persisted for thousands of years (effectively since glaciation, or longer in non-glaciated areas) (Kemperman and Barnes 1976; Jelinski & Cheliak 1992; Ally et al. 2010).

Compared to suckering, recolonization of aspen by seedlings is assumed to be an uncommon occurrence, though there are notable examples of seeding events, particularly across the Intermountain West (Turner et al. 2003; Kreider and Yocom 2021). As a result, documentation of sexual reproduction in aspen has been the subject of comparatively fewer studies than those focused on asexual reproduction (Landhäusser et al. 2019). Despite its relative rarity, sexual reproduction offers a distinct advantage over suckering by increasing genetic diversity (Gill et al. 2017). The resilience afforded by this diversity is crucial for adaptation to changing climate and disturbance regimes, as locally persistent clones may be maladapted to future environmental conditions (Jelinski & Cheliak 1992).

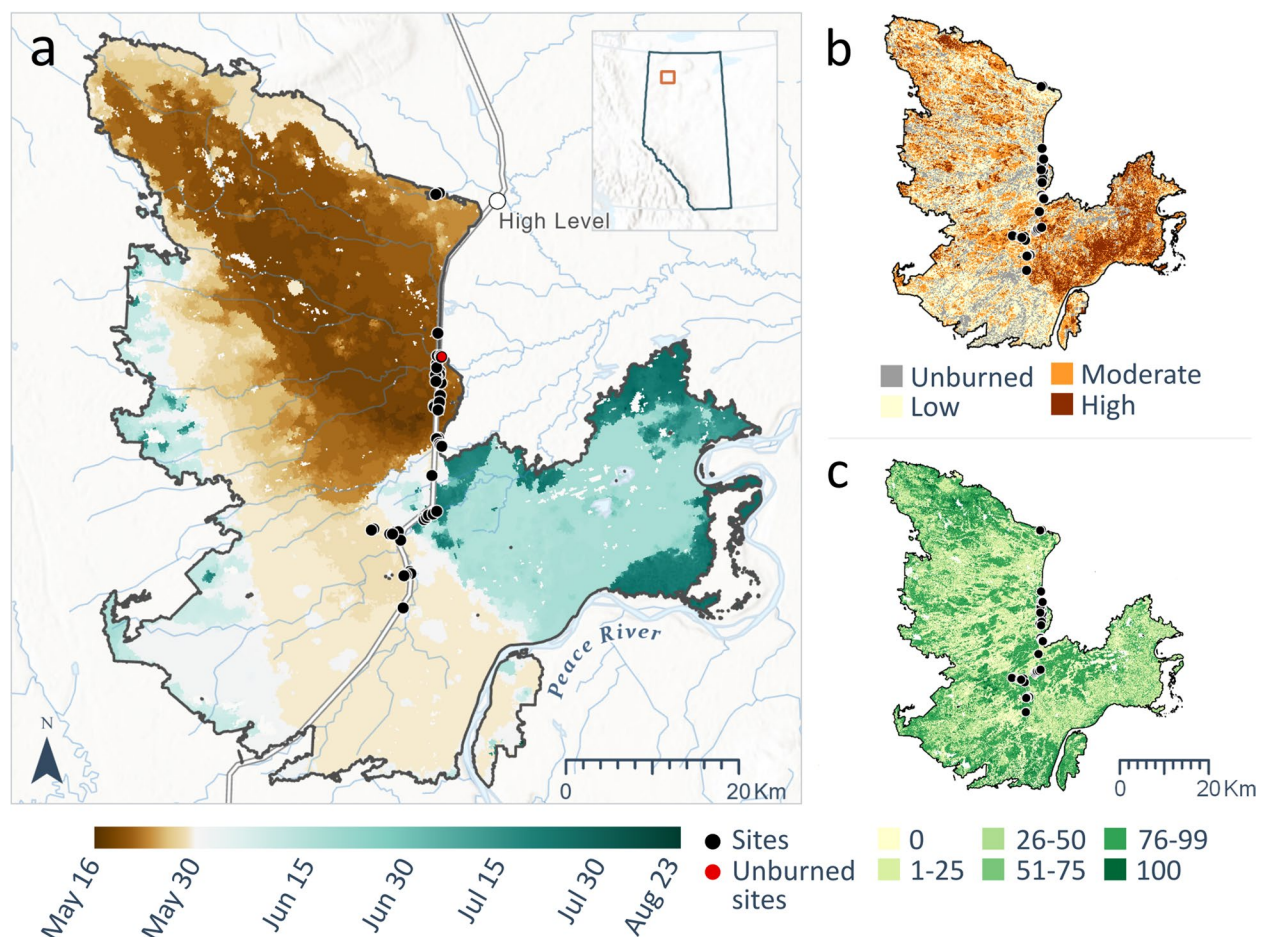
Although wildfires in aspen forests are becoming more common, opportunities to study the recruitment

dynamics of a fire that burned primarily aspen forest remain rare. In this study, we examine the effect of environmental factors affecting aspen sexual and asexual reproduction following a large, high-severity fire in the boreal forest of western Canada. Specifically, we examine (1) the extent to which aspen reproduced by seeds or suckering after the Chuckegg Creek Fire and (2) how phenology, forest stand, and fire severity characteristics are associated with these two recruitment mechanisms. We achieved these objectives by surveying aspen recruitment, forest structure, and fire severity metrics in 46 sites 1 year after the Chuckegg Creek Fire. We then used boosted regression tree models to explore how seedling and suckering recruitment density responded to these pre-fire forest and fire severity variables. We discuss our results in the context of future disturbance regimes and climatic conditions in the western boreal forest of North America.

## Methods

### Study area

Our study was conducted in the 2019 Chuckegg Creek Fire, in northern Alberta, Canada (Fig. 1), which is located partly in the Dry Mixedwood Natural Subregion, with the northeast portion of the fire burning through the Central Mixedwood Natural Subregion (Natural Regions Committee 2006). This area is characterized by upland aspen forest and scattered white spruce (*Picea glauca* (Moench) Voss), with interspersed lowland bogs and fens dominated by black spruce (*Picea mariana* (Mill.) B.S.P.) and tamarack (*Larix laricina* (Du Roi) K. Koch), respectively (Natural Regions Committee 2006). Soils in upland sites are predominantly Luvisols or Gleysols, with lowland sites associated with Gleysols or Organic soils (Soil Classification Working Group 1998). The mean annual precipitation is 430 mm, with a mean warmest month temperature of 16 °C and mean coldest



**Fig. 1** Fire and fuel characteristics of sites (black points) sampled within the 2019 Chuckegg Creek Fire perimeter. **a** Day of burning. **b** Burn severity from the differenced normalized burn ratio (dNBR; Hall et al. 2008). **c** Percent deciduous forest (Guindon et al. 2024). Panel **a** provides the location of the two unburned plots east of the fire perimeter

month temperature of  $-19^{\circ}\text{C}$  (climate normal period 1981–2010, Wang et al. 2016). Three sites within the burn perimeter from the Climate Impacts on Productivity and Health of Aspen (CIPHA) monitoring plot network (Hogg et al. 2005) show that the area experienced defoliation by forest tent caterpillar (*Malacosoma disstria*) in the mid-2000s, which led to a peak annual mortality rate of 15% in 2005 and 2006. Defoliation levels were relatively low in the 10 years prior to the Chuckegg Creek Fire (annual mortality of  $\sim 7\%$  by the last pre-fire measurement year of 2018) (M. Michaelian, unpublished data). Sites have generally experienced declining moisture levels, as measured by the Climate Moisture Index (CMI) since they were established in 2000 (Wang et al. 2016).

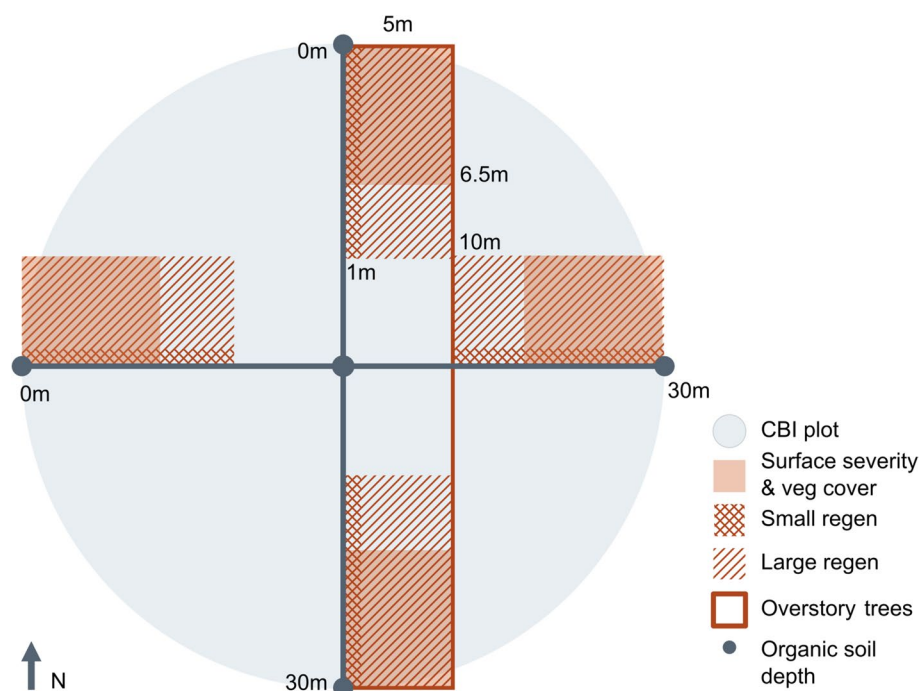
The Chuckegg Creek Fire ignited from lightning on May 12, 2019, under abnormally dry and windy conditions preceded by a 3-year drought (MNP LLP 2020). These extreme weather conditions resulted in two periods of rapid spread. The first occurred between May 17th and 20th, during which the fire advanced 25 km and expanded from 2,300 ha to over 71,400 ha (Fig. 1). On May 29th, the fire made a 30-km run overnight, spotting more than 1 km across the Peace River, along with burning through the Paddle Prairie Métis settlement, destroying 16 homes, and spreading an additional 80,000 ha (MNP LLP 2020). The initial periods of extreme spread occurred before green-up; however, the fire continued to

burn after aspen leaf-out. In total, the Chuckegg Creek Fire burned nearly 310,000 ha of predominantly aspen-dominated forest (Fig. 1).

#### Field methods and data sources

We examined 46 aspen-dominated sites burned by the Chuckegg Creek Fire in August of 2020, 1 year after the fire. Site selection was guided by an initial random sample of sites across a range of potential fire severity, as mapped by the differenced normalized burn ratio (dNBR) (with classification breaks as in Hall et al. 2008). We then refined site selection using on-site assessments of fire severity, as remotely sensed indices of fire severity tend to have lower performance in northern deciduous forests than in other forest types (Holsinger et al. 2021). Three of these sites had been previously sampled by the CIPHA monitoring plot network (Hogg et al. 2005), providing a small sample of detailed pre-fire data. In addition, we sampled two unburned aspen-dominated sites outside of the Chuckegg Creek perimeter to assess baseline recruitment density for the area. Plots were at least 100 m from a road (with one exception 60 m from a minor roadway; mean distance to road 309 m), as well as from each other (minimum inter-plot distance of 115 m).

At each site, we established two perpendicular  $30 \times 5$  m belt transects oriented in the main cardinal directions and intersecting at 15 m (Fig. 2). Within the north–south transect, we recorded the species, diameter at breast



**Fig. 2** Sampling design used to assess post-fire recruitment, fire severity, and forest characteristics at each site



height (DBH), mortality status (live, dead-killed by fire, dead before fire), and fire scorch height of every tree with a  $\text{DBH} \geq 7$  cm. Trees dead before fire (abbreviated DPF in variables) were differentiated by the degree of scorch on the boles, as trees that were dead before a fire tend to experience more severe scorching. When more than 20 trees were present within the transect, we measured the first twenty trees encountered and recorded the total area surveyed. In addition, at each site, we collected tree cores from three large aspen that were alive before the Chuckegg Fire to determine an approximate time since the last major disturbance, a variable considered in model formulation. As nearly all cores were aged to the early 1940s, stand age was considered to be relatively homogenous and was not used in models (Supplemental Table S1).

We differentiated our search for post-fire tree recruitment by two height classes to account for differences in stem density and necessary search effort: small recruits ( $< 1.3$  m) and large recruits ( $\geq 1.3$  m with  $\text{DBH} < 7$  cm). These height and DBH thresholds were selected for consistency with the CIPHA monitoring plot network sampling methods (M. Michaelian, personal communication), as three CIPHA sites were remeasured in this work. Large recruits were measured in four, 5 m-wide, variable-length belt transects at the ends of each larger 30-m transect until a minimum of 10 live aspen were tallied (at which point, the area searched was recorded) or a transect length of 10 m was surveyed (Fig. 2). Small recruits were measured in four, 1 m-wide, variable-length transects. In these transects, we concluded our search after 20 live aspen were measured or we reached the plot length of 6.5 m. For both size classes, we also recorded the dead aspen stems and individuals of other species encountered. For each individual in the small recruit height class, we used the methods of Kreider et al. (2020) to determine if the stem had originated from suckering or seed. In contrast, all large recruits were assigned to the “sucker” class, as it can be safely assumed that only

suckers would have access to energy supplies via the larger genet to grow to the large size class within 1 year (Frey et al. 2003, Kreider et al. 2020).

We assessed in-stand fire severity using three metrics. First, we measured surface fire severity in four  $6.5 \times 5$  m plots (Fig. 2) located at each extremity of the 30-m transects using the surface burn severity index (BSI) (Loboda et al. 2013; Whitman et al. 2018). These measurements were averaged for each site and span values of 0 (unburned) to 4 (mineral soil exposed) (Table 1). Second, at the end of each 30-m transect and in the centre of the plot, we measured the residual organic soil depth (OSD) (five measurements, averaged per site). Finally, we assessed fire severity across forest strata using the Composite Burn Index (CBI; Key and Benson 2006) within a circular 30-m diameter plot, using height thresholds modified for northern forests (Kasischke et al. 2008) (Fig. 2). Similarly to BSI, CBI values are expressed in a range where 0 is unburned and 3 is severely burned (Table 1).

To examine the impact of aspen phenology on recruitment, we used a daily fire spread map from the Canadian Fire Spread database, in which fire progression is interpolated from daily fire detections (Barber et al. 2024; Fig. 1a). The daily fire spread perimeters were used to determine whether each site had burned before or after green-up. We determined that green-up occurred within the first 2 weeks of June (a time period in which none of our sites burned) through a combination of consultation with fireline personnel working on the Chuckegg Creek Fire and exploration of historical green-up timing based on binary daily MODIS NDVI grids, with a cell considered greened-up after reaching 70% of its historical maximum, as per Erni et al. (2020).

### Analysis

We explored the relationship between post-fire aspen recruitment and metrics related to phenology, forest

**Table 1** Predictor variables used in recruitment models

Predictor	Description	Mean	SD	Min	Max
BA DPF aspen	Basal area aspen dead prior to fire ( $\text{m}^2 \text{ha}^{-1}$ )	3.3	3	0	13.2
BA fire-killed aspen	Basal area aspen killed by fire ( $\text{m}^2 \text{ha}^{-1}$ )	27.6	11.9	6.8	69.2
BA live aspen	Basal area aspen not killed by fire ( $\text{m}^2 \text{ha}^{-1}$ )	2.9	8.2	0	38.7
Burn severity index (BSI)	Measurement of surface fire severity. Values range from 0 (unburned) to 4 (mineral soil exposed)	3.2	0.8	1.3	4
Composite burn index (CBI)	Measurement of fire severity across forest strata. Values range from 0 (unburned) to 3 (high severity)	2.2	0.3	1.4	2.7
		# sites leafless		# sites green	
Green-up	Indication of whether the stand had greened up prior to burning (categorical)	39		7	

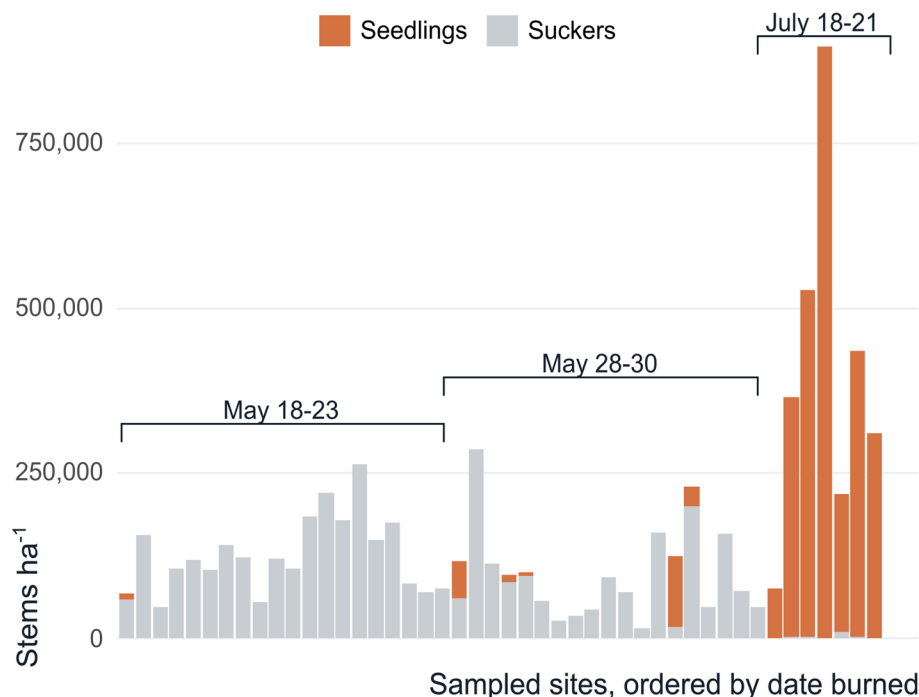
structure, and wildfire severity with boosted regression tree models. Two main models were produced using the following dependent variables: (1) seedling density and (2) sucker density, with a third, all recruits (i.e., combined density of seedlings and suckers), included in the Supplementary Materials (Supplemental Figs. S2 & S3). Specific predictive variables included in all model formulations are provided in Table 1. Variables considered for modelling, but ultimately excluded to simplify model formulation, are reported in Supplemental Table S1, whereas correlation among variables retained in models are presented in Supplemental Fig S1. Variables were selected using a combined approach of prioritizing variables relevant to the study questions (i.e., those representing phenology, forest structure, and fire severity), while eliminating variables consistently unimportant in model formulation, with limited variation across sites to provide predictive power, or with elements redundant to other variables, to simplify the total predictor set (Elith et al. 2008).

All models were processed in the R statistical environment (version 4.2.2; R Core Team 2022) using the caret (Kuhn et al. 2022) and xgboost (Chen et al. 2022) packages. We used the hyperparameter tuning strategy for stochastic gradient-boosted machines documented in Boehmke and Greenwell (2020); hyperparameters used in tuning, along with optimal hyperparameters selected

are provided in Supplemental Table S2. To account for our small sample size, we used tenfold cross-validation, repeated 5 times, with early stopping set to 50 rounds to improve model accuracy and reduce overfitting (Boehmke and Greenwell 2020). Variable importance and partial dependence information used to plot model outputs were extracted using the caret and pdp (Greenwell 2017) packages, respectively.

## Results

Aspen recruitment in the year following the Chuckegg Creek Fire was prolific and varied among the sites surveyed from 14,615 to 896,666 stems  $\text{ha}^{-1}$  (mean 158,117 stems  $\text{ha}^{-1}$ ) (Fig. 3). Aspen recruitment was greatest at sites that burned later in the progression of the Chuckegg Creek Fire (Fig. 3). At these sites, recruitment was strongly dominated by seedlings and was typically higher than that observed in the sites dominated by suckers (an average of 365,159 vs. 110,556 stems  $\text{ha}^{-1}$ , respectively). However, recruitment dominated by suckering was far more common, occurring at 83% of sites. Post-fire recruitment density was much greater than recruitment density at unburned sites; mean stem density (stems < 7 cm DBH) at the two unburned sites surveyed during the summer of our work was 769 stems  $\text{ha}^{-1}$  and was 604 stems  $\text{ha}^{-1}$  at the three CIPHA sites which had been surveyed the year prior to burning in



**Fig. 3** Density of seedlings and suckers at each site, presented in order of when the site burned in the Chuckegg Creek Fire. Clusters of dates during which sites burned are presented above the data

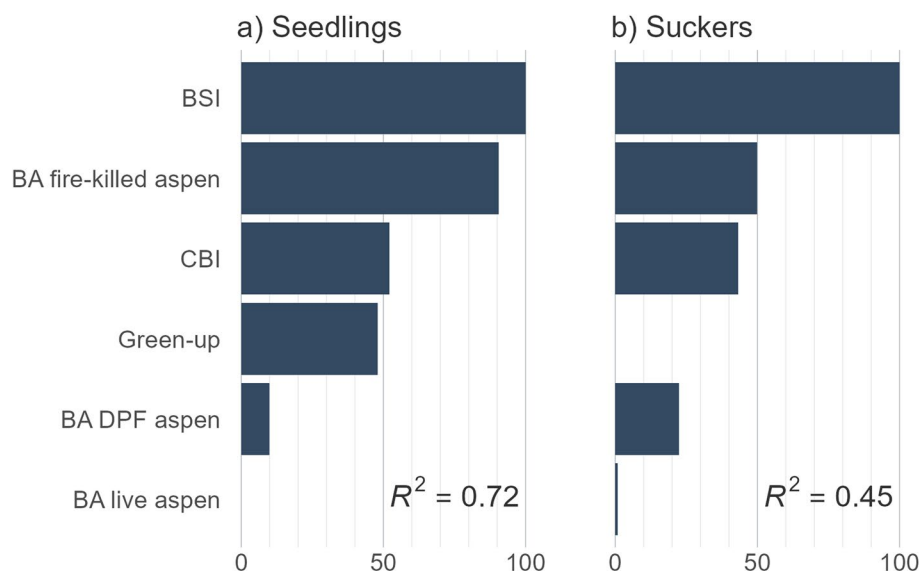
2018 (Supplemental Fig. S4). No coniferous seedlings were found, aligning with the rarity of mature white spruce (*Picea glauca*) within the aspen-dominated stands burned by the Chuckegg Fire. Mature white spruce was found at eight of our sites (max and mean basal area of overstory white spruce of  $1.5 \text{ m}^2 \text{ ha}^{-1}$  and  $0.13 \text{ m}^2 \text{ ha}^{-1}$ , respectively, Supplemental Table S1).

Seedling and suckering stem density were predicted by nearly the same variables (Fig. 4), although their relationship to each variable differed (Fig. 5). BSI was the most important predictor of stem density for both recruitment models (Fig. 4). Seedlings were predicted to be found at high density at sites with high surface fire severity ( $> 3.5$  BSI) (Fig. 5a). In contrast, suckering response to surface fire severity was roughly bimodal, with highest predicted stem density for low ( $< 1.8$  BSI) and moderate (2.4–3 BSI) severity and lowest predicted stem density at very high severity ( $> 3.8$  BSI) (Fig. 5b). Examples of site conditions in which suckering and seedling recruitment each dominated are shown in Fig. 6. Surface fire severity was highly correlated with post-fire organic soil depth (Spearman's  $\rho = 0.9$ ); sites dominated by seedlings had an average organic soil depth of 0.5 cm, as compared to 3.3 cm at sites dominated by suckering, and 8 cm at the two unburned comparison sites.

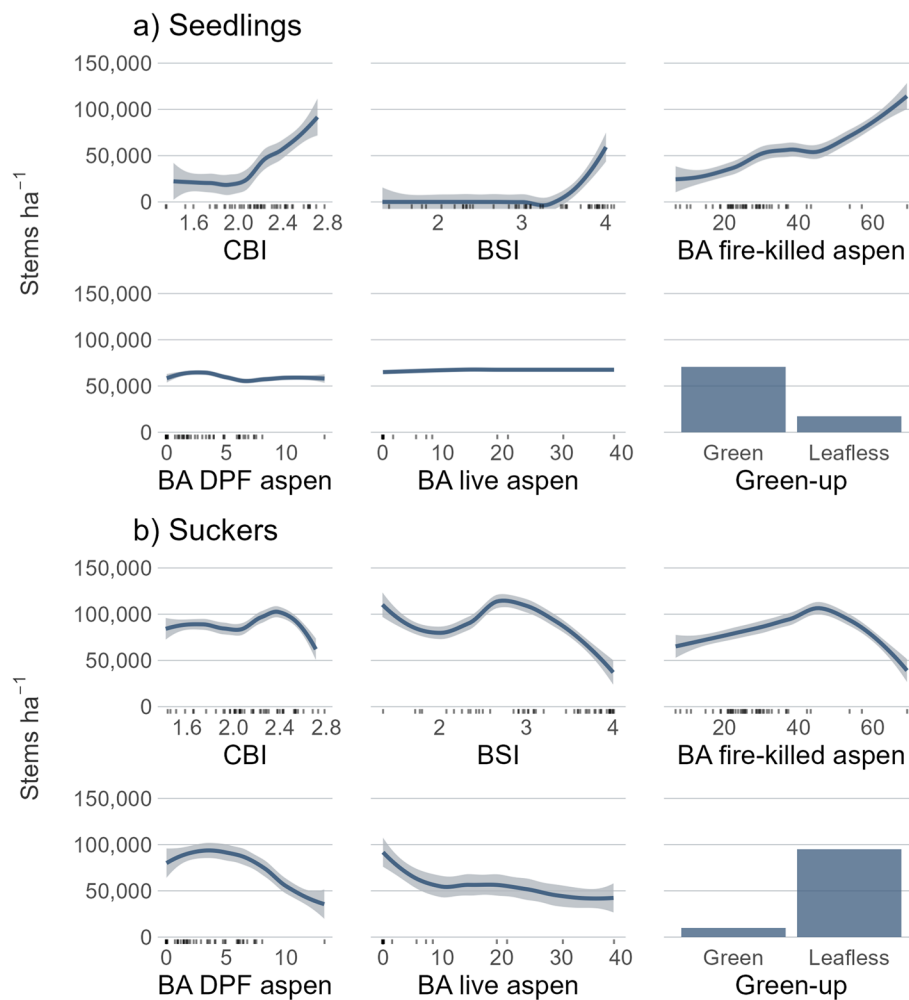
For both the seedling and suckering models, surface fire severity was followed in importance by the basal area of aspen killed by the fire (BA fire-killed aspen) and CBI (Fig. 4). Both BA fire-killed aspen and CBI proved more important to model prediction in the seedling model than suckering model (scaled variable importance of 90.5 and 49.8 for BA fire-killed aspen and 52.2 and 43.1 for

CBI, respectively). Seedling density increased as a function of BA fire-killed aspen, whereas suckering increased with BA fire-killed aspen to approximately  $50 \text{ m}^2 \text{ ha}^{-1}$ , at which point suckering density declined (Fig. 5). Sites with BA fire-killed aspen greater than the  $50 \text{ m}^2 \text{ ha}^{-1}$  threshold tended to have a higher-than-average BSI of 3.6, as compared to a BSI of 3.1 in all sites with lower BA. Notably, nearly all sites experienced high tree mortality (mean percent mortality = 90%; Table S1), and thus, BA fire-killed aspen was representative of the pre-fire total basal area at sites (Spearman's  $\rho = 0.78$ ). In response to CBI, predicted seedling density was low ( $\sim 21,000$  stems  $\text{ha}^{-1}$ , given average conditions for all other variables) until CBI reached moderate levels of around 2.25, at which point density increased with severity (Fig. 5a). Predicted suckering also did not vary substantially at low-to-moderate severity ( $< 2$  CBI), staying at an average prediction of 88,600 stems  $\text{ha}^{-1}$  (Fig. 5b). Sucker density then increased slightly to an average prediction of  $\sim 94,000$  stems  $\text{ha}^{-1}$  at moderate-high severity levels (2 to 2.5 CBI) and decreased again at high severity values ( $> 2.5$  CBI).

The remaining variables varied in order of importance between the seedling and suckering models. For the seedlings model, green-up ranked fourth in importance (scaled importance 48), followed by BA of aspen already dead prior to the fire (BA DPF aspen; scaled importance 9.8), and BA of aspen not killed by the fire (BA live aspen), which had no bearing on model prediction (scaled importance 0) (Fig. 4a). Of these, only green-up displayed a meaningful relationship with seedling density in the partial dependence plots (Fig. 5a). It was impossible to avoid some conflation of variable contributions,



**Fig. 4** Scaled variable importance for **a** seedling and **b** sucker models. Descriptors for abbreviated variables are provided in Table 1



**Fig. 5** Partial dependence plots of stem density (stems  $\text{ha}^{-1}$ ) for variables in models for **a** seedlings and **b** suckers. The blue line shows a smoothed relationship with 95% confidence intervals, in light blue, with rug plot showing raw data values. Bars are used for discrete variables. Descriptors for abbreviated variables are provided in Table 1

as all seedling-dominated sites occurred following green-up (Fig. 1) and registered the highest BSI values (Supplemental Fig. S5). In the suckering model, only BA DPF aspen showed meaningful importance to the model (scaled importance 22.4); variable importance of BA live aspen was 0.9 and green-up had zero importance to the model (Fig. 4b). Model predictions of suckering density generally showed suckering decreasing as BA DPF aspen increased.

## Discussion

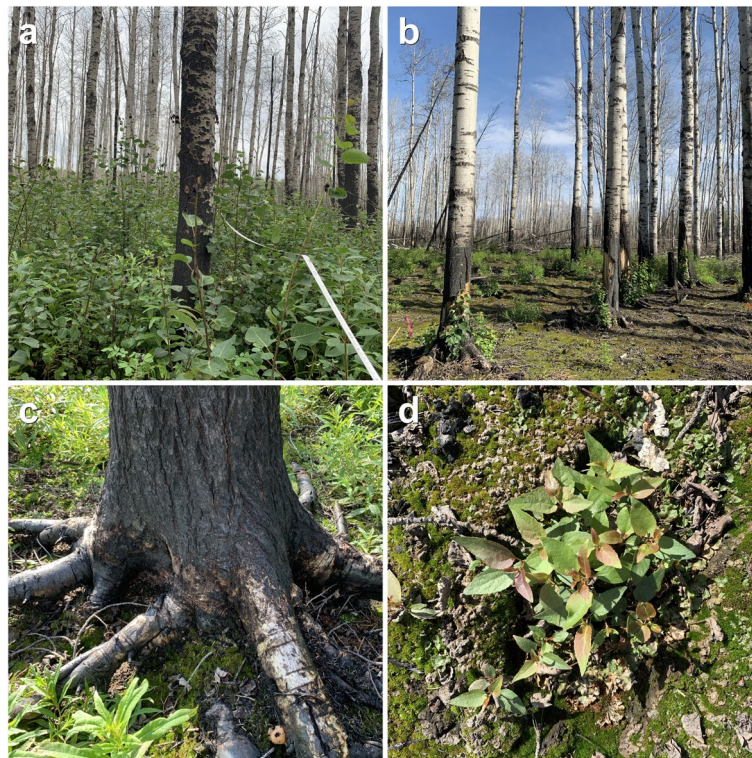
Studying the effect of fire severity, forest structure, and phenology on aspen recruitment strategies is crucial for understanding and projecting future population dynamics in aspen-dominated landscapes. As wildfire and other disturbance regimes respond to climatic fluctuations (Dale et al. 2001), the resilience provided by contrasting

recruitment strategies in aspen, and their effects on forest structure and genetic diversity, will only increase in importance (Gill et al. 2017). Our study documents concentrations of abundant post-fire aspen establishment and outlines the conditions that promote seedlings and suckers. We found that seedling establishment was more likely following burning at high surface severity and in sites that burned after aspen clones had put out leaves. Conversely, vigorous aspen suckering occurred in sites that burned earlier in the season and was associated with a range of low-to-moderate surface fire severities.

## Effects of fire severity and forest stand characteristics

Our models suggest sucker recruitment density was most affected by fire severity. An average sucker recruitment density of 110,556 sucker stems  $\text{ha}^{-1}$  at our sites was consistent with that observed in other studies 1-year





**Fig. 6** Examples of recruitment at sites dominated by **a** suckering and **b** seedlings. Additional photos from the seedling-dominated site show **c** depth of burning into the organic layer and damage to the roots of a mature aspen stem and **d** a microsite harbouring many aspen seedlings

post-fire in western boreal Canada ( $105,944 \text{ stems ha}^{-1}$ , Jean et al. 2020;  $120,000 \text{ stems ha}^{-1}$ , Wang 2003). Suckering density was highest at sites with moderate surface and canopy fire severity but dropped off at high severity levels, as was found in other studies (Horton and Hopkins 1965; Bartos and Mueggler 1981; Wang 2003; Jean et al. 2020). Moderate-high CBI and BA fire-killed aspen indicate mature aspen ramet mortality and release of apical dominance, which, when combined with subsequent soil warming from the removal of canopy cover and the soil organic layer (as reflected by BSI), triggers a suckering response (Farmer 1962; Maini and Horton 1966). However, suckering was reduced at sites of high surface severity burning, as deeply burning fires consume much of the sucker-producing roots that are concentrated at the organic-mineral soil interface, resulting in less prolific sucker initiation from deeper roots (Horton and Hopkins 1965; Frey et al. 2003). Suckers were thus most abundant at sites where fire severity was high enough to kill mature stems and scour the surface, but not so high as to reduce the suckering potential of the roots (Horton and Hopkins 1965).

In our study, seedling density was highest in sites with high surface fire severity that also burned later in the season, after green-up. Aspen seeds have a short window of

viability (Maini 1972), strict requirements for competition-free microsites and adequate moisture for germination (McDonough 1985; Perala 1990), and notably, a need for an alignment in the timing of fire to the ripening and availability of seed sources (Landhäusser et al. 2019). We found seedling-dominated sites aligned with this limited “window of opportunity” for recruitment (Jelinski and Cheliak 1992). Deep burning, often to the mineral soil layer, and the reduction of canopy cover largely removed competition from other vegetation for light and water. Most sites dominated by seedlings had comparatively low suckering density, suggesting partial or full mortality of root buds from which suckers originate. This lack of suckers may have contributed to seedling success, as slower-growing seedlings compete poorly at sites where conditions favour dense, fast-growing suckers (Kreider and Yocom 2021). Our results thus hint at a trade-off between suckering and seedling recruitment, with high surface fire severity conditions detrimental to a suckering response creating a suitable environment for aspen seedlings, providing aspen with an alternate mechanism for achieving forest resilience after fire.

Aspen stand characteristics also significantly influenced post-disturbance recruitment patterns. Our results show that regeneration density for seedlings and suckers

is positively associated with the basal area of aspen killed by fire (which was a reflection of total stand basal area, due to the high rates of fire mortality in our sites). For suckering density, basal area could be an indication of below-ground resources that could support sucker production (DesRochers and Lieffers 2001; Krasnow and Stephens 2015). The relationship could also reflect the effects of greater overstory mortality on recruitment, as described above. Other characteristics of the stand, notably the basal area of aspen that died before fire, seemed to have a negative impact on suckering density. The presence of dead aspen from before the Chuckegg Fire may indicate a history of reduced vigour of the clone due to declining moisture levels and a history of prior defoliation from forest tent caterpillar known to have affected this area (M. Michaelian, unpublished data). Death of individual ramets of an aspen clone can be indicative of lower living root density and carbohydrate stores (Schier 1975; Worrall et al. 2010), thus reducing the capability of the clone to produce new suckers. It should be noted, however, that the standing dead basal area may not perfectly reflect past major mortality events, as dead aspen tend to fall at a faster rate than other species (Hogg et al. 2015).

#### Effects of phenology and timing of establishment

The high proportion of seedlings found at sites burned after green-up suggests that the timing of burning influences aspen recruitment strategy, though it is difficult to isolate its effect from other factors, namely, fire severity, in our study. Although green-up typically reduces both the rate of fire spread and its intensity (Fechner and Barrows 1976), drought conditions led to sites that burned the latest in our study exhibiting pronounced surface fire severity, relative to sites that burned in the spring (MNP LLP 2020). We believe phenology likely interacted with severity to affect the patterns in recruitment densities we observed. Aspen clones that have invested resources in producing leaves deplete carbohydrate reserves in the roots, which can affect sucker growth and thus their competitive ability and survival (Landhäusser and Lieffers 2002; Frey et al. 2004). Depleted post-leaf flush carbohydrate reserves that may have been sufficient to produce suckers at lower fire intensity may have been inadequate to initiate suckers from deeper roots unaffected by higher-severity fire (Schier et al. 1985).

For seedlings, recruitment at later-burning sites may have been facilitated by the alignment between the later timing of burning and that of seed ripening and dispersal. Seed dispersal has been documented to occur in mid-May to mid-June in the central Rockies (Perala 1990) and would be expected to occur later in northern Alberta (Maini 1972). Seed dispersal to the later-burning sites

would reap the benefits of lower competition due to the higher surface fire severity at these sites, as discussed above.

Arguably, sites that burned earlier would also have been exposed to a similar aspen seed rain as those that burned later in the fire's progression. However, earlier burning sites may have been occupied by suckers before aspen seed dispersal, as suckers can initiate as soon as 2 weeks after the death of the mature tree under suitable soil temperature conditions (Fraser et al. 2002). Alternatively, earlier burning sites may have had some initial seedling establishment, but competition from subsequent growth of suckers, or possibly herbaceous or shrubby species, generated too much competition for aspen seedling survival (Kreider and Yocom 2021). Sites that burned at equivalent fire severity earlier in the season had much lower (or absent) seedling densities relative to suckers than those which burned after green-up, further hinting at the interacting effects of fire severity and phenology on recruitment (Supplemental Fig. S5).

Sites may have experienced differing levels of seed rain due to proximity to a seed source and the associated quantity of seed. Despite this, sites with a high proportion of seedlings were further from unburned stands dominated by aspen (as a proxy for possible seed availability) than many without seedlings (Supplemental Fig. S6), suggesting that seedling density at sites was not simply a function of seed rain. Seedling densities at sites will almost certainly shift, as early seedling mortality reduces initial numbers; however, recruitment may continue in subsequent years if safe, competition-free microsites persist, allowing for additional seedling establishment over time (Romme et al. 2005; Landhäusser et al. 2019).

#### Management considerations

Whereas other parts of the boreal region support a mix of broadleaf and conifer species or are strongly dominated by conifers, aspen drives the forest-based economy, the ecology, and the approach to wildfire management in the part of northern Alberta where the Chuckegg Fire burned (Macdonald et al. 2023). Although the area would be expected to be conifer-dominated based on climate alone (Roberts and Hamann 2016), aspen established following fires in the past (Natural Regions Committee 2006), with the forest burned by Chuckegg likely an outcome of large wildfires in the 1940s (Tymstra et al. 2005; also evidenced by stand ages sampled in this study). Large, high-intensity wildfires are thus within the range of historical variability in this part of the boreal zone. While extreme fire-conducive weather can overcome aspen flammability thresholds, aspen stands are less flammable than conifer-dominated ones (Alexander et al. 2010; Parisien

et al. 2023). The past fire-induced shift to aspen, perpetuated by Chuckegg and the post-fire recruitment flush of suckers and seedlings, thus has important implications for future fire risk—and by extension, the forest industry and ecology—within this region.

Climate-induced changes in the fire-climate-vegetation dynamics of boreal North America will produce both risks and opportunities for aspen forests. Projected future climate is expected to drive a northward expansion of aspen parkland in western Canada, as climatic moisture deficits become limiting for most boreal conifer species (Hogg 1994, Hogg and Hurdle 1995). In addition, there is a trend toward increasing abundance of broad-leaf species (aspen and birch [*Betula* spp.]) following fire in northwestern Canada and Alaska (Baltzer et al. 2021, Hogg and Wein 2005, Johnstone et al. 2010, Dawe et al. 2022), as exemplified in our study area. As wildfire activity intensifies in this part of the boreal forest, fire-driven conversion of mixed or conifer-dominated forest to aspen-dominated forests is likely to be reinforced by subsequent fires (Johnstone et al. 2020; Whitman et al. 2022; Walker et al. 2023).

This said, climatic changes and resulting decreased moisture levels due to persistent or repeated droughts may eventually preclude adequate aspen recruitment, limit growth, and increase dieback from a combination of sudden aspen decline (Rehfeldt et al. 2009; Michaelian et al. 2011; Worrall et al. 2013) and associated outbreaks of defoliating insects (Hogg et al. 2002; Chen et al. 2018; Cortini and Comeau 2020). Warmer and drier climatic conditions may limit the germination success of aspen by seed, thereby curtailing the resilience of the species to more severe, compound disturbance (Kulakowski et al. 2013). Future vegetation projections suggest that much of northern Alberta may be too moisture limited to support productive forests and transition to grasslands by the end of the century (Stralberg et al. 2018). Aspen forests of western Canada are thus subject to contrasting driving factors as climatic warming and drying push northward, affecting disturbance regimes and subsequent recruitment by aspen and other boreal species.

Provided future climates can sustain growth, the combination of vegetative and sexual recruitment of aspen may provide a means to respond to changing disturbance dynamics. As seen in our study, aspen seedlings can fill the recruitment gap caused by a lowered suckering response due to increasingly intense wildfire. Reproduction by seed enables long-distance dispersal and colonization of aspen, allowing upslope migration (Landhäusser et al. 2010, Nigro et al. 2022) and post-disturbance recruitment, even when the nearest seed source is several kilometers away (Kay 1993). Genetic recombination allows for local adaptation to changing

environmental conditions, providing an opportunity for aspen to overcome warmer and drier conditions (Long and Mock 2012).

Fire Management aiming for clonal diversity would be cautioned against simply targeting higher-severity fires in aspen stands. Although our results suggest that high-severity surface fire can produce microsite conditions suitable for seedling establishment by limiting sucker production, this does not guarantee successful seedling recruitment or increased genetic diversity. Aspen sexual reproduction is highly episodic and dependent on post-fire environmental conditions, particularly adequate soil moisture at the time of seed dispersal and germination (McDonough 1985). Without sufficient precipitation, even sites that experience severe burning and exposure of mineral soil may fail to support seedling establishment. High surface severity fires, particularly after green-up, are thus most effective for a management objective of curtailing suckering, whereas moderate-high severity fire would be best suited for stimulating a vigorous suckering response. A mosaic of fire severities across the landscape may allow for both the persistence of established clones through suckering and the opportunity for seedling establishment where conditions permit, ultimately enhancing forest resilience to future environmental changes.

### Limitations

Although the Chuckegg Creek Fire afforded a rare opportunity to sample many sites with similar stand composition, age, and topoedaphic setting, we should be cautious in extending our results to other parts of the boreal region. Given the strong correlation between fire severity and phenology at our sites, it was impossible to fully isolate the effects of these two factors, and of other factors to a lesser degree. Future studies examining the impact of phenology and severity on aspen recruitment may wish to stratify their site selection by both variables, if possible, to differentiate their effects. We also did not consider the long-term survivorship of the recruits. Although we can report rapid thinning of recruitment density in the three CIPHA sites that were remeasured in 2022 (Supplemental Fig. S4), the resampling at these sites did not distinguish between seedlings and suckers, thereby preventing us from comparing the survival likelihood of the two recruitment strategies. We also did not consider the effects of herbivory as a factor influencing recruitment success. Although we did not directly observe any evidence of heavy browse pressure on the recruits, herbivore consumption can be a limiting factor to aspen stand renewal after disturbance (Seager et al. 2013). Future research could include these considerations to offer



deeper insights into the dynamics of aspen recruitment strategies following fire.

## Conclusion

Our research capitalizes on the unique opportunity offered by the Chuckegg Creek Fire to gain a deeper understanding of the factors driving aspen regeneration following wildfire events, providing valuable insights into the conditions favouring aspen seedling or vegetative suckering establishment post-fire. Our findings document vigorous suckering alongside several locations of considerable aspen seedling recruitment, while highlighting the particular importance of surface fire severity in influencing aspen recruitment dynamics. Although aspen seedlings have exacting environmental requirements for germination and survival, we found that high surface fire severity likely restricted aspen's suckering response and produced conditions in which aspen recruitment by seed was more successful. Suckering was reduced at sites that burned later in the fire season, hinting at complex interactions between fire severity, phenology, and recruitment strategy success. As climates and disturbance dynamics change, these mechanisms of post-disturbance recruitment in aspen, as observed in our study, will have profound implications for forest structure, fire regimes, genetic diversity, and ecological resilience of the boreal mixedwood of western North America.

## Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-025-00359-2>.

Supplementary Material: Additional figures and tables.

## Acknowledgements

We thank A. Van Dongen, N. Wozney, R. Hermanutz, and M. Gelderman for their assistance in field data collection, N. Wozney for dendrochronological sample processing, D. Letourneau for data processing, D. Stralberg and C. Kuntzman for sharing code for boosted regression tree analysis, and Q. Barber for sharing the fire progression dataset.

## Authors' contributions

MAP, DAD, and EW conceived of the study design; DAD performed data analysis and the preparation and writing of the manuscript; all authors contributed to data acquisition and editing of the manuscript.

## Funding

This work was supported by Natural Resources Canada.

## Data availability

The datasets used and analyzed during the current study are available from the corresponding author upon reasonable request.

## Declarations

## Ethics approval and consent to participate

Not applicable.

## Consent for publication

Not applicable.

## Competing interests

The authors declare that they have no competing interests.

## Author details

<sup>1</sup>Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, 5320 122 Street NW, Edmonton, AB T6H 3S5, Canada. <sup>2</sup>California State Polytechnic University, Humboldt, Humboldt, CA 95521, USA.

Received: 3 December 2024 Accepted: 21 February 2025

Published online: 22 May 2025

## References

- Alexander, M.E. 2010. Surface fire spread potential in trembling aspen during summer in the Boreal Forest Region of Canada. *The Forestry Chronicle* 86 (2): 200–212. <https://doi.org/10.5558/tfc86200-2>.
- Ally, D., K. Ritland, and S.P. Otto. 2010. Aging in a long-lived clonal tree. *PLoS Biology* 8 (8): e1000454. <https://doi.org/10.1371/journal.pbio.1000454>.
- Baltzer, J.L., N.J. Day, X.J. Walker, D. Greene, M.C. Mack, H.D. Alexander, D. Arsenault, J. Barnes, Y. Bergeron, Y. Boucher, L. Bourgeau-Chavez, C.D. Brown, S. Carrière, B.K. Howard, S. Gauthier, M.-A. Parisien, K.A. Reid, B.M. Rogers, C. Roland, L. Sirois, S. Stehn, D.K. Thompson, M.R. Turetsky, S. Veraverbeke, E. Whitman, J. Yang, and J.F. Johnstone. 2021. Increasing fire and the decline of fire adapted black spruce in the boreal forest. *PNAS* 118 (45): e2024872118. <https://doi.org/10.1073/pnas.2024872118>.
- Barber, Q.E., P. Jain, E. Whitman, D.K. Thompson, L. Guindon, S.A. Parks, X. Wang, M.G. Hethcoat, and M.-A. Parisien. 2024. The Canadian Fire Spread Dataset. *Scientific Data* 11 (1): 764. <https://doi.org/10.1038/s41597-024-03436-4>.
- Bartos, D., and W. Mueggler. 1981. Early succession in aspen communities following fire in western Wyoming. *Journal of Range Management* 4 (34): 315–318.
- Boehmke, B., and B.M. Greenwell. 2020. *Hands-on machine learning with R*. Boca Raton, FL: Chapman and Hall/CRC Press.
- Boulanger, Y., S. Gauthier, and P.J. Burton. 2014. A refinement of models projecting future Canadian fire regimes using homogeneous fire regime zones. *Canadian Journal of Forest Research* 44 (4): 365–376. <https://doi.org/10.1139/cjfr-2013-0372>.
- Chen, L., J.-G. Huang, A. Dawson, L. Zhai, K.J. Stadt, P.G. Comeau, and C. Whitehorse. 2018. Contributions of insects and droughts to growth decline of trembling aspen mixed boreal forest of western Canada. *Global Change Biology* 24 (2): 655–667. <https://doi.org/10.1111/gcb.13855>.
- Chen, T., T. He, M. Benesty, V. Khotilovich, Y. Tang, H. Cho, K. Chen, R. Mitchell, I. Cano, T. Zhou, M. Li, J. Xie, M. Lin, Y. Geng, Y. Li, and J. Yuan. 2022. *xgboost: Extreme Gradient Boosting*. R package version 1.6.0.1, <https://CRAN.R-project.org/package=xgboost>.
- Cortini, F., and P.G. Comeau. 2020. Pests, climate and competition effects on survival and growth of trembling aspen in western Canada. *New Forests* 51: 175–190. <https://doi.org/10.1007/s11056-019-09726-9>.
- Dale, V.H., L.A. Joyce, S. McNulty, R.P. Neilson, M.P. Ayres, M.D. Flannigan, P.J. Hanson, L.C. Irland, A.E. Lugo, C.J. Peterson, et al. 2001. Climate Change and Forest Disturbances: Climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. *BioScience* 51 (9): 723–734. [https://doi.org/10.1641/0006-3568\(2001\)051\[0723:CCAFD\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0723:CCAFD]2.0.CO;2).
- David, A.J., J.C. Zasada, D.W. Gilmore, and S.M. Landhäusser. 2001. Current trends in the management of aspen and mixed aspen forests for sustainable production. *The Forestry Chronicle* 77 (3): 525–532. <https://doi.org/10.5558/tfc77525-3>.
- Dawe, D.A., M.-A. Parisien, A.V. Dongen, and E. Whitman. 2022. Initial succession after wildfire in dry boreal forests of northwestern North America. *Plant Ecology* 223: 789–809. <https://doi.org/10.1007/s11258-022-01237-6>.
- DesRochers, A., and V.J. Lieffers. 2001. Root biomass of regenerating aspen (*Populus tremuloides*) stands of different densities in Alberta. *Canadian Journal of Forest Research* 31 (6): 1012–1018. <https://doi.org/10.1139/x01-037>.

- Elith, J., J.R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. *Journal of Animal Ecology* 77 (4): 802–813. <https://doi.org/10.1111/j.1365-2656.2008.01390.x>.
- Erni, S., X. Wang, S. Taylor, Y. Boulanger, T. Swystun, M. Flannigan, and M.-A. Parisien. 2020. Developing a two-level fire regime zonation system for Canada. *Canadian Journal of Forest Research* 50 (3): 259–273. <https://doi.org/10.1139/cjfr-2019-0191>.
- Farmer, R.E. 1962. Aspen root sucker formation and apical dominance. *Forest Science* 8 (4): 403–410.
- Fechner, G.H., and J.S. Barrows. 1976. Aspen stands as wildfire fuel breaks. Eisenhower Consortium Bulletin 4. Fort Collins, Colorado, USA: Colorado State University, Rocky Mountain Forest and Range Experiment Station. [https://digitalcommons.usu.edu/aspen\\_bib/5029/](https://digitalcommons.usu.edu/aspen_bib/5029/).
- Fraser, E.C., V.J. Lieffers, S.M. Landhäusser, and B.R. Frey. 2002. Soil nutrition and temperature as drivers of root suckering in trembling aspen. *Canadian Journal of Forest Research* 32 (9): 1685–1691. <https://doi.org/10.1139/x02-080>.
- Frey, B.R., V.J. Lieffers, S.M. Landhäusser, P.G. Comeau, and K.J. Greenway. 2003. An analysis of sucker regeneration of trembling aspen. *Canadian Journal of Forest Research* 33 (7): 1169–1179. <https://doi.org/10.1139/x03-053>.
- Frey, B.R., V.J. Lieffers, and E.H. (Ted) Hogg, and S.M. Landhäusser. 2004. Predicting landscape patterns of aspen dieback: Mechanisms and knowledge gaps. *Canadian Journal of Forest Research* 34 (7): 1379–1390. <https://doi.org/10.1139/x04-062>.
- Gill, N.S., F. Sangermano, B. Buma, and D. Kulakowski. 2017. *Populus tremuloides* seedling establishment: An underexplored vector for forest type conversion after multiple disturbances. *Forest Ecology and Management* 404 (15): 156–164. <https://doi.org/10.1016/j.foreco.2017.08.008>.
- Greene, D.F., J.C. Zasada, L. Sirois, D. Kneeshaw, H. Morin, I. Charron, and M.-J. Simard. 1999. A review of the regeneration dynamics of North American boreal forest tree species. *Canadian Journal of Forest Research* 29 (6): 824–839. <https://doi.org/10.1139/x98-112>.
- Greenwell, B.M. 2017. pdp: An R Package for Constructing Partial Dependence Plots. *The R Journal* 9(1): 421–436. <https://journal.r-project.org/archive/2017/RJ-2017-016/index.html>
- Guindon, L., F. Manka, D.L.P. Correia, P. Villemaire, B. Smiley, P. Bernier, S. Gauthier, A. Beaudoin, J. Boucher, and Y. Boulanger. 2024. A new approach for spatializing the Canadian National Forest Inventory (SCANFI) using Landsat dense time series. *Canadian Journal of Forest Research* 54 (7): 793–815. <https://doi.org/10.1139/cjfr-2023-0118>.
- Hall, R.J., J.T. Freeburn, W.J. de Groot, J.M. Pritchard, T.J. Lynham, and R. Landry. 2008. Remote sensing of burn severity: experience from western Canada boreal fires. *International Journal of Wildland Fire* 17(4):476–489. <https://doi.org/10.1071/wf08013>.
- Hogg, E.H., and (Ted), and M. Michaelian M. 2015. Factors affecting fall down rates of dead aspen (*Populus tremuloides*) biomass following severe drought in west-central Canada. *Global Change Biology* 21 (5): 1968–1979. <https://doi.org/10.1111/gcb.12805>.
- Hogg, E.H., and (Ted), and R.W. Wein. 2005. Impacts of drought on forest growth and regeneration following fire in southwestern Yukon. *Canada. Canadian Journal of Forest Research* 35 (9): 2141–2150. <https://doi.org/10.1139/x05-120>.
- Hogg, E.H., and (Ted), J.P. Brandt, and B. Kochtubajda. 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951–2000. *Canadian Journal of Forest Research* 35 (3): 610–622. <https://doi.org/10.1139/x04-211>.
- Hogg, E.H., and (Ted), J.P. Brandt, M. Michaelian. 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. *Canadian Journal of Forest Research* 38 (6): 1373–1384. <https://doi.org/10.1139/x08-001>.
- Hogg, E.H., and (Ted). 1994. Climate and the southern limit of the western Canadian boreal forest. *Canadian Journal of Forest Research* 24 (9): 1835–1845. <https://doi.org/10.1139/x94-237>.
- Hogg, E.H., and P.A. Hurdle. 1995. A dry-climate analogue for the future boreal forest? *Water, Air, and Soil Pollution* 82: 391–400. <https://doi.org/10.1007/BF01182849>.
- Hogg, E.H., J.P. Brandt, and B. Kochtubajda. 2002. Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. *Canadian Journal of Forest Research* 32 (5): 823–832. <https://doi.org/10.1139/x01-152>.
- Holsinger, L.M., S.A. Parks, L.B. Saperstein, R.A. Loehman, E. Whitman, J. Barnes, and M.-A. Parisien. 2021. Improved fire severity mapping in the North American boreal forest using a hybrid composite method. *Remote Sensing in Ecology and Conservation* 8 (2): 222–235. <https://doi.org/10.1002/rse2.238>.
- Horton, K.W., and E.J. Hopkins. 1965. *Influence of fire on aspen suckering*. Ottawa, Ontario: Canada Department of Forestry, Forestry Research Branch.
- Jean, S.A., B.D. Pinno, and S.E. Nielsen. 2020. Early regeneration dynamics of pure black spruce and aspen forests after wildfire in boreal Alberta. *Canada. Forests* 11 (3): 333. <https://doi.org/10.3390/f11030333>.
- Jelinski, D.E., and W.M. Cheliak. 1992. Genetic diversity and spatial subdivision of *Populus tremuloides* (Salicaceae) in a heterogeneous landscape. *American Journal of Botany* 79 (7): 728–736. <https://doi.org/10.1002/j.1537-2197.1992.tb13647.x>.
- Johnstone, J.F., T.N. Hollingsworth, F.S. Chapin III, and M.C. Mack. 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology* 16 (4): 1281–1295. <https://doi.org/10.1111/j.1365-2486.2009.02051.x>.
- Johnstone, J.F., G. Celis, F.S. Chapin, T.N. Hollingsworth, M. Jean, and M.C. Mack. 2020. Factors shaping alternate successional trajectories in burned black spruce forests of Alaska. *Ecosphere* 11 (5): e03129. <https://doi.org/10.1002/ecs2.3129>.
- Kasischke, E.S., M.R. Turetsky, R.D. Ottmar, N.H.F. French, E.E. Hoy, and E.S. Kane. 2008. Evaluation of the composite burn index for assessing fire severity in Alaskan black spruce forests. *International Journal of Wildland Fire* 17 (4): 515–526. <https://doi.org/10.1071/WF08002>.
- Kay, C.E. 1993. Aspen seedlings in recently burned areas of Grand Teton and Yellowstone National Parks. *Northwest Science* 67: 94–104.
- Kemperman, J.A., and B.V. Barnes. 1976. Clone size in American aspens. *Canadian Journal of Botany* 54 (22): 2603–2607. <https://doi.org/10.1139/b76-280>.
- Key, C.H., and N.C. Benson. 2006. Landscape assessment (LA): Sampling and analysis methods. In: FIREMON: Fire effects monitoring and inventory system, Technical Report RMRS-GTR-164-CD (pp LA1–LA51). Fort Collins, Colorado, USA: USDA Forest Service, Rocky Mountain Research Station. <https://doi.org/10.2737/RMRS-GTR-164>.
- Krasnow, K.D., and S.L. Stephens. 2015. Evolving paradigms of aspen ecology and management: Impacts of stand condition and fire severity on vegetation dynamics. *Ecosphere* 6 (1): 1–16. <https://doi.org/10.1890/ES14-00354.1>.
- Kreider, M.R., and L.L. Yocom. 2021. Aspen seedling establishment, survival, and growth following a high-severity wildfire. *Forest Ecology and Management* 493: 119248. <https://doi.org/10.1016/j.foreco.2021.119248>.
- Kreider, M.R., K.E. Mock, and L.L. Yocom. 2020. Methods for distinguishing aspen seedlings from suckers in the field. *Journal of Forestry* 118 (6): 561–568. <https://doi.org/10.1093/jofore/fvaa030>.
- Kuhn, M. 2022. *caret: Classification and Regression Training*. R package version 6.0–93. <https://CRAN.R-project.org/package=caret>.
- Kulakowski, D., M.W. Kaye, and D.M. Kashian. 2013. Long-term aspen cover change in the western US. *Forest Ecology and Management* 299: 52–59. <https://doi.org/10.1016/j.foreco.2013.01.004>.
- Kurz, W.A., C.H. Shaw, C. Boisvenue, G. Stinson, J. Metsaranta, D. Leckie, A. Dyk, C. Smyth, and E.T. Neilson. 2013. Carbon in Canada's boreal forest — A synthesis. *Environmental Reviews* 21 (4): 260–292. <https://doi.org/10.1139/er-2013-0041>.
- Landhäusser, S.M., and V.J. Lieffers. 2002. Leaf area renewal, root retention and carbohydrate reserves in a clonal tree species following above-ground disturbance. *Journal of Ecology* 90 (4): 658–665. <https://doi.org/10.1046/j.1365-2745.2002.00699.x>.
- Landhäusser, S.M., D. Deshaies, and V.J. Lieffers. 2010. Disturbance facilitates rapid range expansion of aspen into higher elevations of the Rocky Mountains under a warming climate. *Journal of Biogeography* 37 (1): 68–76. <https://doi.org/10.1111/j.1365-2699.2009.02182.x>.
- Landhäusser, S.M., B.D. Pinno, and K.E. Mock. 2019. Tamm review: Seedling-based ecology, management, and restoration in aspen (*Populus tremuloides*). *Forest Ecology and Management* 432: 231–245. <https://doi.org/10.1016/j.foreco.2018.09.024>.
- Loboda, T.V., N.H.F. French, C. Hight-Harf, L. Jenkins, and M.E. Miller. 2013. Mapping fire extent and burn severity in Alaskan tussock tundra: An analysis of the spectral response of tundra vegetation to wildland fire. *Remote*



- Sensing of the Environment* 134: 194–209. <https://doi.org/10.1016/j.rse.2013.03.003>.
- Long, J.N., and K. Mock. 2012. Changing perspectives on regeneration ecology and genetic diversity in western quaking aspen: Implications for silviculture. *Canadian Journal of Forest Research* 42 (12): 2011–2021. <https://doi.org/10.1139/x2012-143>.
- Macdonald, S. E., P. G. Comeau, C. A. Nock, and B. D. Pinno. 2023. Ecological silviculture for aspen mixedwoods in Western Canada. In: B. J. Palik and A. W. D'Amato (eds) *Ecological Silvicultural Systems: exemplary models for sustainable forest management*. Wiley, Hoboken, NJ. p 169. [https://digitalcommons.usu.edu/aspen\\_bib/8027/](https://digitalcommons.usu.edu/aspen_bib/8027/).
- Maini, J.S. 1972. Silvics and ecology in Canada. In: *Aspen: Symposium Proceedings*. General Technical Report NC-1. St. Paul, MN, USA: USDA Forest Service, North Central Forest Experiment Station. [https://digitalcommons.usu.edu/aspen\\_bib/5401/](https://digitalcommons.usu.edu/aspen_bib/5401/).
- Maini, J.S., and K.W. Horton. 1966. Vegetative propagation of *Populus spp.*: I. Influence of temperature on formation and initial growth of aspen suckers. *Canadian Journal of Botany* 44(9): 1183–1189. <https://doi.org/10.1139/b66-130>.
- McCullough, S.A., A.T. O'Geen, M.L. Whiting, D.A. Sarr, and K.W. Tate. 2013. Quantifying the consequences of conifer succession in aspen stands: Decline in a biodiversity-supporting community. *Environmental Monitoring and Assessment* 185: 5563–5576. <https://doi.org/10.1007/s10661-012-2967-4>.
- McDonough, W.T. 1985. Sexual reproduction, seeds and seedlings. In N.V. DeByle and R.P. Winokur (eds) *Aspen: ecology and management in the western United States* (pp 25–28). Fort Collins, CO, USA: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. [https://digitalcommons.usu.edu/aspen\\_bib/3804/](https://digitalcommons.usu.edu/aspen_bib/3804/).
- Michaelian, M., E.H. Hogg, R.J. Hall, and E. Arsenault. 2011. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biology* 17 (6): 2084–2094. <https://doi.org/10.1111/j.1365-2486.2010.02357.x>.
- MNP LLP. 2020. *Spring 2019 Wildfire Review – Final Report*. Edmonton, AB: MNP LLP. <https://open.alberta.ca/publications/spring-2019-wildfire-review>.
- Natural Regions Committee 2006. *Natural Regions and Subregions of Alberta*. Compiled by D.J. Downing and W.W. Pettapiece. Pub. No. T/852. Government of Alberta. <https://open.alberta.ca/publications/0778545725>.
- Nesbit, K.A., L.L. Yocom, A.M. Trudgeon, R.J. DeRose, and P.C. Rogers. 2023. Tamm review: Quaking aspen's influence on fire occurrence, behavior, and severity. *Forest Ecology and Management* 531: 120752. <https://doi.org/10.1016/j.foreco.2022.120752>.
- Nigro, K.M., M.E. Rocca, M.A. Battaglia, J.D. Coop, and M.D. Redmond. 2022. Wildfire catalyzes upward range expansion of trembling aspen in southern Rocky Mountain beetle-killed forests. *Journal of Biogeography* 49 (1): 201–214. <https://doi.org/10.1111/jbi.14302>.
- Parisien, M.-A., Q.E. Barber, M.D. Flannigan, and P. Jain. 2023. Broadleaf tree phenology and springtime wildfire occurrence in boreal Canada. *Global Change Biology* 29 (21): 6106–6119. <https://doi.org/10.1111/gcb.16820>.
- Peng, C., Z. Ma, X. Lei, Q. Zhu, H. Chen, W. Wang, S. Liu, W. Li, X. Fang, and X. Zhou. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change* 1: 467–471. <https://doi.org/10.1038/nclimate1293>.
- Perala, D.A. 1990. Quaking aspen (*Populus tremuloides* Michx.). In: R.M. Burns and B.H. Honkala (technical coordinators) *Silvics of North America: II. Hardwoods* (pp 555–569) Washington, D.C., USA: USDA Forest Service. <https://research.fs.usda.gov/treearch/1548>.
- Price, D.T., R.I. Alfaro, K.J. Brown, M.D. Flannigan, R.A. Fleming, E.H. Hogg, M.P. Girardin, T. Lakusta, M. Johnston, D.W. McKenney, et al. 2013. Anticipating the consequences of climate change for Canada's boreal forest ecosystems. *Environmental Reviews* 21 (4): 322–365. <https://doi.org/10.1139/er-2013-0042>.
- R Core Team. 2022. *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing URL <https://www.R-project.org/>.
- Rehfeldt, G.E., D.E. Ferguson, and N.L. Crookston. 2009. Aspen, climate, and sudden decline in western USA. *Forest Ecology and Management* 258 (11): 2353–2364. <https://doi.org/10.1016/j.foreco.2009.06.005>.
- Roberts, D.R., and A. Hamann. 2016. Climate refugia and migration requirements in complex landscapes. *Ecography* 39 (12): 1238–1246. <https://doi.org/10.1111/ecog.01998>.
- Romme, W.H., M.G. Turner, G.A. Tuskan, and R.A. Reed. 2005. Establishment, persistence, and growth of aspen (*Populus tremuloides*) seedlings in Yellowstone National Park. *Ecology* 86: 404–418. <https://doi.org/10.1890/03-4093>.
- Schier, G.A. 1975. Deterioration of aspen clones in the middle Rocky Mountains. Vol. 170. Ogden, UT, USA: USDA Forest Service, Intermountain Forest and Range Experiment Station. [https://digitalcommons.usu.edu/aspen\\_bib/5081/](https://digitalcommons.usu.edu/aspen_bib/5081/).
- Schier, G.A., J.R. Jones, and R.P. Winokur. 1985. Vegetative regeneration in aspen: ecology and management in the Western United States. Fort Collins, CO, USA: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. [https://digitalcommons.usu.edu/aspen\\_bib/3758/](https://digitalcommons.usu.edu/aspen_bib/3758/).
- Seager, S.T., C. Eisenberg, S.B. St, and Clair. 2013. Patterns and consequences of ungulate herbivory on aspen in western North America. *Forest Ecology and Management* 299: 81–90. <https://doi.org/10.1016/j.foreco.2013.02.017>.
- Soil Classification Working Group. 1998. *The Canadian System of Soil Classification*, 3rd ed.; Publication 1646; Ottawa, ON, Canada: NRC Research Press, Agriculture and Agri-Food Canada. <https://sis.agr.gc.ca/cansis/publications/manuals/1998-cssc-ed3/index.html>.
- Stralberg, D., X. Wang, M.-A. Parisien, F.-N. Robinne, P. Sólmos, C.L. Mahon, S.E. Nielsen, and E.M. Bayne. 2018. Wildfire-mediated vegetation change in boreal forests of Alberta. *Canada. Ecosphere* 9 (3): e02156–e02156. <https://doi.org/10.1002/ecs2.2156>.
- Turner, M.G., W.H. Romme, R.A. Reed, and G.A. Tuskan. 2003. Post-fire aspen seedling recruitment across the Yellowstone (USA) Landscape. *Landscape Ecology* 18 (2): 127–140. <https://doi.org/10.1023/A:1024462501689>.
- Tymstra, C., D. Wang, and M.P. Rozeau. 2005. Alberta wildfire regime analysis. *Wildfire Science and Technology Report PFCC-01-05*. Edmonton, AB, Canada: Government of Alberta, Alberta Department of Sustainable Resources Development. [https://archive.org/details/albertawildfirer00tym\\_s\\_0/mode/2up](https://archive.org/details/albertawildfirer00tym_s_0/mode/2up).
- Volney, W.J.A., and K.G. Hirsch. 2005. Disturbing forest disturbances. *The Forestry Chronicle* 81 (5): 662–668. <https://doi.org/10.5558/tfc81662-5>.
- Walker, X.J., K. Okano, L.T. Berner, R. Massey, S.J. Goetz, J.F. Johnstone, and M.C. Mack. 2023. Shifts in ecological legacies support hysteresis of stand type conversions in Boreal Forests. *Ecosystems* 26 (8): 1796–1805. <https://doi.org/10.1007/s10021-023-00866-w>.
- Wang, G.G. 2003. Early regeneration and growth dynamics of *Populus tremuloides* suckers in relation to fire severity. *Canadian Journal of Forest Research* 33 (10): 1998–2006. <https://doi.org/10.1139/x03-123>.
- Wang, X., D.K. Thompson, G.A. Marshall, C. Tymstra, R. Carr, and M.D. Flannigan. 2015. Increasing frequency of extreme fire weather in Canada with climate change. *Climatic Change* 130 (4): 573–586. <https://doi.org/10.1007/s10584-015-1375-5>.
- Wang, T., A. Hamann, D. Spittlehouse, and C. Carroll. 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS ONE* 11 (6): e0156720. <https://doi.org/10.1371/journal.pone.0156720>.
- Whitman, E., M.-A. Parisien, D.K. Thompson, R.J. Hall, R.S. Skakun, and M.D. Flannigan. 2018. Variability and drivers of burn severity in the northwestern Canadian boreal forest. *Ecosphere* 9: e02128. <https://doi.org/10.1002/ecs2.2128>.
- Whitman, E., S.A. Parks, L.M. Holsinger, and M.-A. Parisien. 2022. Climate-induced fire regime amplification in Alberta. *Canada. Environmental Research Letters* 17 (5): 055003. <https://doi.org/10.1088/1748-9326/ac60d6>.
- Worrall, J.J., S.B. Marchetti, L. Egeland, R.A. Mask, T. Eager, and B. Howell. 2010. Effects and etiology of sudden aspen decline in southwestern Colorado, USA. *Forest Ecology and Management* 260 (5): 638–648. <https://doi.org/10.1016/j.foreco.2010.05.020>.
- Worrall, J.J., G.E. Rehfeldt, A. Hamann, E.H. Hogg, S.B. Marchetti, M. Michaelian, and L.K. Gray. 2013. Recent declines of *Populus tremuloides* in North America linked to climate. *Forest Ecology and Management* 299: 35–51. <https://doi.org/10.1016/j.foreco.2012.12.033>.

## Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.