DRIVERS OF FIRE SEVERITY IN WESTERN NORTH AMERICAN BOREAL DECIDUOUS FORESTS

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ABSTRACT

DRIVERS OF FIRE SEVERITY

IN WESTERN NORTH AMERICAN BOREAL DECIDUOUS FORESTS

BETSY BLACK

Boreal forests store a large portion of the Earth's terrestrial carbon. Recently, warmer temperatures and drought have driven severe wildfires that result in carbon combustion losses that may exceed what can be sequestered by post-fire regrowth. However, these severe fires sometimes initiate shifts from conifer- to deciduous-forest dominance. Deciduous forests sequester more carbon for longer than the black spruce forests they replace because they accumulate combustion-resistant aboveground biomass more rapidly. However, as the climate of boreal ecosystems continues to warm, it is uncertain if the relative resilience of deciduous trees to wildfire will persist. To understand what a more deciduous boreal forest means for the future of boreal carbon, we quantified carbon combustion and investigated drivers of fire severity in deciduous and mixed conifer-deciduous stands. We sampled 139 plots across eight fire scars in Alaska and the Yukon. We assessed the relative influence of bottom-up variables related to stand composition and top-down climate variables on wildfire carbon combustion. On average, deciduous stands lost half as much carbon to wildfire combustion as conifer stands lost. Pre-fire fuel loads and vegetation stress were the primary controls on fire severity in mixed and aspen stands, whereas birch stand combustion was additionally influenced by spring precipitation. Our findings suggest that if deciduous tree dominance increases, carbon emissions from boreal wildfires will decline substantially, though wildfire carbon emissions from come deciduous forests may increase if climate change makes precipitation more stochastic in the far north.

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Dedication

To my constant friend.

INTRODUCTION

The boreal forest has historically been a net carbon (C) sink that stores a large portion of the Earth's terrestrial C (Pan et al. 2011, Bradshaw and Warkentin 2015). Increasing fire severity and frequency associated with climate change (Kasischke and Turetsky 2006, Balshi et al. 2009b, Kasischke et al. 2010, Turetsky et al. 2011, de Groot et al. 2013) have the potential to jeopardize this sink and transform the boreal biome into a net C source to the atmosphere (Kasischke et al. 1995, Balshi et al. 2009a, Walker et al. 2019). In North America, the western boreal forest is dominated by black spruce (*Picea mariana*) stands that gradually accumulate C over multiple fire cycles in a thick layer of cold, wet organic soil. Recently, warmer temperatures and drought have driven severe fires that burn more deeply into and combust the C-rich organic soil of black spruce forests (Kasischke and Turetsky 2006, Kasischke et al. 2010, Turetsky et al. 2011). When this occurs, black spruce stands can become a net source of C to the atmosphere (Turetsky et al. 2011, Walker et al. 2019). Additionally, severe fires that combust all or most of the organic soil layer and expose underlying mineral soils can initiate shifts to alternate successional trajectories (Johnstone and Kasischke 2005, Johnstone and Chapin III 2006, Johnstone et al. 2010a, 2020, Baltzer et al. 2021). Fast-growing deciduous species such as birch (*Betula spp*.) and aspen (*Populus tremuloides*) are able to germinate on the exposed mineral soil and out-compete black spruce and have consequently been expanding in the boreal forest (Beck et al. 2011, Mann et al. 2012, Baltzer et al. 2021).

A shift to deciduous-dominated forest might slow the climate change-wildfire feedback loop by exerting a fire self-limiting (or self-regulating) pressure on boreal forests. Fire self-limitation occurs when fire changes the landscape in a way that limits the severity or occurrence of future fire (Parks et al. 2015). In the boreal forest, a transition from conifer to deciduous dominance may increase the amount of C sequestered in forests and reduce wildfire C emissions. Deciduous trees sequester C and nitrogen (N) more quickly than black spruce forests (Mack et al. 2021a). Additionally, deciduous forests have historically been less likely to burn, and if they do burn, less likely to burn severely than black spruce forests (Parisien et al. 2011). If fire activity is reduced, deciduous forests should sequester more C longer than the black spruce forests they replace.

While previous studies have investigated the effect of deciduous trees on ignitions (Krawchuk et al. 2006), fire probability (Cumming 2001, Bernier et al. 2016, Dash et al. 2016, Hart et al. 2019), area burned (Rupp et al. 2002, Marchal et al. 2017), and containment failure (Arienti et al. 2006), no studies have quantified their effects on C emissions from boreal wildfires. Furthermore, projections of future climate and fire regimes indicate that fire frequency and severity will likely exceed historical precedents (Flannigan et al. 2005, Balshi et al. 2009b, Veraverbeke et al. 2017). However, these projections are based on the forecasted intensification of fire-promoting weather conditions and do not take into account the potential fire self-limiting effect of a shift in canopy species. The drivers of fire activity in black spruce stands are well documented (Dyrness and Norum 1983, Harden et al. 2000, Beverly 2017, Walker et al. 2018a, 2018b, 2020), but little is known about drivers in deciduous stands. A better understanding of how deciduous forests resist severe burning will begin to illuminate how a warming climate will shape the trajectory of the C they store.

To understand what an increasingly deciduous boreal forest means for the future of boreal C-wildfire interactions, we investigated three questions:

1) How do pre- and post-fire C pools and absolute and proportional wildfire C losses vary across conifer, mixed, aspen, and birch stands in the boreal forest?

2) How do wildfire-caused tree mortality and deciduous trunk scorching vary among mixed, aspen, and birch stands?

3) What variables drive absolute and proportional C combustion in mixed, aspen, and birch stands?

To address these questions, we quantified combustion in recently burned deciduous and mixed-dominance stands in Alaska and the Yukon and compared our findings to combustion data from black spruce stands. We recorded tree mortality and trunk scorching as additional metrics of fire severity effects on mixed and deciduous stands. We also evaluated many potential drivers of combustion in mixed, aspen, and birch stands. Identifying the variables that drive fire severity will help us understand how climate change might alter deciduous fire regimes in the coming decades.

BACKGROUND

Increasing Fire Disturbance and the Carbon Balance

Fire is the primary large-scale natural disturbance in the boreal forest (Bond-Lamberty et al. 2007, Kelly et al. 2013). In the past half-century, northern high-latitude ecosystems warmed at two to four times the global rate (Walsh 2014, Rantanen et al. 2022), leading to the intensification of wildfire disturbance (Kasischke and Turetsky 2006, Turetsky et al. 2011, Kelly et al. 2013). Fire is projected to continue to increase in frequency, size, and severity over the next century throughout the North American boreal forest and could erode the resilience of the boreal forest's role as a C sink (Flannigan et al. 2005, Balshi et al. 2009a, Young et al. 2017). These projections are based on the predicted intensification of top-down drivers of fire, such as fire weather. However, fire severity, or the proportion of combustible aboveground and belowground organic matter that is consumed in a fire (Keeley 2009), is controlled by an interacting array of top-down and bottom-up drivers. Bottom-up drivers of fire severity are factors that modify fuel availability and quality, such as forest composition. It is unknown if bottom-up drivers will slow or mitigate top-down driven acceleration of wildfire in this region.

Studies have documented how increasing wildfire severity is causing parts of the boreal forest to transition from net C sinks to sources (Bradshaw and Warkentin 2015, Walker et al. 2019). Simulations of ground-layer combustion suggest accelerating C emissions from wildfire will exceed C sequestration from post-fire succession in boreal forests in Alaska (Turetsky et al. 2011). However, empirical evidence suggests that when a transition from black spruce to deciduous dominance occurs, C sequestration over succession exceeds instantaneous C loss from wildfire (Mack et al. 2021a). Yet the effect of deciduous-dominance on wildfire C emissions is not yet understood. Because the future of C sequestered in the boreal forest is of great concern for the global C balance, understanding what variables control fire severity in boreal deciduous forests is critically important.

Drivers of Fire Severity

The range of processes thought to influence fire severity can be grouped into top-down and bottom-up drivers. Bottom-up drivers determine the type, quantity, and availability of fuels and include variables such as canopy species composition, time since the last fire, and soil moisture. Top-down drivers are those that create fire-promoting conditions such as weather.

Stand characteristics are primary bottom-up drivers of fire severity. As the majority of boreal forest wildfire C losses come from the combustion of belowground organic soil (Mack et al. 2011, Walker et al. 2018b, 2020), pre-fire organic soil C pool sizes are a key determinant of wildfire C combustion. The tree species that comprise a stand might have traits that promote fire (i.e., flammable resin) or limit fire (i.e., high leaf and wood moisture content). Stand structure characteristics such as stand density and biomass can interact with species composition to drive fire severity. More flammable fuels on a landscape will increase the severity of wildfire, while more fire-resistant fuels on a landscape might limit fire. Stand age is another bottom-up driver of fire severity commonly investigated as a primary mechanism of fire self-limitation. After a stand-replacing burn, fuels reaccumulate gradually. Several studies have found time after fire to be linked to fire probability and severity (Héon et al. 2014, Parks et al. 2014, 2015, 2016, Bernier et al. 2016, Erni et al. 2018). However, age-dependent fire self-limitation has also been observed to be overridden by extreme weather conditions in some cases (Bessie and Johnson 1995, Larsen 1997, Moritz 2003, Barrett et al. 2016, Beverly 2017, Parks et al. 2018).

Landscape characteristics such as moisture, slope, aspect, and elevation are bottom-up drivers of fire severity. Dry, well-drained parts of landscapes on top of hills or on steep, south-facing slopes that experience the most incoming radiation provide conditions that dry fuels and make them more available for combustion. Whereas parts in flat, valley bottoms that collect moisture are characterized by comparatively water-logged and unavailable fuels. In boreal forests that are characterized by discontinuous permafrost, warmer and drier landscape positions may also promote quicker organic soil decomposition and turn-over, resulting in less accumulation of fire-available fuels. Recent work has highlighted the importance of how landscape characteristics associated with the accumulation of wet, combustion-resistant soils can limit fire probability and severity (Kasischke et al. 2010, Walker et al. 2018a, 2018b, 2020, Parks et al. 2018).

Vegetation stress, potentially caused by pathogen infestations or prolonged severe climate conditions, is yet another potential bottom-up driver of fire severity (Parker et al. 2006, Littell et al. 2016). Climate change is resulting in novel distributions and abundances of pests (Bale et al. 2002). Boreal forests affected by pathogens such as aspen leaf miner or spruce budworm, may experience declines in productivity and patchy die-off (Parent and Verbyla 2010, Wagner and Doak 2013). Landscapes with greater fractions of dead fallen and standing snags may burn more severely. Additionally, tree fall gaps or canopy openings that result from tree mortality increase soil drying and promote the growth of understory vegetation that is available for combustion. Likewise, vegetation stress and mortality caused by years of drought or other severe climate conditions may make available fuels more flammable.

The spatial composition of trees is also an important bottom-up driver of fire severity. The array of non-flammable units, such as lakes, or less-flammable units, such as wetlands, on a landscape influences fire severity in forests (Hellberg et al. 2004, Erni et al. 2018). Likewise, the spatial composition of forest species and the relative fire-adapted or fire-resistant characteristics of those species influences the behavior and ignition success of fire (Hély et al. 2000, Cumming 2001, Krawchuk et al. 2006, Parisien et al. 2011, Rogers et al. 2015). A landscape that is dominated by a fire-promoting tree species should be more flammable and sustain more severe fire than one that is more heterogeneous and includes patches of fire-resistant species (Johnstone et al. 2011).

Weather conditions immediately preceding fire are top-down drivers of fire severity. If a stand experiences warmer or drier than normal conditions in the days, weeks, or months preceding ignition, fuels may be drier and burn more readily after an ignition has occurred (Anderegg et al. 2013, Rogers et al. 2018, Parks et al. 2018, Whitman et al. 2019). Furthermore, in boreal deciduous stands, spring climate variables that contribute to the timing of snowmelt and leaf flush (and the "spring window" time frame between those two events) are especially important in driving the likelihood of fire in deciduous stands (Parisien et al. 2023). Consequently, fire conditions can be assessed with variance from long-term climate means.

A Changing Boreal Forest: From Spruce to Deciduous Successional Trajectories

The severity at which a stand burns can determine the post-fire successional trajectory of boreal forests (Johnstone and Kasischke 2005, Johnstone and Chapin III 2006, 2006, Johnstone et al. 2010a, Hart et al. 2019, Coop et al. 2020). For nearly 6,000 years, western boreal forests in North America have been dominated by black spruce (*Picea mariana*) (Higuera et al. 2009). Historically black spruce forests experienced stand-replacing fires every 80-120 years, then re-established easily afterward due to their fire-adapted traits (Yarie 1981, Larsen 1997). Semi-serotinous cones provide an aerial seedbank of large, carbohydrate-rich seeds that are capable of germinating on charred residual soil organic layer (SOL) without desiccating (Johnstone and Chapin III 2006). Associations with productive mosses and slow decomposition rates in cold boreal soils allow black spruce stands to accumulate a thick layer of organic soil in which 60-85% of the surficial, combustible C in these ecosystems is stored (Boby et al. 2010, Melvin et al. 2015, Alexander and Mack 2016). Historically, that thick SOL only partially combusted during fire leading to the carryforward and accumulation of legacy C over many fire cycles (Chapin III et al. 2006, Boby et al. 2010, Pan et al. 2011). Because it is highly porous and often does not retain near-surface moisture, post-fire residual SOL is a poor substrate. However, black spruce have large, carbohydrate-rich seeds that are released from semi-serotinous cones after fire and are able to successfully germinate on these poor-quality substrates (Johnstone and Chapin III 2006). Forest succession for the next fire-free interval is usually locked in during the first few years after a fire so the ability of black spruce to establish readily after fire has made these stands highly resilient for most of the mid- to late-Holocene (Higuera et al. 2009, Johnstone et al. 2020).

In recent decades, however, increasingly severe fires and shorter fire return intervals have increased competition during establishment and reduced black spruce recruitment (Baltzer et al. 2021). Severe fires that combust most or all of the SOL expose the underlying mineral soil. Because mineral soil is a good substrate for germination, plants with small seeds that would typically desiccate on a thick residual SOL are able to successfully germinate when little or no SOL remains (Johnstone and Chapin III 2006). In particular, fast-growing deciduous species, such as birch and aspen, with small, wind-dispersed seeds establish on the newly exposed mineral soil (Johnstone and Chapin III 2006, Johnstone et al. 2010a). When this occurs, the fast-growing deciduous seedlings can outcompete slow-growing black spruce. In the western North

American boreal forest, this phenomenon is causing reductions in black spruce dominance and successional shifts to deciduous-dominated or mixed-dominance forests (Beck et al. 2011, Whitman et al. 2019, Johnstone et al. 2020, Baltzer et al. 2021).

Once forests have switched to deciduous trajectories, those trajectories are likely to be entrenched (Hansen et al. 2021). Deciduous leaf litter inhibits moss growth and comparatively high decomposition rates prevent the accumulation of a thick SOL (Natalia et al. 2008, Jean et al. 2020). The shallow SOL often combusts completely in fires and exposes mineral soils where deciduous seeds can easily germinate, ensuring self-replacement (Johnstone and Chapin III 2006, Johnstone et al. 2010a). Additionally, aspen and birch can quickly resprout post-fire from below-ground rhizomes or stumps, respectively (Van Cleve et al. 1983, Greene et al. 1999).

Palaeoecological records reveal historical precedents for climate- and wildfire-induced switches between deciduous- and spruce-dominated boreal landscapes. Increased fire activity in a warm period triggered a shift to deciduous dominance around 9,000 years ago that, in turn, acted as a negative feedback on fire activity (Higuera et al. 2009). As the climate cooled and moistened around 6,000 years ago, more flammable black spruce began to establish and increased fire activity (Higuera et al. 2009, Kelly et al. 2013, Hoecker et al. 2020). Though the palaeological precedent suggests that deciduous trajectories will act as a negative feedback to a warmer climate by reducing fire activity, the climate is currently changing at an unprecedented rate (Meehl et al. 2007). Projections of near-future climate exceed any historical precedent so the resilience of this negative feedback loop is unknown.

Implications of an Increasingly Deciduous Boreal Forest

The implications of an increasing proportion of deciduous trees throughout the boreal ecosystem are just beginning to be explored. High severity fires, like those that may trigger successional shifts to deciduous trajectories, promote surface deposition of black C aerosols that accelerate melting when deposited on snow and ice (Flanner et al. 2007). Yet, the resulting deciduous forests counter the initial high radiative forcing from the severe fires over many decades via a higher surface albedo than black spruce forests (Randerson et al. 2006). When incoming solar radiation is most extreme in the spring, evergreen black spruce have dark needles, but deciduous trees are leafless allowing the ground snow cover to reflect the radiation (Randerson et al. 2006, Potter et al. 2020).

Furthermore, comparative studies on post-fire trajectories indicate that in the first 100 years after a fire, deciduous forests tend to sequester C four times as quickly and N three times as quickly as black spruce stands, resulting in 1.6 times as much total C storage and comparable N storage after the first 100 years (Mack et al. 2021a). Thus, deciduous trajectories might act as a negative feedback on climate change by creating a larger C sink than the black spruce forests they replace.

Deciduous traits lead to low flammability, slowed fire spread, and low severity burning (Parisien et al. 2011, Rogers et al. 2015). High leaf water content, non-resinous stem wood, and less fire-adapted physiognomy contribute to decreased flammability (Johnson 1996, Hély et al. 2000). Additionally, deciduous stands have higher aboveground net primary productivity than black spruce and drop large amounts of leaf litter that prevents the growth of moss and accumulation of thick SOLs (Alexander et al. 2012, Jean et al. 2020). Consequently, deciduous forests store the bulk of their organic material in combustion-resistant aboveground biomass

(Alexander and Mack 2016, Mack et al. 2021a). A study of the species composition of burns in the boreal forests of Western Canada suggested that black spruce was the most flammable stand class while deciduous was the least flammable (Cumming 2001). As patches of fire-adapted black spruce forests in the sites most vulnerable to severe burning transition to less flammable deciduous forests, it is probable that an increasingly mixed- or deciduous-dominated stand composition will act as a negative feedback and the resulting landscape will have longer fire return intervals, suppress fire spread, and be more resistant to severe burning (Johnstone et al. 2011, Parisien et al. 2011).

Despite the possible stabilizing effects of a regime shift to deciduous forests in boreal ecosystems, many unknowns remain. Because of their characteristic shallow SOL, deciduous forests do not insulate permafrost against thawing which could trigger emissions of long-sequestered permafrost C (Harden et al. 2006, Douglas et al. 2020). It is also unclear if deciduous forests will remain resilient and productive in light of increasing drought stress and insect pathogens associated with climate change (Anderegg et al. 2013, Boyd et al. 2019, 2021). Most concerningly, projections of future climate and fire regimes indicate fire frequency and severity will likely exceed any historical precedent (Kelly et al. 2013). For this reason, it is essential to quantify wildfire C losses and determine what drives fire severity in deciduous forests. Doing so will help us anticipate the effects of intensifying fire conditions on boreal wildfire C emissions.

Objective

To determine the effects of a greater proportion of deciduous-dominated forests on the future C balance of the boreal forest, it is necessary to understand what factors drive fire severity in deciduous forests under current conditions. While the drivers of fire severity are well-studied in black spruce stands, little is known about the drivers in deciduous stands. To explore these unknowns, we surveyed recently burned deciduous-dominated (>66% deciduous) and mixed-dominance (33-66% deciduous) stands in Alaska and the Yukon to quantify total and proportional C combustion and identify the variables that drive fire severity.

RESEARCH QUESTIONS

To investigate the effects of climate change and an altered vegetation regime on boreal forest C combustion dynamics we asked three questions:

1) How do pre- and post-fire C pools and absolute and proportional wildfire C losses vary across conifer, mixed, aspen, and birch stands in the boreal forest?

2) How do wildfire-caused tree mortality and deciduous trunk scorching vary among mixed, aspen, and birch stands?

3) What variables drive absolute and proportional C combustion in mixed, aspen, and birch stands?

HYPOTHESES

Question 1: C Pools and Losses

How do pre- and post-fire C pools and absolute and proportional wildfire C losses vary across conifer, mixed, aspen, and birch stands in the boreal forest?

We hypothesized that aspen and birch stands would contain significantly more pre-fire C, lose less C to wildfire combustion, and contain more post-fire C than conifer stands due to stand differences in above and belowground C stocks and their relative availability for combustion. Specifically, both relative and absolute C combustion in deciduous stands should be low compared to conifer stands because the components of deciduous forests that are likely to burn (litter, understory vegetation, a thin SOL, and tree leaves and fine branches) comprise a comparatively smaller portion of the C of those forests than the combustion available components of black spruce forests (a thick SOL and resinous coarse and fine branches) (Alexander et al. 2012, Melvin et al. 2015, Alexander and Mack 2016). The bulk of the C in deciduous stands is protected in large, fire-resistant tree boles and, at maturity (100 years old), deciduous stands tend to contain more C than conifer stands (Alexander and Mack 2016, Mack et al. 2021a). Due to the influence of black spruce, aspen, and birch trees on stand characteristics, we expected mixed stands to have greater pre-fire and post-fire C pools and less C losses than conifer stands, but smaller pre-fire and post-fire C pools and greater C losses than deciduous stands.

Question 2: Mortality and Scorching

How do wildfire-caused tree mortality and deciduous trunk scorching vary among mixed, aspen, and birch stands?

We expected that mixed stands would experience slightly higher tree mortality and trunk scorching than aspen and birch stands on account of greater fractions of conifer trees in mixed stands that increase fire severity in the stand. We also expected tree mortality to be greater in mixed stands than deciduous stands due to thicker SOLs (facilitated by greater proportions of conifer stems (Natalia et al. 2008, Jean et al. 2020)) in which fire could potentially smolder for longer, killing tree roots. Similarly, we expected trunk scorch height would be greater in mixed stands than in deciduous stands due to the fire-promoting characteristics of conifer trees, such as ladder fuels and resinous leaves and branches, that might promote more intense fire with greater flame heights.

Question 3: Drivers of Combustion

What variables drive absolute and proportional wildfire C combustion in mixed, aspen, and birch stands?

Bottom-up Drivers

Stand Characteristics

We expected that absolute and proportional wildfire C combustion would decrease with greater pre-fire aboveground biomass in aspen and birch stands. Stand biomass is a proxy for fuel quantity, but species traits determine fuel availability. While greater black spruce biomass means more combustion-available fuels (ladder fuels and resinous coarse and fine woody debris), greater aspen and birch biomass mean wetter, fire-resistant stem wood and leaves and thus should decrease fire severity and absolute and proportional C combustion (Johnson 1996). Furthermore, we expected that the shade and evaporative moisture provided by deciduous tree foliage would create microclimates that were relatively inhospitable to fire compared with the open structure of conifer stands (Johnson 1996). For the same reasons, we expected both absolute and proportional combustion to decline as the relative proportion of deciduous trees in a stand increased. Alternatively, if deciduous trees experience a window of higher vulnerability to combustion in the early spring between snowmelt and leaf flush (Parisien et al. 2023), greater deciduous stand aboveground biomass may be linked to greater wildfire C loss. Because larger SOL C pools occur in parts of the landscape that are more resistant to decomposition (poorly-drained, colder aspects or parts underlain with nearer-surface permafrost) (Thompson et al. 2017), we expected greater pre-fire belowground C pools to be associated with greater absolute combustion (due to the larger available C pools), but lower proportional combustion (due to deeper fraction of SOL being wet and unavailable for combustion). As stand age co-varies with both tree biomass and, at least in conifer stands, SOL accumulation (Jean et al. 2017, 2020), and we expected that SOL C combustion would comprise the bulk of C loss (in conifer stands, SOL combustion can account for 90% of C emissions (Walker et al. 2018b)), we expected to see a positive correlation between stand age and absolute combustion, but a negative correlation between stand age and proportional combustion. However, because deciduous litter inhibits the growth of mosses that are the primary components of SOL in conifer stands (Natalia et al. 2008, Jean et al. 2017, 2020), SOL C pools in deciduous stands might not co-vary with stand age and therefore we hypothesized that both absolute and proportional combustion would be negatively correlated with stand age because if SOL pool sizes remain fairly constant and aboveground biomass increases, the dampening effect of deciduous increasing tree biomass on wildfire C losses will be the only thing that changes with stand age.

Vegetation Stress

We expect that declines in forest health associated with stress from climate warming and pathogen outbreaks will cause both mixed and deciduous forests to experience greater fire severity as a result of fuel accumulation and drying. Stands that have experienced several years of drought, declines in winter snow accumulation, pathogens infestations, or other changes that might exert stress on trees are likely to have greater loads of dead and drying snags and CWD available for combustion. Similarly, more stressed stands might experience more tree mortality and therefore may have proportionally more canopy gaps that allow sunlight to penetrate to the forest floor and dry out soils. Vegetation stress might be a more important driver of fire severity in mixed stands than in deciduous stands because black spruce trees facilitate the accumulation of greater loads of SOL C that will dry in stress-induced canopy gaps (Alexander and Mack 2016). Alternatively, vegetation stress in deciduous stands might have a greater effect on fire severity by reducing deciduous leaf litter inputs that inhibit understory vegetation productivity (Natalia et al. 2008, Jean et al. 2017, 2020), allowing for the accumulation of more organic material available for combustion. If a greater increase in fire severity is observed in deciduous stands affected by pathogens or drought than in similarly afflicted mixed stands, it may be on account of a greater proportional effect of stress on the flammability of deciduous trees themselves. Black spruce trees are already very flammable in non-stressed conditions, so a disease outbreak or drought may not result in a large magnitude change in the flammability of a stand. Comparatively, deciduous trees, which are typically less flammable, might experience a large magnitude change in relative flammability under stress.

Landscape Composition

We expected that the tree species composition of the greater landscape surrounding a stand would modify fire severity in that stand. The presence of non-flammable units (such as bodies of water) has been shown to decrease fire activity in nearby stands (Erni et al. 2018), so we expect that fire severity in a stand may similarly be influenced by the relative flammability of surrounding forest. We expected that if the surroundings were dominated by more flammable conifer trees, the stand would experience greater fire severity than if the surroundings were dominated by less flammable deciduous trees (Hély et al. 2000, 2001, Cumming 2001, Krawchuk et al. 2006). Conversely, fire severity should decrease in a stand if the area surrounding it is proportionally more deciduous due to the lower flammability of deciduous stands (Hély et al. 2000, 2001, Cumming 2001, Krawchuk et al. 2006).

Top-down Drivers

Variance from Climate Normals

We expected that greater than normal spring temperatures and lower than normal spring precipitation accumulation would cause greater wildfire C combustion. Higher than normal temperatures and lower than normal precipitation will influence SOL moisture and therefore, the availability of SOL for combustion. As mixed stands contain black spruce trees that facilitate greater SOL accumulation (Jean et al. 2017, 2020), we expect SOL drying to be more of a risk for mixed stands than for deciduous stands. Spring departures from normal, in particular, have the potential to control the timing of snowmelt and leaf flush and therefore control the length of the window of time (the time between these two phenological events) in which deciduous trees are particularly vulnerable to combustion (Parisien et al. 2023). Likewise, spring climate will influence soil moisture and thus may have an even greater effect on stands that carry a greater fraction of their C belowground than aboveground. Greater than normal temperatures and lower than normal precipitation should result in greater fire severity in deciduous and especially in mixed stands.

METHODS

Study Region

We conducted this study in the Alaska Boreal Interior and Boreal Cordillera ecoregions (US EPA 2021). These ecoregions encompass a portion of Alaska bounded by the Brooks Range to the north and the Alaska Range to the south and the southern portion of the Yukon Territory (US EPA 2021). Both ecoregions have continental climates characterized by long, cold winters and short, moderate summers. The region experiences freezing temperatures for 6-8 months of the year and is underlain by discontinuous permafrost (Osterkamp and Romanovsky 1999, US EPA 2021). Using Climate NA, we extracted climate metric normals from a 30-year period (1981 to 2010) for each site in the study. We calculated fire scar-weighted means for each metric. The normal mean temperature at our sites was -3.2 ± 0.6 °C, the warmest month mean temperature was 14.8 ± 0.4 °C, and the coldest month mean temperature was -21.4 ± 1.1 °C (Wang et al. 2016). In this same period, our sites received mean annual precipitation of 376 ± 16 mm (132 ± 11 mm of which was received as snow) (Wang et al. 2016). The 17 million ha of forested area in the Alaskan boreal forest are comprised of black spruce (42%), white spruce (29%), birch (12%), *Populus spp*. (8%), and mixed-spruce ecosystems (the remainder) (Yarie and Billings 2002). The vegetation makeup of the Boreal Cordillera is similar to that of the Alaska Boreal Interior but includes lodgepole pine in the southern extent of the ecoregion (*Pinus contorta*) (Johnstone and Chapin III 2003).

Site Identification and Selection

To ensure accurate post-fire measurements, we restricted our study to include only fires that occurred in the seven years preceding sampling (2015 – 2021). We identified fires using the

Alaska Large Fire Database (Bureau of Land Management n.d.) and constrained site candidacy to include only portions of burn scars within 2 km of roads to ensure accessibility (State of Alaska, Department of Transportation & Public Facilities 2022). We also limited site candidacy to portions of burn scars that contained deciduous-dominated canopy (>66% deciduous and >30% tree cover) or mixed deciduous-conifer canopy (33-66% deciduous and >30% tree cover) using a Landsat-based deciduous fraction map (Massey et al. in review). Difference Normalized Burn Ratio (dNBR), calculated with Google Earth Engine using Landsat imagery from the year before, of, and after each fire, was used to stratify potential sites across a range of fire severities (high severity = >52%, moderate severity = <52% & >20%, and low severity = <20%). We applied a minimum threshold of -0.5% dNBR to reduce the inclusion of unburned sites. As no year after fire imagery existed for 2022 at the time of this endeavor, dNBR for 2021 was calculated using only 2020 and 2021 data. We used these remotely-sensed indices to guide us to promising regions of fire scars, then deployed a DJI Mavic 3 unmanned aerial vehicle (UAV) to locate sites. From each site, we flew the UAV to visually search the surrounding landscape for the nearest patch of burned mixed or deciduous forest that was at least 100 m away. In total, we surveyed 85 sites that included 239 plots of mixed-, aspen-, or birch-dominated canopy across eight fire scars (Figure 1). Our sites were evenly distributed among fire scars (10-16 sites per fire scar) except for Isom Creek, which had few accessible burned deciduous stands (2 sites).

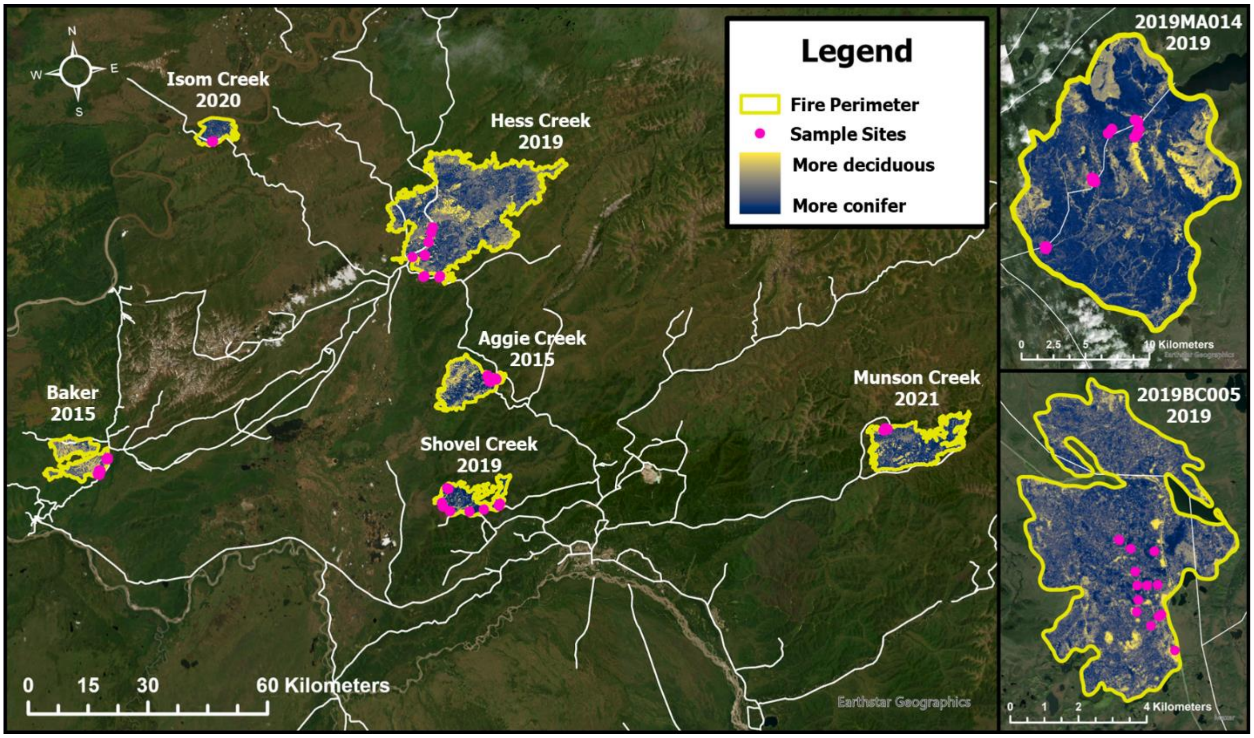


Figure 1: Map of Field Sites. Fire scars sampled in Alaska (left) and the Yukon Territory (upper and lower right) in this study. Fire scar perimeters (yellow polygons) are labeled with the fire name and year. The blue and yellow raster is a remotely-sensed metric of the pre-fire deciduous canopy cover derived using Landsat surface reflectance measurements from 2015 (Massey et al. in review). White lines are roads and pink points are sites measured in this study. Maps were created using ArcGIS Pro.

Site Measurements

In each site, we established three 10 m x 2 m belt transect plots (A, B, and C). If the site occurred on a slope, we oriented the transects to be perpendicular to the major aspect, otherwise, the transects were oriented randomly. We laid the three plots down in a continuous 30 m belt transect unless limits due to the size or shape of the deciduous patch forced us to lay the plots down parallel to one another. Parallel plots were laid down between 3 m and 20 m apart depending on the availability of burned mixed or deciduous forest. At each site, we recorded latitude, longitude, and elevation with a Garmin GPS device (error limited to 15 m 95% of the time) and slope and aspect with a clinometer and compass, respectively. We also assigned a site topo-edaphic moisture class ranging from xeric to subhygric (Johnstone et al. 2008). Additional measurements we recorded but did not use in this study can be found in Supplemental Materials.

To approximate site stand age, we sampled a tree disk from a representatively mature, unrotten tree killed by the fire in each plot. If multiple species were represented within a site, we took at least one tree disk from each species. Tree disks were dried, sanded, and then scanned at a resolution of 1200 DPI using an Epson Perfection V700 Photo scanner. Tree rings were counted along two paths using WinDENDRO 2021 software (Regent Instruments Inc., Quebec, Canada). The stand age for all three plots in a site was estimated as the age of the oldest tree in the site.

Aboveground Characteristics and C Pools

Within each plot, we inventoried all trees that had been alive and were rooted (or if greater than 50% of the stem was rooted) within the 2 m belt at the time of fire. We recorded tree species and alive or dead status. For each deciduous tree, we recorded the maximum height of fire scorching on the trunk. For trees taller than 1.3 m, we recorded diameter at breast height (DBH) and for all other trees, we recorded basal diameter (BD). For each tree, we visually estimated proportional combustion (0%, 25%, 50%, 75%, or 100%) of three pools: coarse branches, fine branches, and foliage. We used allometric equations to estimate pre-fire total, foliage, live crown, and standing dead biomass from DBH or BD of each tree (Alexander et al. 2012). Live crown estimates were parsed into coarse and fine branches (85% coarse and 15% fine for deciduous trees; 40% coarse and 60% fine for conifers) (Ruark and Bockheim 1987, Mack et al. 2008). We calculated combusted biomass of each tree component by multiplying coarse branch, fine branch, and foliage combustion estimates with the corresponding pre-fire biomass estimates. Total combusted biomass was calculated as the sum of coarse branch, fine branch, and foliage combustion plus standing dead biomass (8.8% of total biomass for conifers and 1.4% of total biomass for deciduous trees). Post-fire biomass was calculated by subtracting total combusted biomass from total pre-fire biomass. We transformed these estimates into total g C m^{-2} by multiplying each biomass estimate by 50% to estimate grams of C and then dividing each plot sum by the plot area: 20 m^2.

We inventoried all shrubs that had been alive at the time of fire and rooted within 1 m of the transect (if the site was located on a non-0° slope, we conducted the shrub inventory on the down-slope side of the transect, if not, we randomly assigned one side of the transect for the shrub inventory). We recorded shrub genera, BD, and proportional combustion of stems, fine branches, and foliage. For three shrubs for which we recorded DBH, we used a *Salix* taper equation based on *Salix* inventory data (Truettner *et al*. manuscript in preparation) to approximate BD (BD = DBH * 1.05131 + 0.94935). We used allometric equations to estimate pre-fire total shrub aboveground biomass, stem biomass, branch biomass, and new growth biomass (Berner et al. 2015). Boreal Alaska equations were used for *Alnus* and *Salix* and Boreal Yakutia equations were used for *Betula* shrubs. To estimate the dry biomass (g) of shrubs that were recorded as "unknown," we calculated the relative basal area of known shrubs in each site and assigned the unknowns to the most abundant genera. For six sites that contained only unknown species of shrubs, we assigned shrub genera based on the dominant shrub genera in the closest sites. We then applied our combustion estimates to the pre-fire biomass estimates. Combusted biomass was calculated as the sum of combusted foliage, fine branches, and stems. Postfire biomass was calculated as total pre-fire biomass minus combusted biomass. We transformed these estimates into total g C m^{-2} by multiplying each biomass estimate by 50% to estimate g C and then dividing each plot sum by the plot area: 10 m^2.

Stand Type Classification

Using the total biomass (g m^{-2}) and density (stems m^{-2}) of each tree species in each plot, we calculated deciduous, aspen, birch, and poplar indices: the sum of relative biomass and relative density divided by two times 100. Using these indices, we established a deciduous index of 0-100% deciduous. We used the deciduous index to categorize plots as deciduous (deciduous index>=66%), mixed (deciduous index<66% & deciduous index>=33%), or conifer (deciduous index<33%). We also established species-specific deciduous indices that we used to assign plots as: aspen (deciduous index>=66%, aspen index>birch index, & aspen index>poplar index), birch (deciduous index>=66%, birch index>aspen index, & birch index>poplar index), poplar (deciduous index>=66%, poplar index>aspen index, and poplar index>birch index), mixed (deciduous index<66% & deciduous index>=33%), or conifer (deciduous index<33%). Our initial survey included 264 plots spread among 88 sites, but we removed 25 plots that were balsam poplar- or conifer-dominant or contained no trees from the study. Consequently, some sites contained fewer than three plots.

Belowground C Pools

In each plot we collected one soil organic layer (SOL) sample approximately 10 cm x 10 cm in length and width and the entire depth of the SOL. Two lengths, two widths, and two depths were measured in the field. SOL sample depth excluded any post-fire (green) moss growth but included everything from below green moss to the top of the mineral soil. The samples were wrapped in foil and frozen until subsequent laboratory analysis. The C content of each organic soil sample was calculated using standard laboratory techniques (see Supplemental Materials: Residual Organic Soil Processing and C Pool Calculation & Table A). The C content of these samples was used to extrapolate the post-fire C pool of each plot in g C m^{-2} (see Supplemental Table B).

To estimate pre-fire SOL depth and C pools, we used Alaska forest inventory data from our study ecoregions for mature (>29 years old) aspen, birch, and mixed-dominance stands. We acquired data from three forest inventory databases: the US Forest Service Alaska Forest Inventory Analysis (Burrill et al. 2021), the Cooperative Alaska Forest Inventory (Malone et al. 2009), and the Bonanza Creek LTER Regional Site Network (Ruess 2015, Van Cleve et al. 2021, Ruess et al. 2023); and from studies that included a forest inventory (Alexander and Bonanza Creek LTER 2014, Melvin and Bonanza Creek LTER 2018, Mack et al. 2021b, Jean et al. 2022, Melvin et al. 2022). The data we compiled included measures of organic soil depth as well as stand and landscape characteristics from unburned stands. To accommodate data constraints (ranges in our sample data variables that exceeded ranges in inventory data variables: see Supplemental Table C), we selected aspect, slope, moisture class, and stand density for inclusion as predictor variables in our final models. We used 355 plot level measurements in a random forest analysis. We also tested the impact of summarizing plot-level measurements to site level (see Supplemental Materials: Plot-level versus site-level soil depth random forest models) and confirmed that soil depth predictions were similar. Therefore, we chose to keep the within-site variability in our final model as it was a better fitting model.

We trained random forest models for each stand type (mixed-, aspen-, and birch-dominated based on the deciduous index). We assessed the strength of several candidate random forest models by comparing model adjusted R^2, Root Mean Squared Error (RMSE), and Mean Absolute Error (MAE) (see Supplemental Table D). We assessed the ability of each model to accurately predict soil depth (based on predicted versus actual depth R^2 adj.) when the inventory data was split into training (75%) and validation (25%) data. We opted for models that minimized error while maximizing fit between predicted and actual soil depth on split data frames. The final models used a repeated cross-validation resampling method, 20 k-folds, three repeats, 1,000 trees, and model Root Mean Squared Error as a metric for selecting the optimal model (see Supplemental Table D). Model performance ranged from $R^2 = 0.28$ to 0.50 and RMSE ranged from 1.29 cm to 3.6 cm. The random forest models were then used to predict pre-fire soil depth in our sample data. The models were created using the R packages randomForest (Cutler and Wiener 2022), caret (Kuhn et al. 2023), and pdp (Greenwell 2022).

Burn depth was calculated as the difference between modeled pre-fire soil depth and measured post-fire soil depth. If the post-fire soil depth was greater than the modeled pre-fire depth, we assumed 0 cm of soil combusted and used post-fire depth as the pre-fire depth. To calculate the C content of combusted soil, we used SOL C pool data from a previous study where soil C pools were measured in unburned mixed, aspen, and birch stands in interior Alaska (Alexander et al. 2012, Alexander and Mack 2016). We classified the total unburned organic soil depths from both our study sites and the previous study's sites as shallow (< 5 cm), intermediate (5 – 10 cm), or deep (> 10 cm) (Alexander et al. 2012, Alexander and Mack 2016). Then we used the average C pool and depth of soil profile subsections (0-5, 5-10, and 10+) within each depth class from the previous study's SOL C pool data to estimate the C content of combusted SOL in our sites (Alexander et al. 2012, Alexander and Mack 2016) (see Supplemental Table E).

Pre-fire Vegetation Stress

The 2-band Enhanced Vegetation Index (EVI2) is a remotely-sensed, reflectance-derived metric of vegetation greenness and can be used to infer plant productivity, stress, and mortality (Jiang et al. 2008, Rogers et al. 2018, Berner et al. 2020, Boyd et al. 2021). As a proxy for vegetation stress potentially caused by prolonged pathogen or climate stress, we calculated annual mean summer (July 15 – August 15) EVI2 values for 10 years preceding each fire at each of our sites using Landsat imagery (Berner et al. 2023). Mean EVI2 values were calculated from a 90 m x 90 m area around each of our sites' GPS coordinates. Vegetation stress trends were obtained by calculating the slope of a linear relationship between year and mean summer EVI2. Positive trend values, therefore, indicate vegetation greening, negative trend values indicate vegetation browning, and trend values of 0 indicate no change in vegetation reflectance.

As an additional metric of pre-fire vegetation stress, we recorded the presence or absence of aspen canker on every aspen tree in our study. Unlike other tree pathogens such as aspen leaf miner or spruce budworm, it was possible to detect aspen canker post-fire due to the characteristic scars left behind on aspen trunks (see Supplemental Figure A). As not all sites contained aspen trees, we had a smaller sample size for this metric than for any other metric we investigated and therefore analyzed the effect of aspen canker on combustion separately.

Landscape Composition

To characterize the tree species composition of the greater landscape surrounding each of our sites, we used deciduous fraction and tree cover map products for the years 2010 and 2015 that were derived from 30 m resolution Landsat imagery (Massey et al. *in review*). We calculated the mean proportion of deciduous canopy of pixels in a 100 m buffer around each of our sites'

GPS coordinates. (Massey et al. 2022). We created additional spatial metrics based on outlining patches of deciduous forest by hand with ArcGIS Pro and high-resolution imagery from Planet Labs. However, as high-quality imagery was not available for all sites (and not all stands we measured were composed of discrete deciduous forest patches), our sample size was reduced from 239 to 129 plots for these metrics. Additionally, these patch-based metrics were unsuccessful in detecting any landscape composition effect on combustion in preliminary data exploration so they were excluded from our models.

Year-of-fire Climate Variance

Climate metrics were acquired for every site using ClimateNA (v7.30) software (Wang et al. 2016). Climate "normals" for each site were calculated as the thirty-year mean of each metric from 1981 to 2010. We extracted spring (March, April, and May) average temperature (°C) and total precipitation (mm). Year-of-fire climate variance from normal was calculated as the difference between the 30-year climate normal and the year-of-fire climate metric. Therefore, positive values indicated greater than normal mean temperatures or precipitation accumulations and negative values indicated lower than normal spring temperatures or precipitation accumulations.

Statistical Analyses

Comparing C Pools and Combustion Among Stand Types

We acquired pre-existing data from burned conifer stands (Mack et al. 2021a) for use in a comparison with the burned mixed, aspen, and birch stands we sampled. To ensure appropriate comparisons between our data and the (Mack et al. 2021a) data, for all analyses including conifer data the aboveground C pool only included tree C. We tested for pool size differences among stand types in aboveground, belowground, and total (above plus below) C pools for pre-fire, post-fire, and combusted C pools. We also tested for differences in proportional combustion (combusted C / pre-fire C) among stand types in aboveground, belowground, and total C pools. We used General Least Squares (GLS) models in the R package nlme (Pinheiro et al. 2023) with varIdent variance structures to account for hetereroscedascity among stand types and Gaussian spatial correlations to account for the spatial non-independence of plots located within sites and fire scars. Aboveground and belowground C pools were assessed for outliers with Bonferroni Outlier Tests that assessed for points that violated normality assumptions using the R package car. 22 outlier plots were removed for all subsequent analyses that included cross-stand type comparisons (Fox et al. 2023). Shapiro-Wilk Normality tests were conducted using the R core package stats (R Core Team 2023). Model heteroscedasticity was assessed visually using Q-Q plots and fitted values versus residuals using the R package performance (Lüdeck et al. 2023). When models still violated GLS assumptions after applying variance and spatial correlation structures, we tested and applied log or square root response variable transformations if they improved model assumptions. Model fit estimates (means and standard errors), p-values, and t-values were obtained with the R packages emmeans (Lenth et al. 2023) and sjPlot (Lüdecke et al. 2023) and base R (R Core Team 2023).

Comparing Wildfire-caused Tree Mortality and Scorching Among Mixed, Aspen, and Birch Stands

We designated each plot as having experienced complete mortality (0% of trees survived fire) or incomplete mortality (>0% of trees survived fire). To investigate if mortality differed between stand types, we calculated the proportion of plots of each stand type that experienced complete mortality and compared the numbers across stand types qualitatively.

We compared how mean deciduous trunk scorch height differed among stand types using linear regressions (R Core Team 2023). We extracted modeled mean scorch heights for each stand type using the emmeans package (Lenth et al. 2023). To examine scorch height's effectiveness as a proxy for fire severity, we used linear regressions to see if there was a significant relationship between mean plot scorch height and both absolute and proportional aboveground and total C combustion (R Core Team 2023).

Assessing Drivers of Combustion in Mixed, Aspen, and Birch Stands

To assess drivers of absolute and proportional C combustion in mixed, aspen, and birch stands, we created models using all the variables we hypothesized would drive fire severity as predictors (Table 1). We included shrub C in our measures of aboveground C for these analyses (on average, shrub C comprised only 3.1 ± 0.6% of pre-fire aboveground C in our sites, but accounted for 14.6 ± 1.6% of aboveground combusted C). We tested the strength of our hypothetical model for predicting absolute and proportional aboveground, belowground, and total C combustion in each stand type using GLS models with Gaussian spatial correlations to account for the spatial non-independence of plots located within sites and fire scars using the R package nlme (Pinheiro et al. 2023). All predictor variables were scaled (R Core Team 2023). For each model, we examined residual plots for homoscedasticity and normality and, as needed, applied the appropriate correlation structures (fixed, power, or exponential variance structures)(R Core Team 2023). We extracted the significance and standardized coefficient effect size for each predictor variable and the model R^2 using the base R summary function and the R package sjPlot

(R Core Team 2023, Lüdecke et al. 2023). We also extracted the estimated marginal mean effect of each predictor variable when all of the other variables were held constant at their means using the package emmeans (Lenth et al. 2023). We extracted each predictor variable's slope from each full model for creating figures using the R package effects (Fox et al. 2022).

Table 1: Bottom-up and Top-down Variable Means. Raw mean (± SE) and range (minimum – maximum) of bottom-up and top-down drivers at our sites and the hypothesized directionality of relationships between each driver and combustion (Absolute / Proportional, where N is negative and P is Positive). Aboveground (tree plus shrub) and belowground (SOL) C are measured in (g C m^{-2}). Deciduous index is the measured % deciduous tree biomass and density of each plot. Stand age is the age in years of trees in each plot at the time of fire. 10-year EVI2 trend is the slope of the linear relationships between year and mean summer EVI2. The 100 m buffer average deciduous is the remotely-sensed mean deciduous canopy of a 100 m buffer around each site (Massey et al. in review). Year-of-fire climate variance metrics were calculated by subtracting the year-of-fire mean metric (mean spring temperature or total precipitation) from the mean of a 30-year period from 1981 – 2010.

Variable Group		Variable	Mixed Stands (n = 61)		Aspen Stands (n = 93)		Birch Stands (n = 85)		Hypothesis
Bottom-Up Drivers	Stand Characteristics	Aboveground C	4907 ± 458	(209 - 17478)	5316 ± 458	(736 - 20593)	7389 ± 545	(219 - 26861)	(N / N)
		Belowground C	3917 ± 196	(2474 - 9622)	2401 ± 85	(1255 - 6542)	4531 ± 168	(2457 - 10211)	(P / N)
		Deciduous Index	55 ± 1	(35 – 66)	87 ± 1	(66 – 100)	93 ± 1	(66 – 100)	(N /N)
		Stand Age	84 ± 3	(43 - 165)	93 ± 2	(43 - 196)	91 ± 3	(63 - 212)	(P / N)
	Vegetation Stress Trends	10-year EVI2 Trend	-0.0009 ± 0.0004	(-0.0052 - 0.0061)	-0.0014 ± 0.0003	(-0.0060 - 0.0086)	-0.0020 ± 0.0003	(-0.0079 - 0.0033)	(N / N)
	Landscape Composition	100m buffer Avg. Deciduous	34 ± 2	(7 - 75)	36 ± 1	(4 - 69)	52 ± 1	(10 - 89)	(N / N)
Top-down Drivers	Year-of-fire Climate Variance	Spring Temperature	2.8 ± 0.1	(-1.8 - 3.8)	2.8 ± 0.1	(-1.8 - 3.8)	1.8 ± 0.3	(-1.8 - 3.8)	(P /P)
		Spring Precipitation	8 ± 1	(-14 - 37)	6 ± 1	(-14 - 29)	17 ± 1	(-14 - 38)	(N /N)

Additionally, we conducted separate analyses to assess the effect of aspen canker pathogen stress on wildfire C combustion on the subset of our plots that contained aspen trees (n = 145). We compared absolute and proportional total and tree C combustion in plots where aspen canker was present to plots where aspen canker was not present using GLS models with spatial correlation structures using the package nlme (Pinheiro et al. 2023) and extracted model means using the emmeans package (R Core Team 2023, Lenth et al. 2023). We also compared absolute and proportional C combustion between individual aspen trees with and without canker using simple linear regressions and extracted model means using the emmeans package (R Core Team 2023, Lenth et al. 2023).

RESULTS

C Pools and Absolute C Combustion Across Stand Types

Mixed, aspen, and birch stands combusted less C and retained more C post-fire than conifer stands (Figure 2; Supplemental Table F). This effect was largely due to the differential distribution of C among stand types: mixed, aspen, and birch stands stored the bulk of their C in aboveground pools that were fairly combustion-resistant while conifer stands stored most of their C in belowground pools that were highly susceptible to combustion (Figure 2; Supplemental Table F).

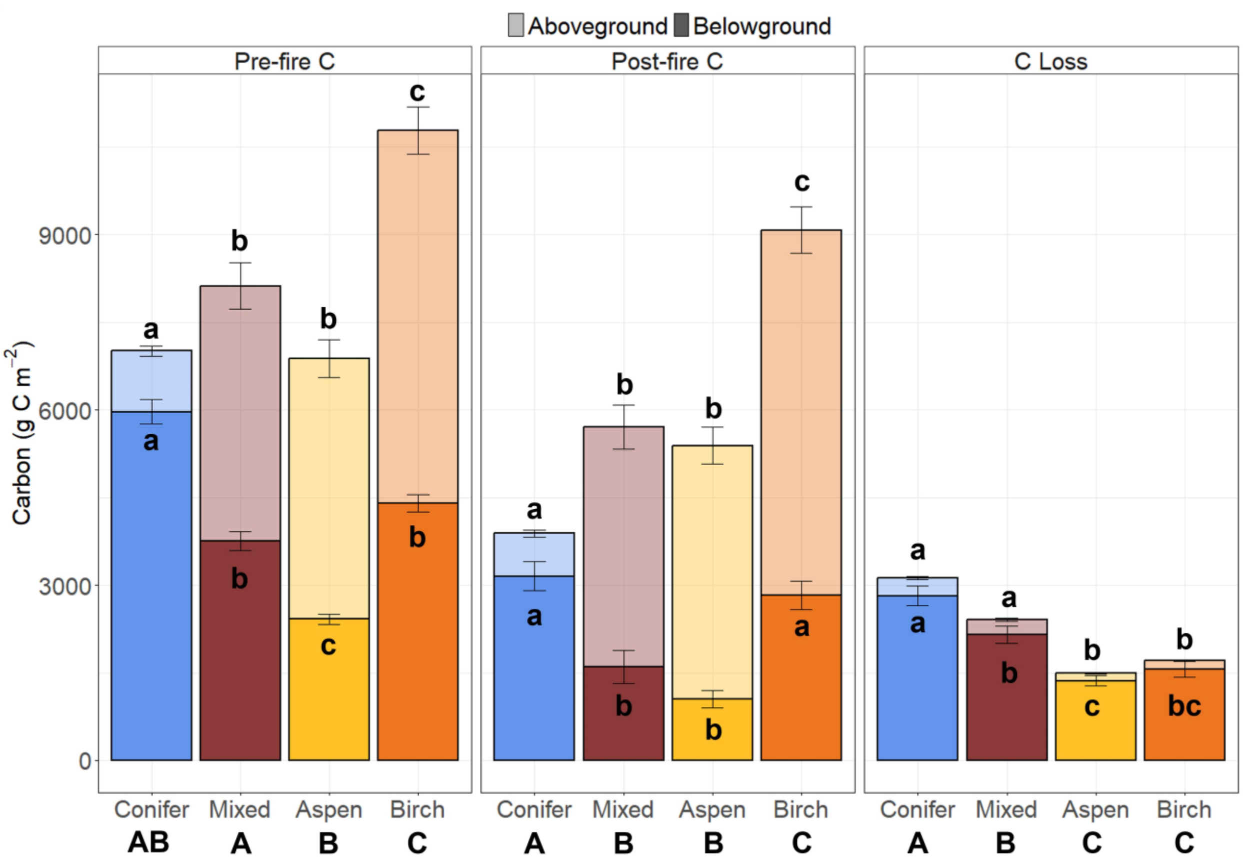


Figure 2: Pre-fire C, Post-fire C, and C Loss in aboveground, belowground, and total C pools among stand types. Lowercase letters above bars denote significant differences among stand types in aboveground pools, lowercase letters in lower bars denote significant differences among belowground pools, and uppercase letters below the graph denote significant differences

in total (aboveground plus belowground) C pools. Error bars are raw standard errors (±1 SE of the mean). (For model statistics see Supplemental Table F.)

Aboveground C pools and losses varied across stands. Pre-fire aboveground C pools were more than four times as large in mixed and aspen stands as in conifer stands and more than six times as large in birch stands as in conifer stands (Figure 2; Supplemental Table F). Mixed, aspen, and birch stands retained substantially more aboveground C post-fire than conifer stands (more than five times as much in mixed and aspen stands and nearly nine times as much in birch stands, Figure 2; Supplemental Material: Table F). Birch and aspen stands lost significantly less aboveground C to combustion than mixed or conifer stands (Figure 2; Supplemental Material: Table F). Across stand types, aboveground combustion accounted for only a small fraction of total C loss (10% for conifer stands, 11% for mixed stands, and 8% for both aspen and birch stands).

Belowground C pools and losses varied with stand type. Aspen stands had the smallest pre-fire belowground C pools – less than half as much as conifer stands, which contained the most. Post-fire, birch and conifer stands retained the most residual belowground C. Aspen stands lost the least belowground C to combustion and conifer stands lost significantly more than any other stand type (Figure 2; Supplemental Material: Table F). Regardless of stand type, the majority of C lost came from the combustion of belowground SOL (90% for conifer stands, 89% for mixed stands, and 92% for both aspen and birch stands).

Lastly, total C pools and losses were different in different stand types. Birch stands had the largest total pre-fire and post-fire C pools. Conifer stands retained significantly less total post-fire C than all other stand types. In total, aspen and birch stands lost around half as much C to combustion as conifer stands and mixed stands lost around three-quarters as much C to combustion as conifer stands (Figure 2; Supplemental Table F).

Proportional C Loss Across Stand Types

Mixed, aspen, and birch stands combusted a significantly smaller fraction of their aboveground C pools than conifer stands (Figure 3, see Supplemental Table F), likely due to the relative fire-resistance of deciduous tree biomass compared with conifer tree biomass. However, the proportional combustion of belowground C pools was comparatively much more homogenous across stand types (Figure 3, see Supplemental Table F). The only significant difference in proportional combustion of belowground C was between birch and mixed stands: birch stands experienced significantly less proportional combustion of their belowground C than mixed stands (Figure 3, see Supplemental Table F). Overall, mixed, aspen, and birch stands experienced significantly less proportional total combustion than conifer stands (see Supplemental Table F).

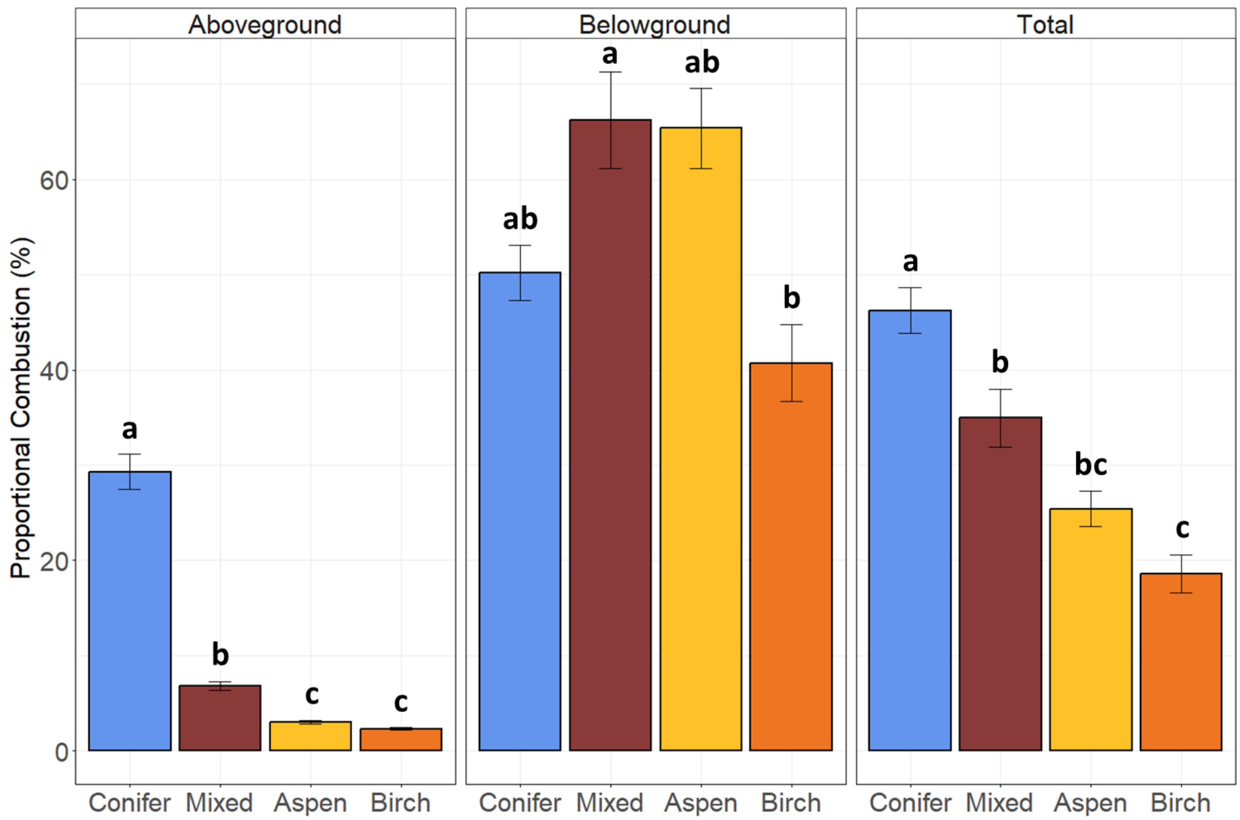


Figure 3: Proportional C Loss in aboveground, belowground, and total C pools among stand types. Letters above bars denote significant differences in the proportion of pre-fire C that was combusted in each pool (aboveground, belowground, or total). Error bars are raw standard errors (±1 SE of the mean). (For model statistics see Supplemental Table F.)

Wildfire-caused Tree Mortality and Scorching

We assessed tree mortality and trunk scorching as additional metrics of fire severity in mixed, aspen, and birch stands. Mortality was nearly ubiquitous in our study sites: only 77 out of 2,436 (3.1%) total trees inventoried survived fire (21 out of 782 [2.7%] in mixed stands, 6 out of 750 [0.1%] in aspen stands, and 50 out of 904 [5.5%] in birch stands). However, we observed that complete mortality (0% tree survival in a plot) was less common in the birch-dominated plots we measured (77% of birch plots had at least one surviving tree) than in mixed (90% of mixed plots had at least one surviving tree) or aspen plots (98% of aspen plots had at least one surviving tree).

The height of deciduous trunk scorching was highest on the deciduous stems in mixed plots (287 ± 17 cm), next highest in birch-dominated plots (261 ± 9 cm), and lowest in aspen-dominated plots (210 ± 8 cm). Average scorch height was significantly higher in mixed stands than in aspen stands ($P = 0.02$), but birch stand average scorch height was not significantly different from either aspen or mixed stands. Mean plot scorch height was significantly ($P < 0.05$) greater in sites that experienced higher absolute tree combustion ($R^2 = 0.17$), proportional tree combustion ($R^2 = 0.11$), and absolute total combustion ($R^2 = 0.05$). Plot scorch height was not significantly related to plot proportional total combustion.

Drivers of C Combustion in Mixed, Aspen, and Birch Stands

Drivers of absolute and proportional C combustion varied across stand type (mixed, aspen, or birch) and C pool (aboveground (Figure 4), belowground (Figure 5), or total (Supplemental Figures E & F)), but some common trends emerged. Models of belowground and total combustion were very similar, likely due to belowground C losses accounting for approximately 90% of total C combustion across stand types. (For results of total C combustion models, see Table 2 and Supplemental Materials: Drivers of Total C Combustion & Figures E & F). Every combustion response metric we tested was significantly related to at least one of our bottom-up driver predictor variables (Tables 2 & Table 3). Contrastingly, no top-down drivers were significantly related to any of our combustion metrics in mixed or aspen stands. Though absolute and proportional belowground and total combustion in birch stands were significantly lower following springs with greater precipitation accumulation.

Table 2: Absolute C Combustion Driver Standardized Coefficients. Model fit (R^2) and predictor variable standardized coefficient effect sizes (±1 SE of the mean) of fitted absolute C

combustion driver models in mixed, aspen, and birch stands. Driver variables with effect sizes in bold were significant ($P < 0.05$). “AG” is pre-fire aboveground C, “BG” is pre-fire belowground C, “Age” is stand age, “DI” is plot deciduous index, “EVI” is 10-year EVI2 trend, “100m” is the 100 m buffer mean deciduous canopy, “Temp” is the year-of-fire mean spring temperature variance from normal, and “Precip” is the year-of-fire total spring precipitation variance from normal. For model estimated mean marginal effects, see Supplemental Table G.

Combustion Response		Variance Structure	Bottom-up Drivers						Top-down Drivers		R^2
			AG	BG	Age	DI	EVI	100m	Temp	Precip	
Aboveground Combustion	Mixed	varFixed (AG)	**219 ± 43**	45 ± 35	8 ± 35	-10 ± 27	25 ± 31	28 ± 34	38 ± 31	-1 ± 32	0.40
	Aspen	varExp (Temp)	**75 ± 12**	7 ± 10	**-29 ± 13**	**-45 ± 11**	19 ± 12	-10 ± 13	20 ± 10	-3 ± 13	0.49
	Birch	varPower (BG)	**81 ± 9**	-10 ± 8	4 ± 12	**-49 ± 9**	**27 ± 10**	-7 ± 12	1 ± 24	-17 ± 22	0.45
Belowground Combustion	Mixed	varPower (EVI)	208 ± 151	**-796 ± 127**	-189 ± 130	-126 ± 112	132 ± 138	-91 ± 102	69 ± 157	5 ± 106	0.51
	Aspen	varFixed (BG)	100 ± 68	**-424 ± 71**	28 ± 91	-23 ± 58	47 ± 88	43 ± 88	108 ± 104	5 ± 92	0.28
	Birch	None	**-312 ± 140**	**-289 ± 122**	167 ± 129	-12 ± 124	37 ± 144	-32 ± 147	174 ± 152	**-604 ± 142**	0.40
Total Combustion	Mixed	varFixed (Age)	**433 ± 189**	**-802 ± 128**	-267 ± 158	-125 ± 122	**246 ± 118**	-137 ± 131	88 ± 147	42 ± 130	0.55
	Aspen	varFixed (BG))	**190 ± 72**	**-401 ± 78**	11 ± 89	-93 ± 64	58 ± 86	46 ± 86	129 ± 102	-5 ± 90	0.34
	Birch	None	-223 ± 142	**-288 ± 124**	168 ± 131	-66 ± 125	65 ± 147	-36 ± 150	180 ± 155	**-613 ± 145**	0.40

Table 3: Proportional C Combustion Driver Standardized Coefficients. Model fit (R^2) and predictor variable standardized coefficient effect sizes (± SE) of fitted proportional C combustion driver models in mixed, aspen, and birch stands. Driver variables with effect sizes in bold were significant ($P < 0.05$). “AG” is pre-fire aboveground C, “BG” is pre-fire belowground C, “Age” is stand age, “DI” is plot deciduous index, “EVI” is 10-year EVI2 trend, “100m” is the 100 m buffer mean deciduous canopy, “Temp” is the year-of-fire mean spring temperature variance from normal, and “Precip” is the year-of-fire total spring precipitation variance from normal. For

model estimated mean marginal effects, see Supplemental Table G.

Combustion Response		Variance Structure	Bottom-up Drivers						Top-down Drivers		R^2
			AG	BG	Age	DI	EVI	100m	Temp	Precip	
Aboveground Combustion	Mixed	varFixed (BG)	-1.15 ± 0.91	0.88 ± 0.92	-0.44 ± 0.84	**-1.83 ± 0.7**	1.17 ± 0.7	0.06 ± 0.68	1.14 ± 0.93	-0.19 ± 0.7	0.32
	Aspen	None	**-1.61 ± 0.59**	0.14 ± 0.61	**-1.8 ± 0.6**	**-1.18 ± 0.59**	**1.35 ± 0.59**	-0.74 ± 0.61	0.73 ± 0.65	-0.16 ± 0.6	0.26
	Birch	varPower (AG)	-0.25 ± 0.16	0.05 ± 0.18	-0.06 ± 0.16	**-1 ± 0.2**	0.26 ± 0.19	0.14 ± 0.22	0 ± 0.21	0.01 ± 0.19	0.35
Belowground Combustion	Mixed	varFixed (Age)	8.72 ± 6.05	**-29.98 ± 4.1**	-6.98 ± 5.06	-1.74 ± 3.92	3.74 ± 3.79	-3.01 ± 4.22	0.34 ± 4.72	-2.29 ± 4.17	0.57
	Aspen	varPower (BG)	5.19 ± 3.21	**-31.08 ± 3.54**	-0.31 ± 3.75	0.92 ± 2.9	-0.2 ± 3.66	0.9 ± 3.65	4.17 ± 4.34	-1.8 ± 3.8	0.43
	Birch	varPower (BG)	**-9.16 ± 3.15**	**-11.55 ± 2.01**	5.52 ± 3.18	-0.5 ± 2.8	-0.62 ± 3.05	-0.27 ± 3.29	5.68 ± 3.08	**-13.08 ± 3.24**	0.48
Total Combustion	Mixed	varFixed (BG)	**-6.21 ± 2.67**	**-13.73 ± 2.68**	**-5.74 ± 2.46**	-2.82 ± 2.06	**4.66 ± 2.03**	-2.14 ± 1.99	1.02 ± 2.72	-1.71 ± 2.05	0.62
	Aspen	None	**-7.2 ± 1.49**	**-6.96 ± 1.46**	-2.22 ± 1.53	-1.7 ± 1.46	-0.01 ± 1.5	1.88 ± 1.56	3.29 ± 1.67	-1.98 ± 1.53	0.44
	Birch	None	-8.09 ± 1.86	**-4.57 ± 1.55**	0 ± 1.8	0.89 ± 1.59	0.19 ± 1.91	-0.52 ± 1.93	2.96 ± 2.02	**-4.01 ± 1.88**	0.40

Drivers of Aboveground C Combustion

Counter to our expectations, aboveground combustion increased when pre-fire aboveground C pools were larger in all stand types (Figure 4: 1A, Table 2). Additionally, pre-fire aboveground C had the largest effect on absolute aboveground combustion across stand types (Table 2). Proportional aboveground C combustion decreased with greater pre-fire aboveground C in aspen stands (as expected), but not in birch or mixed stands (Figure 4: 1B, Table 3). Aboveground combustion was not significantly related to stand age in mixed or birch stands, but older aspen stands tended to experience less absolute and proportional aboveground combustion (Figure 4: 2A & 2B). In all but one case (mixed stand absolute combustion), the more deciduous a stand was, the less absolute and proportional aboveground C combustion occurred (Figure 4: 3A & 3B, Tables 2 & 3). Notably, how deciduous a plot was was the only significant predictor of proportional aboveground combustion in mixed and birch stands. Lastly, aspen stand proportional aboveground combustion and birch stand absolute aboveground combustion were both greater when 10-year EVI2 trends were higher, meaning that, contrary to our expectations, more combustion occurred if the stands trended greener over the 10 years preceding fire (Figure 4: 4A & 4B, Tables 2 & 3). None of the remaining predictor variables we included in our models (pre-fire belowground C pools, % deciduous canopy of a 100 m buffer, spring temperature, or spring precipitation) were significant predictors of absolute or proportional aboveground C combustion in any stand type (Supplemental Figure B, Tables 2 & 3).

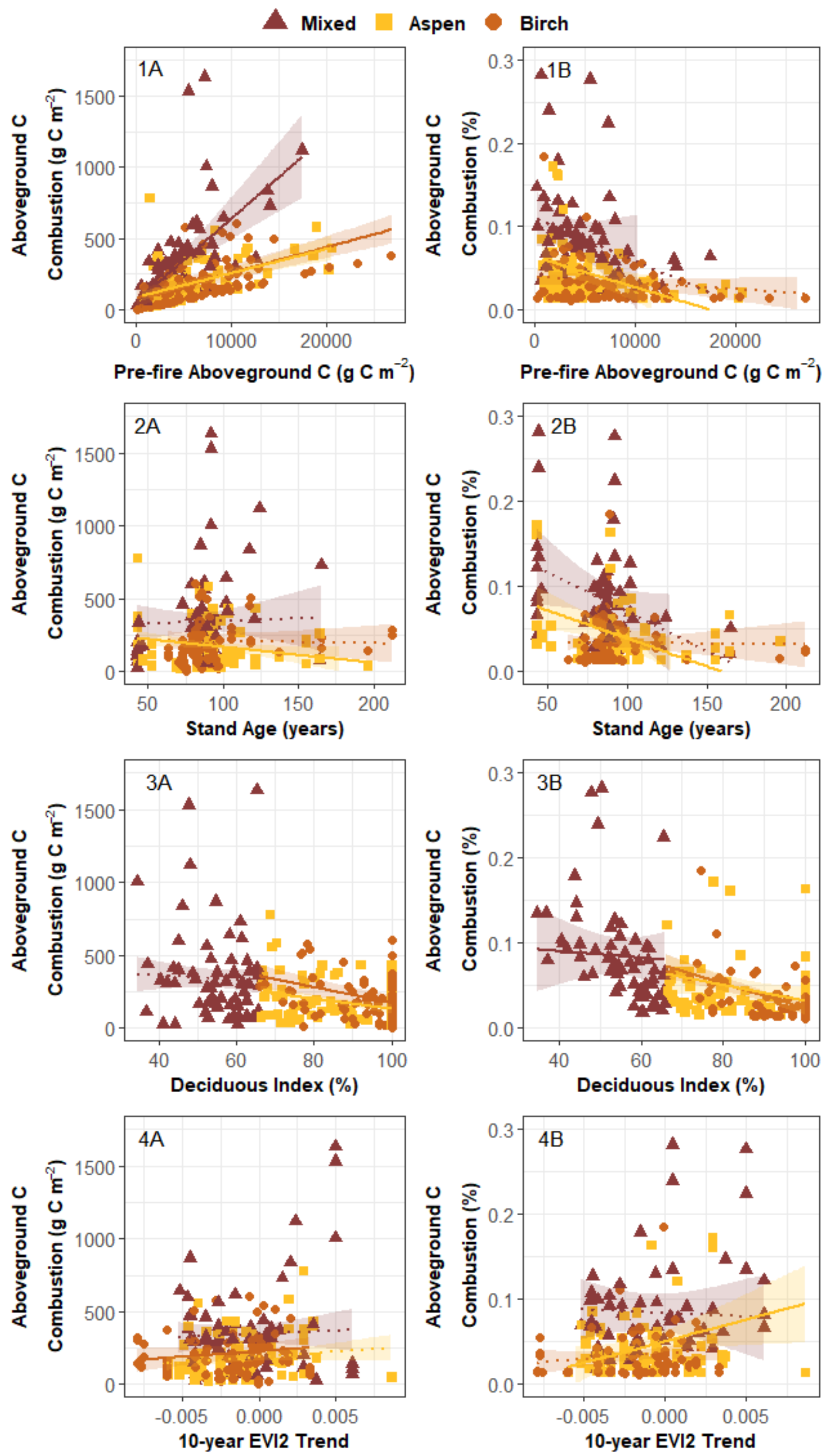


Figure 4: Drivers of Aboveground C Combustion. Relationship between aboveground combustion and selected hypothetical fire severity predictor variables in mixed, aspen, and birch stands. Trend lines are solid lines if the variable was a significant predictor ($P < 0.05$) of the

combustion response metric in full model, otherwise trend lines are dotted (Tables 2 & 3). For variables not included in this figure, see Supplemental Table B.

Drivers of Belowground C Combustion

Absolute and proportional belowground combustion decreased with increasing pre-fire aboveground C in birch stands, but not in mixed and aspen stands (Figure 5: 1A & 1B, Tables 2 & 3). In all stands, absolute and proportional belowground combustion decreased with pre-fire belowground C (Figure 5: 2A & 2B, Tables 2 & 3). This result was counter to our hypotheses for absolute belowground combustion, but supported our hypotheses for proportional belowground combustion. Further, pre-fire belowground C was the only significant predictor of absolute and proportional belowground combustion in mixed and aspen stands. In birch stands, absolute and proportional belowground combustion were greater if less precipitation accumulated in the spring than normal. Spring precipitation had the largest effect on birch belowground combustion of any predictor we tested (Figure 5 3A & 3B, Tables 2 & 3). None of the other predictor variables impacted belowground combustion (Supplemental Figures C & D, Tables 2 & 3).

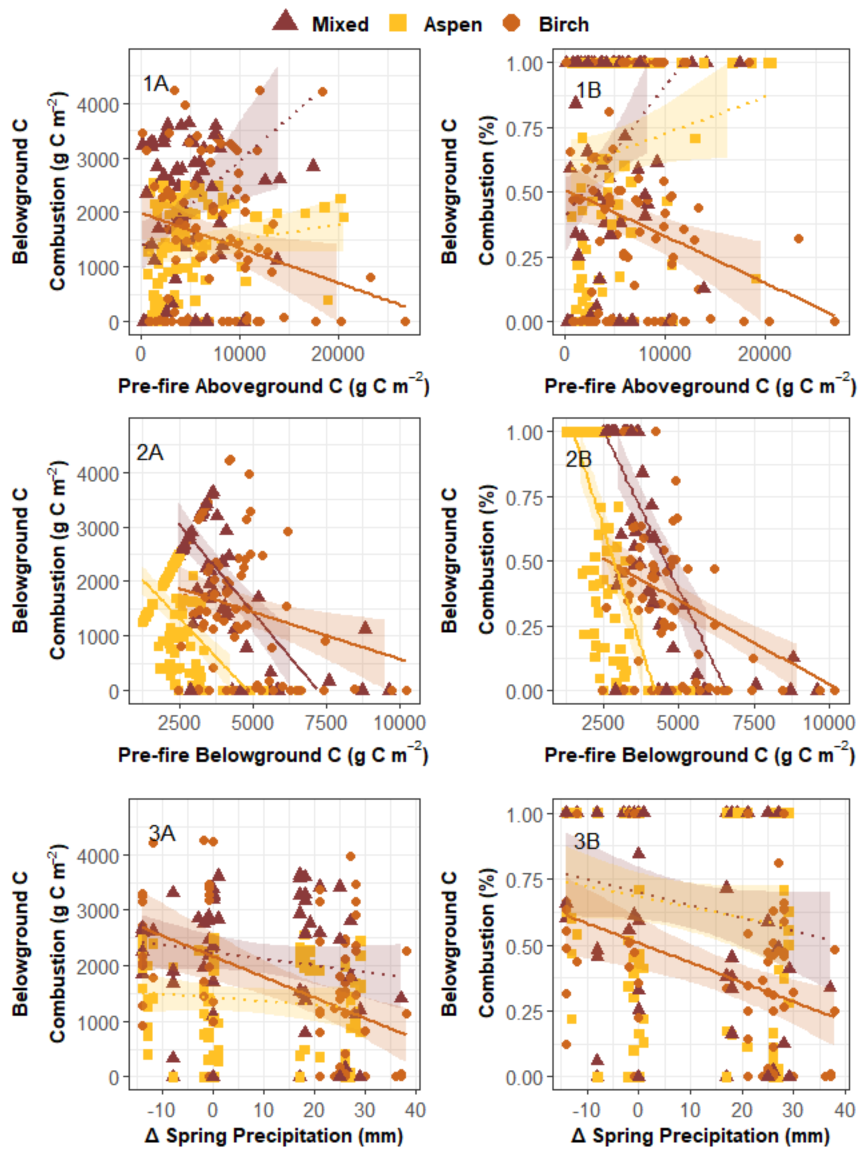


Figure 5: Drivers of Belowground C Combustion. Relationship between belowground combustion and selected hypothetical fire severity predictor variables in mixed, aspen, and birch stands. Trend lines are solid lines if the variable was a significant predictor ($P < 0.05$) of the combustion response metric in full model, otherwise trend lines are dotted (Tables 2 & 3). For variables not included in this figure, see Supplemental Figures C & D.

Aspen Canker as a Driver of C Combustion

Aspen canker was present in 55% of the plots that contained aspen trees and, overall, 33% of individual aspen trees surveyed had aspen canker. Trees in plots with aspen canker did not experience significantly different mean absolute or proportional total or aboveground combustion than plots without any aspen canker (See Supplemental Table H). However, individual tree absolute combustion was significantly (R^2 adjusted = 0.02, $P < 0.001$) greater in aspen trees afflicted with aspen canker (779 ± 53 g C m^{-2}) than those that were unafflicted (526 ± 34 g C m^{-2}). Similarly, individual tree proportional combustion was significantly (R^2 adjusted= 0.02, $P = 0.006$) greater in aspen trees afflicted with aspen canker (2.6 ± 0.2 %) than those that were unafflicted (2.2 ± 0.1 %).

DISCUSSION

Differences in C Pools and Combustion Across Stand Types

While other studies have documented the ability of deciduous trees to reduce ignitions (Krawchuk et al. 2006), fire probability (Cumming 2001, Bernier et al. 2016, Dash et al. 2016, Hart et al. 2019), area burned (Marchal et al. 2017), and containment failure (Arienti et al. 2006), our study is the first to demonstrate that wildfires combust less C in mixed and deciduous stands than wildfires in conifer stands in western North American boreal forests. On average, birch and aspen stands lost around half as much and mixed stands lost around three-quarters as much C to wildfire combustion as the dominant stand type, black spruce. Furthermore, mixed, aspen, and birch stands lost proportionally less of their pre-fire C than conifer stands. For mixed and aspen stands, this effect was not, as we had expected, due to much larger pre-fire total C pools (mixed and aspen stands did not have significantly more pre-fire C than conifer stands), but rather to lower proportional losses of C. Interestingly, only birch stands had significantly more total pre-fire C than conifer stands and birch stands lost the least C proportionally. The differences in combustion were likely caused by disparate distributions of C between aboveground and belowground pools and the relative flammability of those pools among stand types. The majority of C loss came from the combustion of belowground fuels for all stand types, but mixed and deciduous stands stored much less of their C in combustion-available belowground pools than conifer stands. Instead, mixed and deciduous stands stored the majority of their pre-fire C in aboveground pools that experienced relatively little combustion.

Aboveground C Pools and Combustion

Aboveground C combustion accounted for only a small fraction of total wildfire C loss across all stand types. Consistent with previous studies, we found mixed, aspen, and birch stands had significantly larger pre-fire aboveground C pools than conifer stands (Alexander et al. 2012, Mack et al. 2021a). However, we also found that mixed and deciduous stands lost proportionally less of their pre-fire aboveground C pools to combustion than conifer stands. These effects may be caused by differences in the traits of aspen, birch, and black spruce trees. Aspen and birch trees have higher leaf and stem wood moisture content and lack the resin and ladder fuels that characterize black spruce trees (Johnson 1996). Additionally, aspen and birch trees allocate less C to leaves and fine branches than black spruce, and therefore have more C locked in fire-resistant stem wood (Alexander et al. 2012). While previous research did not detect significant differences between the aboveground C pools of mature birch and aspen stands (Alexander and Mack 2016), the birch stands we measured contained significantly more pre-fire aboveground C than aspen. Since birch and aspen stands lost comparable amounts of aboveground C to combustion, birch stands ended up with significantly more post-fire aboveground C than aspen stands.

Belowground C Pools and Combustion

Consistent with previous studies (Boby et al. 2010, Turetsky et al. 2011, Walker et al. 2018a, 2018b, 2020), we found the bulk of C losses in conifer stands came from the combustion of belowground C pools. We also found the same to be true for mixed, aspen, and birch stands. Because proportional combustion of belowground C did not vary substantially among stand types, the differences in absolute belowground C loss we observed resulted from differences in pre-fire belowground C pool sizes. Conifer stands store 60-85% of their surficial, combustion-available C belowground (Boby et al. 2010, Alexander and Mack 2016). We found that for both aspen and birch stands, pre-fire belowground C only accounted for around 40% of total pre-fire C. Alexander and Mack (2016) found similar distributions of C in mature unburned birch stands, but reported only ~20% of total C was belowground for unburned aspen stands. Notably, that study only included two mature aspen stands. We also expanded upon that previous research (Alexander and Mack 2016) by parsing out an intermediate class—mixed stands—that stored around 50% of their C in belowground pools.

Mixed and deciduous stands had smaller pre-fire belowground C pools than conifer stands, likely as a result of the inhibition of moss growth caused by deciduous leaf litter inputs (Natalia et al. 2008, Jean et al. 2017, 2020). Consistent with previous work (Alexander and Mack 2016), birch stands had significantly more belowground C than aspen stands: an amount comparable with mixed stands. Previous work has highlighted the greater occurrence of aspen stands in warmer, well-drained parts of the landscape as compared with birch stands (Van Cleve and Alexander 1981, Van Cleve et al. 1983). Warmer SOL conditions promote faster SOL turnover, possibly resulting in the differences we observed between aspen and birch pre-fire belowground pools (Van Cleve et al. 1983). Alternatively, differences in soil moisture, litter and woody debris C:N ratios, or understory vegetation compositions may also create conditions prone to faster decomposition or less organic soil accumulation in aspen stands.

Post-fire, mixed and aspen stands contained significantly less belowground C than conifer stands, whereas birch stand residual belowground C did not differ significantly from conifer stand residual belowground C. The small belowground C pool size of mixed stands compared with conifer stands could make mixed stands more likely to transition from mixed to deciduous-dominant forest following wildfire (Johnstone and Chapin III 2006, Johnstone et al. 2010b, 2020).

Total C Pools and Combustion

Our analysis showed pre-fire total C pools were similar among conifer, mixed, and aspen stands and were larger in birch stands, highlighting the importance of considering aspen and birch stands separately. For aspen stands, this finding aligns with previous research showing that total C pool size would remain relatively unchanged with a successional shift from conifer to aspen and birch trajectories (Alexander and Mack 2016). This study (Alexander and Mack 2016) classed stands aged 60-100 years together into a mature class and therefore may not have detected differences in total C pool sizes that developed even later in succession. The burned aspen and birch stands we surveyed were around 90 years old on average and ranged up to around 200 years old and therefore captured much older deciduous stands than the previous study. Our finding in birch stands is more consistent with previous research where aspen and birch were lumped into a single deciduous class and deciduous stands were found to contain significantly more total C than conifer stands at maturity (Mack et al. 2021a). Our study therefore highlights the importance of considering aspen and birch trajectories separately.

Mixed and deciduous stands lost less C to combustion and retained more residual C post-fire than conifer stands. This finding suggests that if the North American boreal forest becomes increasingly mixed and deciduous and those stands remain highly productive (Mann et al. 2012, Mekonnen et al. 2019, Hansen et al. 2021, Baltzer et al. 2021), more C will be sequestered on the landscape (Mack et al. 2021a), and less of it will combust in wildfire. However, even though aspen and birch stands lost comparable amounts of C to combustion, birch stands had greater total C pools post-fire than all other stand types. Future projections of boreal C pools and wildfire C losses should take the different pre- and post-fire pool sizes of aspen and birch stands into account.

Tree Mortality and Scorch Height in Mixed, Aspen, and Birch Stands

Complete mortality (0% tree survival in a plot) was less common in birch stands than in mixed or aspen stands. This result agrees with the differences we observed among stand types in our other metrics of fire severity. The survival of just one or a few trees in a stand could have implications for the trajectory of post-fire forest recovery. Following fire, deciduous trees readily resprout, giving them an advantage over slow-growing black spruce seedlings (Van Cleve and Alexander 1981, Van Cleve et al. 1983, Greene et al. 1999, Walker et al. 2023). Aspen and birch trees do not need to survive a wildfire to resprout and quickly recolonize their immediate surroundings following fire. Yet, a surviving deciduous tree in a large fire scar could produce windborne seeds that are able to spread to more severely burned portions of the fire scar in the critical window of establishment post-fire (Johnstone et al. 2020).

Even though birch stands were more likely to have one or more surviving trees post-fire, most trees in this study (97%) were still killed by fire. This near-complete mortality may have important implications in light of the shift from belowground to aboveground C pools that accompanies deciduous successional trajectories (Alexander and Mack 2016). Carbon that is protected from combustion in the form of deciduous trees will remain on the landscape post-fire in the form of dead biomass. Post-fire, aspen stands had six times and birch stands had nine times as much residual aboveground C as conifer stands. While this C is protected from instantaneous loss to the atmosphere at the time of fire, dead stems might fall and be assimilated into belowground C pools or they might ultimately be decomposed and respired to the atmosphere. Dead tree C may even remain locked on the landscape as woody debris until the next fire, at which time the C may be more likely to combust due to drying. The traits of deciduous tree woody debris—greater diameter boles (Alexander et al. 2012)—might slow its decomposition (Trofymow et al. 2002), causing deciduous tree woody debris to be a potentially more stable, longer-lasting repository of C on the landscape than black spruce woody debris. Alternatively, the chemical traits of deciduous woody debris may make it decompose more readily than conifer woody debris (Strukelj et al. 2013), resulting in C losses to the atmosphere. Understanding the fate of dead deciduous tree C will be critical for further comprehending what a more deciduous boreal forest means for the fate of boreal C.

Scorch height on deciduous stems was, as expected, highest in mixed stands. The effect could be caused by the fire-promoting traits of black spruce trees present in mixed stands (Johnson 1996). Scorch height was significantly lower in aspen stands than in mixed stands, but scorch height in birch strands did not differ significantly from scorch height in either mixed or aspen stands. Though by other metrics (complete mortality, belowground combustion) birch stands experienced less severe fire than aspen stands, a possible explanation for the greater scorch height in birch stands than in aspen stands is the divergent physiognomy and traits of aspen and birch trees. Birch trees have more flammable bark and ladder fuels that could carry flames upward into the tree crown than aspen trees even if neither tree species is likely to experience much significant stem wood combustion. Additionally, our analyses showed that scorch height was significantly correlated with several metrics of C combustion, meaning it could be a useful tool for rapidly assessing fire severity in the field.

Drivers of C Combustion in Mixed, Aspen, and Birch Stands

Despite the prevalence of wildfire risk indices (Wagner 1987, Field et al. 2015) that are informed by top-down drivers, recent work has highlighted the importance of bottom-up variables in driving C combustion in boreal conifer forests (Walker et al. 2018a, 2018b, 2020, Stralberg et al. 2020). We investigated multiple top-down and bottom-up variables as potential drivers of aboveground, belowground, and total wildfire C combustion in mixed, aspen, and birch stands. At least one bottom-up driver of combustion was significantly associated with every combustion response metric we tested. Conversely, only belowground and total birch C losses were significantly affected by a top-down driver of combustion.

A class of possible bottom-up drivers of combustion that we did not investigate were landscape topo-edaphic position metrics: slope, aspect, and moisture class. These metrics control the quantity and availability of belowground fuel loads and are consequently among the most influential drivers of combustion in some boreal conifer forests (Walker et al. 2018a, 2018b, 2020, Stralberg et al. 2020). However, we used slope, aspect, and moisture class to model pre-fire soil depth, and therefore could not include them in our fire severity models alongside pre-fire soil depth without confounding our models. Yet, as these landscape topo-edaphic position metrics were important drivers of soil depth, which in turn was an important driver of belowground and total C combustion in our sites, it is likely that they play an important role in driving fire severity in boreal mixed, aspen, and birch stands. Greater plot slope was associated with thinner SOL depth, north-facing aspects were associated with greater SOL depths than south-facing aspects, and grater plot moisture was associated with deeper SOLs. Thus, plots that were poorly-drained and wetter tended to have larger SOL C pools.

The metric we used to investigate possible spatial effects of surrounding forest species' traits on fire severity (the % deciduous canopy in a 200 m radius buffer around each site) was not significantly associated with combustion for any C pool or stand type. One explanation for this is that C combustion in stands is not influenced by the species traits of trees in their greater surroundings. Yet, we observed many unburned patches of deciduous forest within burn scars (see Supplemental Figure G) which leads us to suppose that the lack of significance could be due to the metrics that we assessed not appropriately capturing such a spatial effect. The fire scars we surveyed in this study were all predominantly black spruce matrices containing patches of mixed and deciduous forest (Figure 1). The fact that we did not identify any fire scars to sample that were predominantly deciduous may be indicative of a spatial effect of black spruce on wildfire severity in deciduous stands. Landscapes more fragmented with deciduous trees may lower the overall severity of wildfire (Johnstone et al. 2011). Possibly, landscapes dominated by deciduous trees seldom burn, potentially explaining why we only found small patches of burned deciduous trees within burned black spruce-dominant forests to sample. Indeed, studies using larger scale remote-sensing or modeling approaches have documented the fire-limiting effects of deciduous trees (Cumming 2001, Rupp et al. 2002, Epting and Verbyla 2005, Krawchuk et al. 2006, Duffy et al. 2007, Marchal et al. 2017, Rupasinghe and Chow-Fraser 2021, Foster et al. 2022). Future studies should seek to quantify how the spread and directionality of fire in relation to the surrounding tree composition relate to wildfire C loss in deciduous stands.

Drivers of Aboveground C Combustion in Mixed, Aspen, and Birch Stands

Across mixed, aspen, and birch stands, how proportionally deciduous a plot was and/or how much aboveground biomass it contained pre-fire were the strongest drivers of aboveground

C combustion. As expected, plots that were more proportionally deciduous had lower absolute and proportional aboveground combustion (this effect was not significant for mixed stand absolute aboveground combustion, but the trend was the same). This result was likely due to comparatively fire-resistant traits of deciduous trees: a lack of resin, less C allocation to fire available components such as leaves and fine branches, and comparatively more C allocation to wet, fire-resistant boles than black spruce trees (Alexander et al. 2012). Aboveground C losses were greater in stands with more pre-fire aboveground biomass, implying that deciduous tree biomass does not directly constrain fire severity, as we had expected it might, via the facilitation of a wetter, less fire-promoting local microclimate. Instead, more pre-fire aboveground C meant more combustion-available fuel. However, as expected, stands with greater aboveground biomass experienced lower proportional aboveground combustion, likely because the larger a deciduous tree is, the more of its C, proportionally, is stored in combustion-unavailable boles (Alexander et al. 2012).

Older aspen stands experienced less proportional aboveground C combustion, likely due to the link between stand age and the distribution of aboveground biomass between available and unavailable tree components: larger trees have proportionally more of their aboveground C stored in stems than in leaves and branches than smaller trees. However, stand age is also linked with the accumulation of combustion-available snags and woody debris. Previous work has shown how, at maturity, deciduous stands begin to accumulate snags and woody debris due to the onset of senescence (Alexander et al. 2012). The combustion of those snags may increase the overall residency time and intensity of fire in a stand, possibly causing living tree biomass to gradually dry out and combust. Therefore, we expected that absolute aboveground combustion would be greatest in the oldest stands. Stand age was not a significant driver of aboveground combustion in mixed or birch stands. However, older aspen stands experienced lower absolute aboveground combustion. This result could be due to the extremely stratified physiognomy of aspen trees: they retain few low branches and therefore the largest (and likely oldest) aspen trees have little by way of ladder fuels. Additionally, the warmer, south-facing landscape positions that aspen tend to occur on (Van Cleve and Alexander 1981, Van Cleve et al. 1983) may promote fast decomposition of any senesced branches and snags, limiting the potential C pools available for combustion.

Pre-fire belowground biomass did not influence the combustion of aboveground biomass in mixed, aspen, or birch stands. Boreal wildfires can smolder for weeks to years (Scholten et al. 2021) after ignition in the deep SOL common in black spruce stands. Therefore, we expected that larger belowground fuel loads that could sustain fire longer might lead to greater tree combustion. However deciduous stands typically have comparatively shallower SOL than black spruce stands (Alexander and Mack 2016) and thus might only accumulate large quantities of organic soil under circumstances that make that organic soil especially combustion-resistant, such as in wet-parts of the landscape.

A surprising finding was greater aboveground C combustion in stands that had trended greener in the 10 years preceding fire, which was only significant for birch absolute aboveground combustion and aspen proportional aboveground combustion. We expected gradual vegetation browning pre-fire would serve as a proxy for trees experiencing stress and mortality (Rogers et al. 2015, Boyd et al. 2019, 2021) and would therefore be linked to greater aboveground fuel availability. Indeed, the presence of aspen canker was correlated with greater individual aspen tree combustion. Therefore, it is possible that the 10-year EVI2 metric we used did not capture the effect of climate- and pathogen-tree stress or, alternatively, that such stress did not increase C losses. However, in other Arctic ecosystems, greater productivity (measured via pre-fire NDVI trends) preceding fire has been linked to greater probability of fire and severe burning (Gaglioti et al. 2021). In tundra, it is conjectured that fire is limited by fuel availability, and greening pre-fire signals the accumulation of fuels. As EVI2 can capture changes in greenness caused by shrub growth, it is possible that higher productivity preceding fire in mixed and deciduous stands, similarly, results in more tree and shrub fuels available for combustion. This finding aligns with the relationship between combustion and pre-fire aboveground C pools we observed.

Neither of the top-down predictors we assessed (spring temperature and precipitation anomalies) significantly influenced aboveground combustion. While we had expected that spring temperature and precipitation potentially control “spring window” length (time between snowmelt and leaf flush when deciduous trees are particularly vulnerable to combustion (Parisien et al. 2023)), this finding is consistent with previous studies that have found climate metrics to be poor predictors of fire severity in boreal forests due to the overwhelming importance of bottom-up controls on fire severity (Walker et al. 2018b, 2020).

Drivers of Belowground and Total C Combustion in Mixed, Aspen, and Birch Stands

Our models of belowground and total combustion were very similar because the bulk of C combustion in mixed, aspen, and birch stands came from the combustion of belowground C. Absolute and proportional belowground and total C combustion were lowest in sites with the greatest pre-fire belowground C pools in every stand type (and almost always the most influential predictor). That proportional belowground C combustion was lowest in stands with the most SOL C pre-fire is consistent with trends in black spruce stands (Walker et al. 2018a). Pre-fire belowground C pools tend to be smallest in well-drained parts of the landscape that are likely to experience complete combustion and greatest in wet parts of the landscape where they are likely to experience only partial combustion (Walker et al. 2018a, 2018b, 2019, 2020, Stralberg et al. 2020). Yet we observed that absolute combustion was lowest in sites with the greatest pre-fire belowground C pool size, a finding inconsistent with the findings of previous studies in conifer dominated systems (Walker et al. 2019). In black spruce stands, greater C accumulation is correlated with stand age and moisture (Walker et al. 2018a, 2018b). It is conceivable that the only circumstances under which deciduous stands (which generally have significantly smaller SOL C pools than conifer stands (Alexander and Mack 2016)) accumulate greater SOL C pools is in cold, wet, decomposition-resistant parts of the landscape, resulting in larger SOL C pools that are more unavailable for combustion. This idea is supported by the trends demonstrated in our random forest models: wet, poorly-drained parts of the landscape had deeper SOLs.

We expected aboveground biomass to limit SOL C pool accumulation—via greater deciduous leaf litter inputs (Natalia et al. 2008, Jean et al. 2017, 2020)—and therefore limit absolute belowground and total C loss by virtue of smaller available SOL fuel loads. However, pre-fire aboveground and belowground C pools were not significantly correlated in any stand type in our preliminary analyses. Therefore, we were surprised that with greater pre-fire aboveground C, birch stands had lower absolute belowground C losses and mixed and aspen stands had greater absolute total C losses. A possible explanation for the effect in birch stands may be that birch stands with the greatest aboveground biomass tended to occur in more poorly-drained parts of the landscape—such as on palsas (see Supplemental Material: Figure H)—that made belowground C pools more unavailable for combustion. In contrast to birch stands, mixed and aspen stand belowground C combustion was not influenced by pre-fire aboveground C pools. The greater total C loss in mixed and aspen stands with greater pre-fire aboveground C then is likely attributable to the effect of pre-fire aboveground C on aboveground C losses in those stands.

Stand age only had a significant relationship with mixed stand proportional total combustion: older mixed stands experienced proportionally less total C loss. As stand age is linked to the accumulation of aboveground and belowground C pools (especially in stands with black spruce trees that characteristically accumulate thick SOLs with age (Jean et al. 2017)), the effect was probably due to greater fractions of C unavailable to combustion (deep, wet SOL C and C bound in tree boles). That the effect of stand age was only significant in mixed and not deciduous stands is consistent with research that has demonstrated the SOL C pools (which comprise the bulk of total C loss) increase with stand age in conifer, but not in deciduous stands (Jean et al. 2017, 2020, Mack et al. 2021a).

As we observed for aspen and birch aboveground C combustion, mixed stand total C combustion was significantly greater in stands that had trended greener in the 10 years preceding fire. Why deciduous stands only experienced a significant influence of vegetation greening on aboveground combustion, but mixed stands experienced a significant effect for total C combustion may have to do with the presence of black-spruce facilitated mosses in mixed stands. Deciduous trees inhibit moss growth (Natalia et al. 2008, Jean et al. 2020), so the lower fraction of deciduous trees in mixed stands probably allows more sphagnum and feather mosses to grow. It is plausible that while aspen and birch stand tree and shrub productivity drove the greening effect that resulted in greater aboveground C losses in deciduous stands, the greening effect in mixed stands is attributable to moss productivity and therefore, the accumulation of available belowground C.

Neither of the top-down drivers we tested (spring temperature or precipitation variance) was a significant predictor of belowground or total combustion in mixed or aspen stands. This is consistent with studies that have found climate metrics to be poor predictors of fire severity in boreal black spruce forests (Walker et al. 2018b, 2020). However, absolute and proportional belowground and total C combustion in birch stands were significantly greater following springs that received lower than normal precipitation. Moreover, spring precipitation had the strongest effect on combustion of any predictor in all but the birch absolute total C combustion model. Recent work has highlighted the importance of the window of time between snowmelt and deciduous tree leaf flush in driving early-season fires in deciduous stands (Parisien et al. 2023). Spring precipitation variance may be a proxy for this window: lower spring precipitation in the form of snow might hasten the melting of snow accumulated during the winter. It is possible that we observed an effect of spring precipitation variance on belowground, but not on aboveground C combustion because birch trees were not made any more combustion-available when they were leafless, but contrastingly, birch stand SOLs were able to dry out when incoming solar radiation was not blocked by snow or foliage. That birch stands contained more SOL C than aspen stands (and therefore have more fuel available for drying by a longer spring window), explains why we might see this effect for birch, but not aspen stands.

Implications of a More Deciduous Boreal Forest

Fire Self-Limitation in the Boreal Forest

As climate change increases the frequency and severity of wildfires in boreal black spruce stands, causing more of the landscape to transition from black spruce self-replacement to less flammable deciduous trajectories (Mann et al. 2012, Mekonnen et al. 2019, Baltzer et al. 2021), we can expect to see more C sequestered on the landscape in the form of less-combustible deciduous trees (Mack et al. 2021b). Consequently, we should see a latent decline in wildfire C emissions. Indeed, studies on other parts of the boreal forest undergoing similar state changes project increasing fire frequency and size throughout the 21st century followed by declines in the 22nd century as a result of the eventual dominance of less flammable vegetation (Huang et al. 2021). Our findings suggest that the expected decreases in wildfire frequency and size that may result from a more deciduous boreal forest, will likely be accompanied by reduced wildfire C emissions when those deciduous forests burn. Therefore, if it proceeds as projected (Mann et al. 2012, Mekonnen et al. 2019), the climate change-initiated shift in western North American boreal forest composition from black spruce to aspen and birch will likely reduce future fire severity. This finding provides support for an effect of fire self-limitation in the western North American boreal forest.

Quantifying the fire limiting effects of boreal deciduous forests is critically important for fire management efforts in the boreal forest and beyond. While this study quantified combustion in deciduous stands that *did* burn in order to quantify emissions, a frequent complication to our site selection was encountering deciduous stands within fire scars that were unburned (see Supplemental Figure G). While our study did not aim to quantify the effect of deciduous stands on fire spread or fire probability, other studies (Hély et al. 2000, Cumming 2001, Krawchuk et al. 2006, Bernier et al. 2016, Marchal et al. 2017) have found that deciduous forests do limit fire under certain conditions. Additionally, palaeological studies of past forest composition and fire regimes in the western North American boreal forest suggest that vegetation-mediated fire self-limitation has likely occurred in the past (Higuera et al. 2009, Kelly et al. 2013, Hoecker et al.

2020). With insight in hand from this study and the previous ones, managers can look to protect people, property, and natural resources with natural fire-breaks of less flammable aspen and birch stands in the western North American boreal forest. Furthermore, efforts to use fire-limiting vegetation to mitigate risk in the boreal forest can serve as a model for ecosystems experiencing climate change-intensified fire regimes around the world.

Bottom-up Drivers of Combustion

While mixed and deciduous reliably lost only a fraction of the C to wildfire emissions that conifer stands lost, it is still important to investigate drivers of the range of fire severity we observed within mixed and deciduous stands to infer how their relative fire resistance will hold up in projected future conditions. Bottom-up predictor variables (C pool size, species composition, age, and greening trends) dominated our models of combustion almost universally. Our findings suggest that the lower wildfire C losses from deciduous stands compared with conifer stands are a consequence of their divergent stratification of C between above and belowground pools. That effect can be further explained by the stratification of deciduous aboveground C to primarily combustion-unavailable components: boles rather than leaves and fine branches. However, as greater aboveground C did not limit absolute C losses (with the exception of absolute belowground C losses in birch stands), we did not find support for the general fire-suppressing effect of deciduous tree biomass that we hypothesized might occur as a result of deciduous trees making their microclimates less hospitable to fire.

That stands that trended greener preceding fire and aspen trees afflicted with canker experienced greater combustion deserves further investigation. Previous work found negative correlations between aspen leaf miner outbreaks and vegetation productivity using the vegetation greenness metric, NDVI (Boyd et al. 2019). We expected that EVI2 trends might similarly serve as a proxy for pre-fire aspen leaf miner stress or other vegetation stressors. (We should note that though we were unable to assess stands post-fire for the pre-fire presence of aspen leaf miner, leaf miner was ubiquitous on regrowth, possibly making it more likely that stands were afflicted pre-fire (see Supplemental Figure I)). However, instead of vegetation browning—presumably caused by aspen leaf miner outbreaks and other sources of vegetation stress—resulting in more available C pools and greater C losses, we observed greater C losses after vegetation greening had occurred. This implies that fuel quantity was a stronger driver of C losses than any fuel-availability changes detected with our EVI2 trends. However, aspen trees with canker lost more C to combustion on average, meaning that to some extent, pathogen stress could drive more severe wildfire C losses. (Notably, EVI2 trends were not correlated with the presence of aspen canker at our sites). As climate change is expected to modify future pathogen distributions and abundances, future studies should explore new methods for quantifying the effects of pathogens on wildfire C losses.

Aspen Versus Birch Trajectories

While aspen and birch stands inventoried in our study lost similar amounts of C to wildfire combustion, differences in their projected distributions, unburned and residual C pool sizes, and fire severity responses to top-down variables could have important implications for the future of boreal C storage. The distribution of aspen and birch in future boreal landscapes will likely be influenced by ongoing state changes initiated by severe fires in black spruce stands (Baltzer et al. 2021). Birch is the most common alternate successional trajectory for severely burned black spruce stands in the Boreal Cordillera while aspen is the most prevalent in the Alaska Boreal Interior (Baltzer et al. 2021).

Birch trees stored more C and lost proportionally less of it to fire than aspen stands, meaning that their net ecosystem C flux from the previous fire to the current fire was a greater C sink. However, because of this, birch stands also had the largest post-fire dead tree C pools, which, as discussed, are of uncertain fate. Aspen stands combusted the least belowground C by virtue of containing the least pre-fire. In fact, complete aspen belowground SOL C combustion was common. As lower belowground C pools were associated with lower overall C emissions across stand types, the small belowground C pools of aspen stands might limit C losses by decreasing fire residency time in a stand.

Most significantly, aspen stand C losses were not influenced by either of the top-down climate variables we assessed: spring temperature and precipitation variance. This implies that aspen stands may be relatively resilient to the direct effects of weather extremes. Birch stands, on the contrary, experienced significantly greater C losses following springs that had lower than normal precipitation. While past trends and projections of future boreal climate consistently indicate rising temperatures (Walsh 2014), the projections of boreal precipitation are much more uncertain (Scaff et al. 2015). In general, trends indicate that mean annual precipitation may increase, but that precipitation events may become more stochastic and extreme and droughts will become more common (Zhang et al. 2013, Wang et al. 2014, Bennett and Walsh 2015, Wendler et al. 2017). Droughts or more stochastic precipitation may result in more severe fires if anomalously dry conditions allow greater SOL drying in birch stands. This effect could endanger large C sink of boreal birch stands. Our findings highlight the importance of considering the distinct characteristics of aspen and birch stands when projecting future boreal forest net ecosystem C balance.

CONCLUSION

In this study we filled a critical knowledge gap in boreal wildfire ecology by quantifying the wildfire C losses in mixed, aspen, and birch stands. Deciduous stands lost half as much C to wildfire emissions as conifer stands, suggesting that as deciduous forest becomes more prevalent across the western North American boreal landscape (Mann et al. 2012, Mekonnen et al. 2019, Baltzer et al. 2021), boreal C will become more resistant to combustion. Within the gradient of fire severities in boreal mixed, aspen, and birch stands, bottom-up controls of fuel quantity and quality (and not top-down fire weather conditions) were the only important drivers of total wildfire C losses for mixed and aspen stands, suggesting that C stored in these stands may be somewhat resilient to projected climate intensification. Birch stand C losses, conversely, were strongly influenced by variations in spring precipitation. Consequently, the residence of the larger C pools stored in birch stands could be more destabilized by projected future conditions than the C pools of aspen stands. Yet, deciduous trees significantly limit wildfire C emissions in boreal forests compared with the historic dominant species black spruce. This suggests that in response to climate change, boreal forests are exhibiting a fire self-limiting effect that may act as a negative feedback on the climate change-wildfire feedback loop.

SUPPLEMENTAL MATERIALS

Supplemental Figure A: Aspen Tree with Aspen Canker. A photograph of an aspen tree taken in 2022 in the Shovel Creek 2019 fire scar outside of Fairbanks, AK. The image depicts how aspen trees afflicted with aspen canker pre-fire can be easily distinguished post-fire from characteristic aspen-canker scars.

Measurements Not Used in this Study

Site-level Measurements

In addition to recording the presence or absence of aspen canker on every aspen tree in our sites, we also recorded whether or not aspen canker was present in the general area of each of our sites. This was intended to capture the effect of being in a stand in which aspen canker was present even if none of the trees in our plot were infected. We also noted the presence of aspen leaf miner on regrowth (saplings and seedlings). We captured aerial UAV imagery of every site from directly above the center of each 30 m transect from 30, 45, and 50 m. We also took photos of each site from the 0 m end of the transect tape with data collection iPads.

Tree Inventory

We recorded the standing or fallen status of every tree. For deciduous trees, we also recorded whether the crown had fallen off of the tree since the fire.

Tree Regrowth Inventory

All tree seedlings and saplings inside of a 1 x 1 m quadrat placed on the upslope side of the transect tape (or on the side opposite of our shrub inventory) at the 3 m, 6 m, and 9m points within each plot were counted. Additionally, three representative basal diameters were taken for each species present for each class (sapling or seedling).

Coarse Woody Debris Inventory

All down and standing wood that was dead pre-fire was classed as Coarse woody debris (CWD). We measured CWD using a line-intercept method. The species and decay class (soft, crumbly, or hard) of every piece of CWD that crossed the transect line and was greater than or equal to 5 cm in diameter was recorded. Diameter was recorded as the diameter of each piece of CWD where it intersected the transect line. For CWD recorded as an “unknown” species, the relative basal area of tree species from the tree inventory in a plot was used to estimate a proportional species contribution to biomass. Pre-fire biomass of CWD was estimated using allometric equations and specific gravities from (Alexander et al. 2004), (Delisle et al. 1988), and Nalder *et al*. 1999. For CWD <7 cm in diameter, biomass was estimated using Nalder *et al*. 1999 Southern Northwest Territories black spruce, white spruce, and aspen equations (aspen equations were applied to birch and poplar CWD). For CWD >= 7 cm in diameter, (Alexander et al. 2004) equations and (Delisle 1986) specific gravities were used to calculate pre-fire biomass of deciduous (aspen specific gravities used for aspen, birch, and poplar) and conifer (white spruce specific gravities used for black spruce and white spruce) CWD. “Sound” specific gravities were used for CWD pieces with a decay class of hard and “soft” specific gravities were used for pieces recorded as soft or crumbly. All equations yielded pre-fire biomass estimates in units of Mg/ha so biomass was transformed to gC/m^{-2} by multiplying each CWD biomass estimate by ((1000000/10000)/2). Total pre-fire CWD biomass was calculated as the sum of CWD in each plot. Combusted biomass was estimated by multiplying each pre-fire biomass estimate by the combustion estimate. Post-fire CWD biomass was calculated as the total pre-fire CWD biomass minus the combusted CWD biomass.

Residual Organic Soil Processing and C Pool Calculation

Soil profile samples were thawed for 24-48 hours. To account for any compression that had occurred since collection, we fluffed each sample out to its original dimensions. Each sample was cut in half bilaterally and half was reserved for future analyses. The remaining halves were cut into 5 cm depth subsections with the deepest subsections being of variable depth depending on the location of the organic/mineral soil interface. Two measurements each of depth, height, and width and wet weight were obtained for each subsection. Each subsection increment was homogenized by hand and parsed out into homogenized soil, coarse organic material (anything that could not be easily shredded by hand such as sticks or roots>2mm), and rocks. Rock volume was measured using water displacement in a graduated cylinder. A wet mass of homogenized soil and coarse organic material was recorded. Both the coarse organic material and up to 50g subsamples of the homogenized soil were dried in an oven at 60° C for 48 hours. Dry masses of each component were recorded. The homogenized soil was ground using a coffee grinder and re-dried for at least 48 hours. With careful attention to not expose samples to air moisture for longer than necessary, 3 mg (± 0.2 mg) of each ground and dried soil sample was measured and rolled into a 4x6 mm ultra-light weight pressed tin capsule. The samples were combusted using a Costech Elemental Analyzer calibrated with NIST peach leaf standard 1547 to determine percent C. To calculate the residual soil C pools, we calculated volume, soil bulk density, coarse density, and coarse and soil C pools using the formulas in Table A.

Supplemental Table A: SOL C Pool Calculation Formulas. Formulas were used to calculate the total residual C pools (g C m^{-2}) of each plot.

Metric	Formula
Total subsection volume (cm^{-3})	Subsection average length * Subsection average width * Subsection average depth
Soil volume (ml)	Total subsection soil volume – rock volume
Soil moisture (%)	1 – ((Wet homogenized soil subsample weight – Dry homogenized soil subsample weight) / Wet homogenized soil subsample weight)
Bulk density (g cm^{-3})	(Whole subsection homogenized soil wet weight * Soil moisture) / Soil volume
Soil C pool (g C m^{-2})	Bulk density * (Percent C / 100) * Subsection average depth * 10000
Coarse density (g cm^{-3})	Coarse dry weight / Soil volume
Coarse C pool (g C m^{-2})	(Coarse density / 2) * Subsection average depth * 100
Total subsection C pool (g C m^{-2})	Soil C pool + Coarse C pool
Total sample C pool (g C m^{-2})	Sum of all sample subsection C pools

Supplemental Table B: Residual Organic Soil Horizon Characteristics. Mean (± standard error) and range (minimum-maximum) of residual organic soil depth, bulk density, C%, soil C pool, coarse woody material C pool, and total C pool for each 5 cm soil profile subsection for each stand type for all plots that contained residual organic soil post-fire. No standard errors are reported for subsections that only had one sample.

Forest Type	Subsection (cm)	Depth (cm)	Depth Range (cm)	Bulk Density (g C m^{-2})	Bulk Density Range (g C m^{-2})	C%	C% Range	n
Mixed	0-5	4.1 ± 0.3	0.8-6.8	0.16 ± 0.02	0.05-0.32	37 ± 2	22-50	31
Mixed	5-10	4.9 ± 0.1	4.0-5.5	0.20 ± 0.03	0.04-0.31	29 ± 3	22-50	10
Mixed	10-15	6.3		0.18		26		1
Mixed	15-20	4.0		0.36		33		1
Aspen	0-5	3.4 ± 0.2	1.3-6	0.17 ± 0.01	0.04-0.32	32 ± 1	21-48	43
Aspen	5-10	4.4 ± 0.7	2.9-6.8	0.15 ± 0.03	0.08-0.25	32 ± 5	21-45	5
Aspen	10-15	5.0		0.14		32		1
Birch	0-5	4.6 ± 0.2	0.8-11	0.12 ± 0.01	0.01-0.54	40 ± 1	21-52	70
Birch	5-10	5.1 ± 0.1	4.3-6.5	0.14 ± 0.01	0.03-0.32	34 ± 2	20-53	29
Birch	10-15	4.4 ± 0.3	3.0-5.3	0.19 ± 0.04	0.03-0.37	30 ± 3	21-47	9
Birch	15-20	4.8 ± 0.3	4.0-5	0.14 ± 0.04	0.02-0.23	32 ± 7	20-46	4
Forest Type	**Subsection (cm)**	**Soil C (g C m^{-2})**	**Soil C Range (g C m^{-2})**	**Coarse C (g C m^{-2})**	**Coarse C Range (g C m^{-2})**	**Total C (g C m^{-2})**	**Total C Range (g C m^{-2})**	**n**
Mixed	0-5	1979 ± 218	562-7345	242 ± 29	33-621	2221 ± 229	595-7700	31
Mixed	5-10	2536 ± 333	1100-4013	511 ± 159	118-1844	3047 ± 268	1671-4196	10
Mixed	10-15	3036		1663		4699		1
Mixed	15-20	4647		63		4711		1
Aspen	0-5	1630 ± 114	569-3713	261 ± 48	0-1869	1892 ± 128	701-4095	43
Aspen	5-10	1908 ± 406	1276-3499	218 ± 59	83-381	2126 ± 411	1359-3724	5
Aspen	10-15	2232		297		2529		1
Birch	0-5	1704 ± 85	341-4100	569 ± 80	22-4937	2273 ± 127	363-6565	70
Birch	5-10	2092 ± 146	870-4590	375 ± 35	86-899	2467 ± 148	1251-5060	29
Birch	10-15	2014 ± 325	581-3989	232 ± 55	81-539	2246 ± 311	845-4168	9
Birch	15-20	1667 ± 415	466-2366	93 ± 43	11-207	1760 ± 451	477-2573	4

Supplemental Table C: Data Used to Train Soil Depth Models. Attributes of data used to train unburned soil depth models (Training Data) compared with our data (Sample Data). Mean (± SE) and range (minimum to maximum) of each variable were assessed for inclusion in models to predict pre-fire soil depth based on attributes that could be measured post-fire. Variables designated with an * (aspect (°), slope (°), moisture class (1 – 3; 1 = dry, 2 = intermediate, 3 = wet), and stand tree density (n m^{-2})) were used as predictors in the final models. Biomass (g m^{-2}), stand age (years), and elevation (m) were excluded from the models because the ranges represented by the training data were smaller than the ranges present in the sample data.

	Training Data						**Sample Data**					
Variable	**Mixed (n = 121)**		**Aspen (n = 87)**		**Birch (n = 147)**		**Mixed (n = 61)**		**Aspen (n = 93)**		**Birch (n = 85)**	
Unburned SOL Depth	8.9 ± 0.3	(2.4-19.4)	5.2 ± 0.2	(1.7-10.3)	8.8 ± 0.3	(2.1-23.1)						
Aspect*	139 ± 9	(0-345)	167 ± 9	(0-344)	158 ± 7	(0-354)	172 ± 12	(8-352)	152 ± 8	(11-352)	171 ± 11	(8-363)
Slope*	7 ± 1	(0-33)	8 ± 1	(0-36)	8 ± 1	(0-29)	9 ± 1	(0-32)	16 ± 1	(0-34)	14 ± 1	(0-32)
Moisture Class*	1.9 ± 0.1	(1-3)	2.1 ± 0.1	(1-3)	2.0 ± 0.1	(1-3)	1.8 ± 0.1	(1-3)	1.4 ± 0.1	(1-3)	1.7 ± 0.1	(1-3)
Density*	0.56 ± 0.04	(0.01-2.25)	0.35 ± 0.03	(0.03-1.21)	0.40 ± 0.03	(0.00-1.35)	0.64 ± 0.05	(0.10-2.25)	0.40 ± 0.03	(0.10-1.05)	0.53 ± 0.03	(0.05-1.50)
Biomass	5289 ± 341	(224-20749)	7270 ± 596	(43-33433)	8543 ± 523	(25-28020)	9565 ± 910	(419-34958)	10488 ± 924	(254-41186)	14376 ± 1087	(439-53723)
Stand Age	61 ± 2	(31-158)	55 ± 2	(31-120)	57 ± 2	(30-158)	85 ± 3	(43-165)	93 ± 3	(43-196)	92 ± 3	(63-212)
Elevation	328 ± 16	(91-884)	435 ± 14	(125-823)	328 ± 12	(91-823)	543 ± 35	(134-999)	557 ± 31	(134-1050)	532 ± 22	(250-955)

Plot-level versus Site-level Soil Depth Random Forest Models. We created random forest models to predict soil depth in unburned mixed, aspen, and birch stands using pre-existing forest inventory data from mature, unburned stands (Malone et al. 2009, Alexander et al. 2012, Ruess 2015, Melvin et al. 2015, Alexander and Mack 2016, Jean et al. 2020, Burrill et al. 2021, Van Cleve et al. 2021, Mack et al. 2021a, Ruess et al. 2023). We tested models created using the data at plot-level (cumulative n = 355) and using the data summarized to site level (cumulative n = 141). Due to the larger size of the training data set, models created using the plot-level data performed substantially better than models created using the summarized data. However, using the un-summarized data introduced the potential of a pseudo-replication effect. Yet because running the models on either data set yielded similar soil depth predictions (linear relationships between soil depth predictions based on plot-level and site-level data were significantly correlated for all stand types: adjusted R^2 for mixed stands = 0.67, for aspen stands = 0.65, and for birch stands = 0.56), we opted to use the stronger models created with plot-level data.

Supplemental Table D: Soil Depth Random Forest Model Fit Statistics. Model fit statistics (R^2, RMSE, and MAE) and the % increase in Mean Squared Error (MSE) that each variable's removal would cause are reported. Additionally, R^2 adjusted values of the linear relationships between predicted and actual soil depth when we trained the data models on a random subset of the data and tested it on the remainder (75% train and 25% test data). The linear relationships between predicted and actual soil depth were significant ($P < 0.05$) for all of the split data models.

Forest Type	**Mixed**	**Aspen**	**Birch**
Model R^2	0.50	0.65	0.28
Model RMSE	2.83	1.29	3.60
Model MAE	2.04	0.82	2.43
Variable % Increase MSE			
Aspect	3.69	0.89	2.41
Density	1.29	1.05	1.28
Moisture Class	4.87	0.36	3.12
Slope	2.97	1.74	3.08
Train/Test Split Prediction R^2 adj.	0.32	0.71	0.14

Supplemental Table E: Organic Soil C Pool Characteristics from Alexander and Mack 2016 Data used to Estimate Combusted Organic Soil C from Modeled Pre-fire Soil Depths. Mean (± standard error) depth, bulk density, percent carbon, and carbon pool for each soil profile subsection within each soil depth class and stand type. The depth class designation indicates if the measurements came from a sample with a full depth profile less than 5 cm (shallow), between 5 and 10 cm (intermediate), or greater than 10 cm (deep). The subsection (0-5, 5-10, or 10+) indicates which depth strata of a soil profile the subsample measurements came from. Residual soil C was calculated as: (modeled subsection depth / 5 cm (or average depth for 10+ subsection)) * average subsection C pool. No standard errors are reported for deep aspen stand measurements because there was only one deep aspen sample. Only the bolded values were used to project C pools of combusted soil for this study (none of the projected mixed or birch depths fell into the shallow depth class and none of the projected aspen depths fell into the deep depth class).

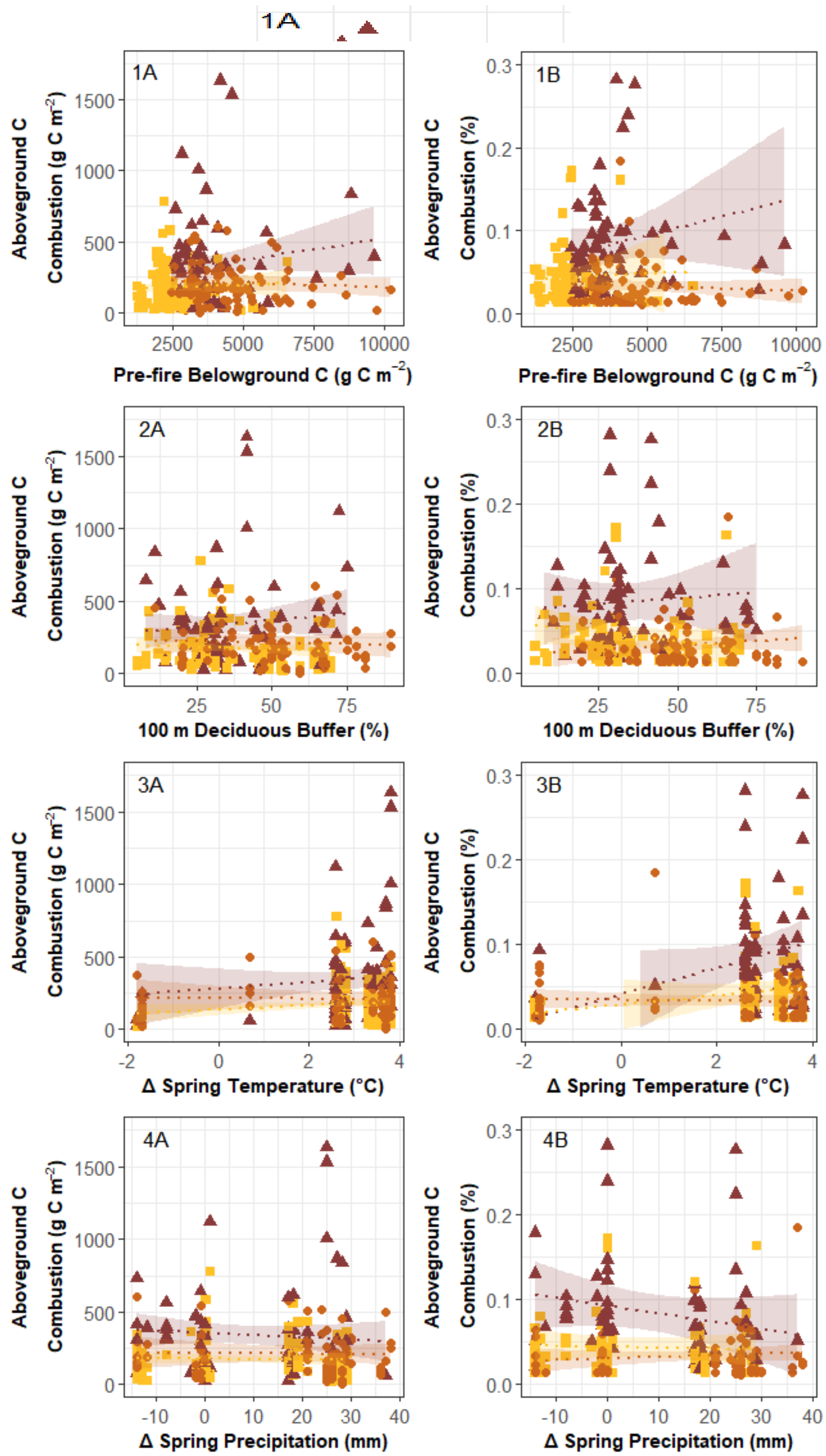
Forest Type	Depth Class	Subsection (cm)	Depth (cm)	Bulk Density (g m^{-2})	C%	C Pool (g C m^{-2})	n
Mixed Stands	Shallow	0-5	4.6 ± 0.2	0.14 ± 0.02	33 ± 1	2055 ± 226	23
	Intermediate	**0-5**	**5.0 ± 0.0**	**0.09 ± 0.01**	**39 ± 2**	**1725 ± 139**	**17**
	Intermediate	**5-10**	**3.9 ± 0.4**	**0.15 ± 0.02**	**32 ± 2**	**1773 ± 210**	**17**
	Deep	**0-5**	**5.0 ± 0.0**	**0.06 ± 0.01**	**45 ± 1**	**1497 ± 157**	**8**
	Deep	**5-10**	**5.0 ± 0.0**	**0.09 ± 0.01**	**43 ± 2**	**1994 ± 219**	**8**
	Deep	**10+**	**10.4 ± 1.5**	**0.13 ± 0.04**	**32 ± 2**	**4160 ± 1051**	**8**
Aspen Stands	**Shallow**	**0-5**	**4.1 ± 0.2**	**0.13 ± 0.01**	**32 ± 1**	**1596 ± 100**	**34**
	Intermediate	**0-5**	**5.0 ± 0.0**	**0.11 ± 0.01**	**35 ± 2**	**1891 ± 214**	**15**
	Intermediate	**5-10**	**3.4 ± 0.3**	**0.16 ± 0.02**	**28 ± 2**	**1434 ± 184**	**15**
	Deep	0-5	5.0	0.13	33	2141	1
	Deep	5-10	5.0	0.17	33	3018	1
	Deep	10+	5.0	0.44	22	5206	1
Birch Stands	Shallow	0-5	4.2 ± 0.2	0.13 ± 0.01	34 ± 2	1820 ± 110	20
	Intermediate	**0-5**	**5.0 ± 0.0**	**0.08 ± 0.01**	**42 ± 1**	**1830 ± 135**	**25**
	Intermediate	**5-10**	**3.4 ± 0.3**	**0.17 ± 0.02**	**32 ± 1**	**1769 ± 187**	**25**
	Deep	**0-5**	**5.0 ± 0.0**	**0.08 ± 0.01**	**42 ± 5**	**1677 ± 126**	**4**
	Deep	**5-10**	**5.0 ± 0.0**	**0.13 ± 0.02**	**36 ± 6**	**2402 ± 282**	**4**
	Deep	**10+**	**2.3 ± 0.6**	**0.28 ± 0.08**	**29 ± 3**	**1461 ± 332**	**4**

Supplemental Table F: C Pool and C Loss Model-estimated Means and Model Statistics. Pre-fire C, post-fire C, C Loss in aboveground, belowground, and total (aboveground plus belowground) C pools. Proportional C Loss in aboveground, belowground, and total C pools. Mean (± SE) estimates are based on GLS models with C pool (or %C pool loss) as a response variable and stand type as a predictor variable. P-values designate differences from the intercept (conifer stands). Transformations were applied to the response variables when untransformed models violated model assumptions and a transformation improved model assumptions.

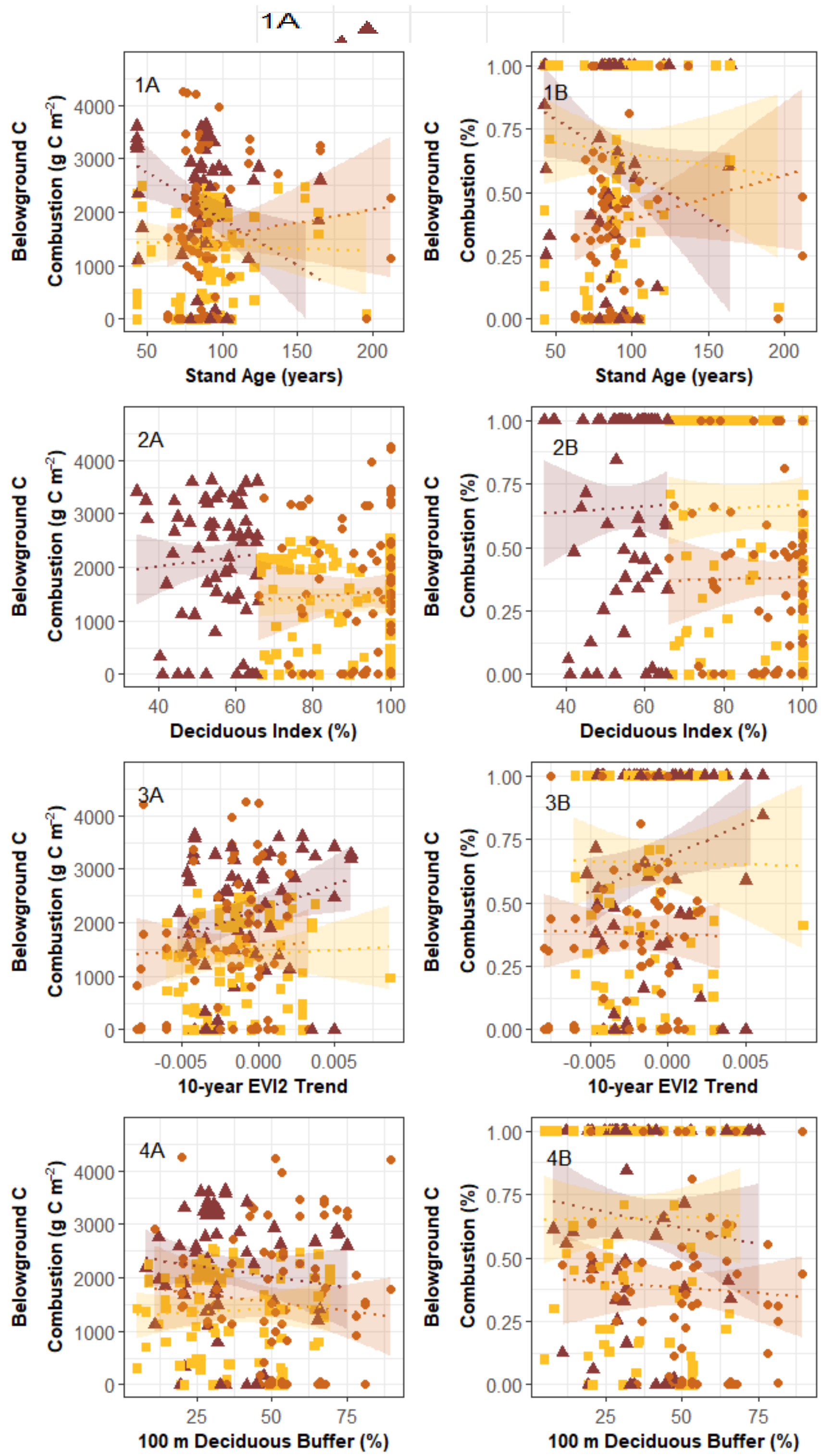
Pool		Conifer Stands (n = 63)			Mixed Stands (n = 57)			Aspen (n = 88)			Birch (n = 78)			Y
		Mean (± SE)	T value	P-value	Mean (± SE)	T value	P-value	Mean (± SE)	T value	P-value	Mean (± SE)	T value	P-value	Transform
Above-ground	Pre-fire	940 ± 93	20.13	**<0.001**	3983 ± 450	8.38	**<0.001**	4065 ± 424	9.05	**<0.001**	6016 ± 533	12.48	**<0.001**	Sq. Root
	Post-fire	657 ± 67	19.59	**<0.001**	3748 ± 427	9.56	**<0.001**	3939 ± 410	10.56	**<0.001**	5871 ± 518	14.07	**<0.001**	Sq. Root
	C Loss	264 ± 46	11.48	**<0.001**	220 ± 33	-0.791	0.430	115 ± 17	-3.4	**<0.001**	138 ± 18	-2.803	**0.005**	Sq. Root
	%C Loss	22.8 ± 2.8	-11.91	**<0.001**	5.2 ± 0.4	-10.09	**<0.001**	2.7 ± 0.2	-14.9	**<0.001**	2.2 ± 0.1	-16.82	**<0.001**	Log
Below-ground	Pre-fire	5677 ± 298	164.47	**<0.001**	3682 ± 181	-6.02	**<0.001**	2402 ± 123	-11.74	**<0.001**	4139 ± 195	-4.48	**<0.001**	Log
	Post-fire	2864 ± 290	19.73	**<0.001**	977 ± 307	-3.97	**<0.001**	674 ± 189	-6.07	**<0.001**	2038 ± 345	-1.79	0.075	Sq. Root
	C Loss	2797 ± 168	16.64	**<0.001**	2113 ± 170	-2.86	**0.005**	1348 ± 102	-7.38	**<0.001**	1603 ± 166	-5.05	**<0.001**	None
	%C Loss	48.8 ± 3.5	13.85	**<0.001**	61 ± 6.8	1.58	0.115	57.1 ± 6.5	1.12	0.263	41.7 ± 5.5	-1.08	0.281	None
Total	Pre-fire	6795 ± 218	275.21	**<0.001**	7765 ± 390	2.24	**0.026**	6233 ± 334	-1.39	0.167	10041 ± 453	0.39	**<0.001**	Log
	Post-fire	3643 ± 238	30.58	**<0.001**	5339 ± 469	3.37	**<0.001**	4936 ± 357	3.08	**0.002**	8479 ± 508	9.35	**<0.001**	Sq. Root
	C Loss	3106 ± 172	18.04	**<0.001**	2368 ± 170	-3.05	**0.003**	1477 ± 104	-8.1	**<0.001**	1750 ± 167	-5.66	**<0.001**	None
	%C Loss	43.3 ± 2.7	32.01	**<0.001**	28.3 ± 3.6	-3.2	**0.002**	20.3 ± 2.5	-6.03	**<0.001**	15.6 ± 2.5	-7.06	**<0.001**	Sq. Root

Supplemental Table G: Estimated Marginal Mean Effects of C Combustion Drivers. Estimated marginal mean effect sizes (± SE) of variables in fitted absolute and proportional aboveground, belowground, and total combustion driver models in mixed, aspen, and birch stands. "Abs" designates models of absolute combustion and "%" designates models of proportional combustion. "AG" is pre-fire aboveground C, "BG" is pre-fire belowground C, "Age" is stand age, "DI" is plot deciduous index, "EVI" is 10-year EVI2 trend, "100m" is the 100m buffer mean deciduous canopy, "Temp" and "Precip" are the year-of-fire spring temperature and precipitation variance from normal.

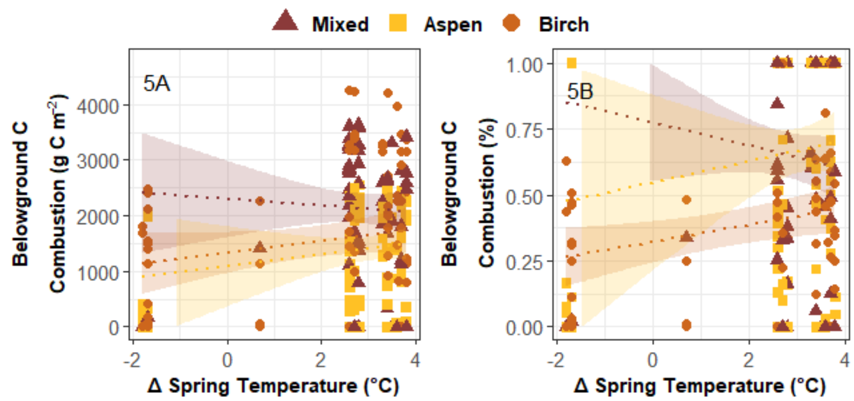
Combustion Response			Variance Structure	Intercept	Bottom-up Drivers						Top-down Drivers		R^2
					AG	BG	Age	DI	EVI	100m	Temp	Precip	
Aboveground Combustion	Mixed	Abs	varFixed (AG)	365 ± 33	**0.06 ± 0.01**	0.03 ± 0.02	0.3 ± 1.4	-1 ± 3	7888 ± 9872	2 ± 2	32 ± 26	-0.06 ± 2.29	0.40
	Mixed	%	varFixed (BG)	8.65 ± 0.64	-0.0003 ± 0.0003	0.0006 ± 0.0006	-0.018 ± 0.034	**-0.22 ± 0.09**	369 ± 220	0.004 ± 0.04	0.98 ± 0.8	-0.01 ± 0.05	0.32
	Aspen	Abs	varExp (Temp)	175 ± 11	**0.02 ± 0.003**	0.01 ± 0.01	**-1.1 ± 0.5**	**-4 ± 1**	7234 ± 4413	-1 ± 1	14 ± 7	-0.19 ± 0.82	0.49
	Aspen	%	None	4.38 ± 0.56	**-0.0004 ± 0.0001**	0.0002 ± 0.0007	**-0.066 ± 0.022**	**-0.09 ± 0.05**	**508 ± 222**	-0.04 ± 0.03	0.53 ± 0.48	-0.01 ± 0.04	0.26
	Birch	Abs	varPower (BG)	221 ± 25	**0.02 ± 0.002**	-0.01 ± 0.005	0.1 ± 0.4	**-5 ± 1**	**9359 ± 3550**	-0.4 ± 0.7	0.5 ± 10	-1.08 ± 1.36	0.45
	Birch	%	varPower (AG)	2.98 ± 0.21	-0.00005 ± 0.00003	**0 ± 0.0001**	-0.002 ± 0.006	**-0.11 ± 0.02**	92 ± 67	0.01 ± 0.01	-0.001 ± 0.09	0 ± 0.01	0.35
Belowground Combustion	Mixed	Abs	varPower (EVI)	2144 ± 102	0.06 ± 0.04	**-0.52 ± 0.08**	-7.7 ± 5.3	-15 ± 14	41800 ± 43446	-6 ± 6	59 ± 135	0.34 ± 7.53	0.51
	Mixed	%	varFixed (Age)	65.35 ± 3.53	0.0024 ± 0.0017	**-0.0196 ± 0.0027**	-0.284 ± 0.206	-0.21 ± 0.48	1180 ± 1200	-0.19 ± 0.26	0.29 ± 4.05	-0.16 ± 0.3	0.57
	Aspen	Abs	varFixed (BG)	1358 ± 88	0.02 ± 0.02	**-0.52 ± 0.09**	1 ± 3.4	-2 ± 5	17427 ± 33125	2 ± 5	79 ± 76	0.35 ± 5.87	0.28
	Aspen	%	varPower (BG)	65.28 ± 3.61	0.0012 ± 0.0007	**-0.0379 ± 0.0043**	-0.011 ± 0.138	0.07 ± 0.23	-74 ± 1370	0.05 ± 0.2	3.05 ± 3.17	-0.12 ± 0.24	0.43
	Birch	Abs	None	1483 ± 127	**-0.06 ± 0.03**	**-0.19 ± 0.08**	5.9 ± 4.6	-1 ± 13	13007 ± 49954	-2 ± 9	74 ± 65	**-37.6 ± 8.84**	0.40
	Birch	%	varPower (BG)	38.07 ± 3.1	**-0.0018 ± 0.0006**	**-0.0075 ± 0.0013**	0.195 ± 0.113	-0.05 ± 0.3	-215 ± 1060	-0.02 ± 0.19	2.41 ± 1.31	**-0.81 ± 0.2**	0.48
Total Combustion	Mixed	Abs	varFixed (Age)	2500 ± 110	**0.12 ± 0.05**	**-0.53 ± 0.08**	-10.8 ± 6.4	-15 ± 15	**77525 ± 37284**	-9 ± 8	76 ± 126	2.99 ± 9.25	0.55
	Mixed	%	varFixed (BG)	34.2 ± 1.86	**-0.0017 ± 0.0007**	**-0.009 ± 0.0018**	**-0.233 ± 0.1**	-0.35 ± 0.25	**1470 ± 641**	-0.13 ± 0.13	0.88 ± 2.34	-0.12 ± 0.15	0.62
	Aspen	Abs	varFixed (BG))	1534 ± 85	**0.04 ± 0.02**	**-0.49 ± 0.09**	0.4 ± 3.3	-7 ± 5	21716 ± 32278	3 ± 5	95 ± 74	-0.31 ± 5.72	0.34
	Aspen	%	None	24.72 ± 1.44	**-0.0016 ± 0.0003**	**-0.0085 ± 0.0018**	-0.082 ± 0.056	-0.14 ± 0.12	-5 ± 560	0.1 ± 0.09	2.41 ± 1.22	-0.13 ± 0.1	0.44
	Birch	Abs	None	1675 ± 129	-0.04 ± 0.03	**-0.19 ± 0.08**	6 ± 4.7	-7 ± 13	22405 ± 50914	-2 ± 9	76 ± 66	**-38.1 ± 9**	0.40
	Birch	%	None	17.25 ± 1.68	-0.0016 ± 0.0004	**-0.0029 ± 0.001**	-0.0001 ± 0.064	0.09 ± 0.17	67 ± 663	-0.03 ± 0.11	1.26 ± 0.86	**-0.25 ± 0.12**	0.40



Supplemental Figure B: Drivers of Aboveground C Combustion. Relationship between aboveground combustion and hypothetical fire severity predictor variables not included in the main text in mixed, aspen, and birch stands. Trend lines are solid lines if the variable was a significant predictor ($P < 0.05$) of the combustion response metric in full model, otherwise trend lines are dotted (Tables 2 & 3). Line slopes are extracted from each stand type's full model.



Supplemental Figure C: Drivers of Belowground C Combustion. Relationship between belowground combustion and hypothetical fire severity predictor variables not included in the main text in mixed, aspen, and birch stands. Trend lines are solid lines if the variable was a significant predictor ($P < 0.05$) of the combustion response metric in full model, otherwise trend lines are dotted (Tables 2 & 3). Line slopes are extracted from each stand type's full model.



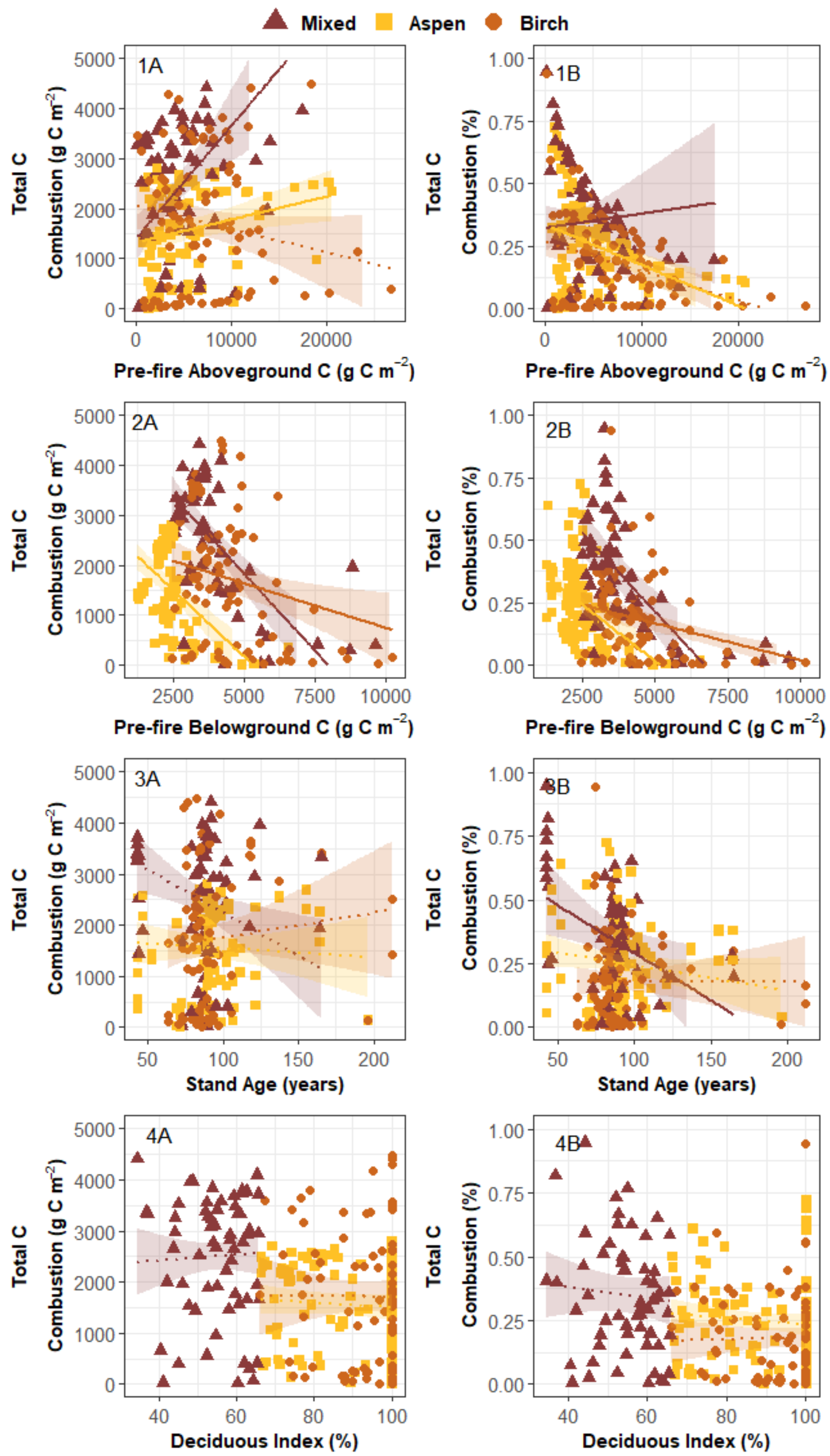
Supplemental Figure D: Additional Drivers of Belowground C Combustion. Relationship between belowground C combustion and hypothetical fire severity predictor variables not included in the main text in mixed, aspen, and birch stands. Trend lines are solid lines if the variable was a significant predictor ($P < 0.05$) of the combustion response metric in full model, otherwise trend lines are **dotted** (Tables 2 & 3). Line slopes are extracted from each stand type's full model.

Supplemental Table H: Mean C combustion in plots with and without aspen canker. Model-estimated means (± SE) of absolute and proportional total and tree combustion in plots with and without canker. Plots with canker and plots without canker did not exhibit significant differences in C combustion in any case.

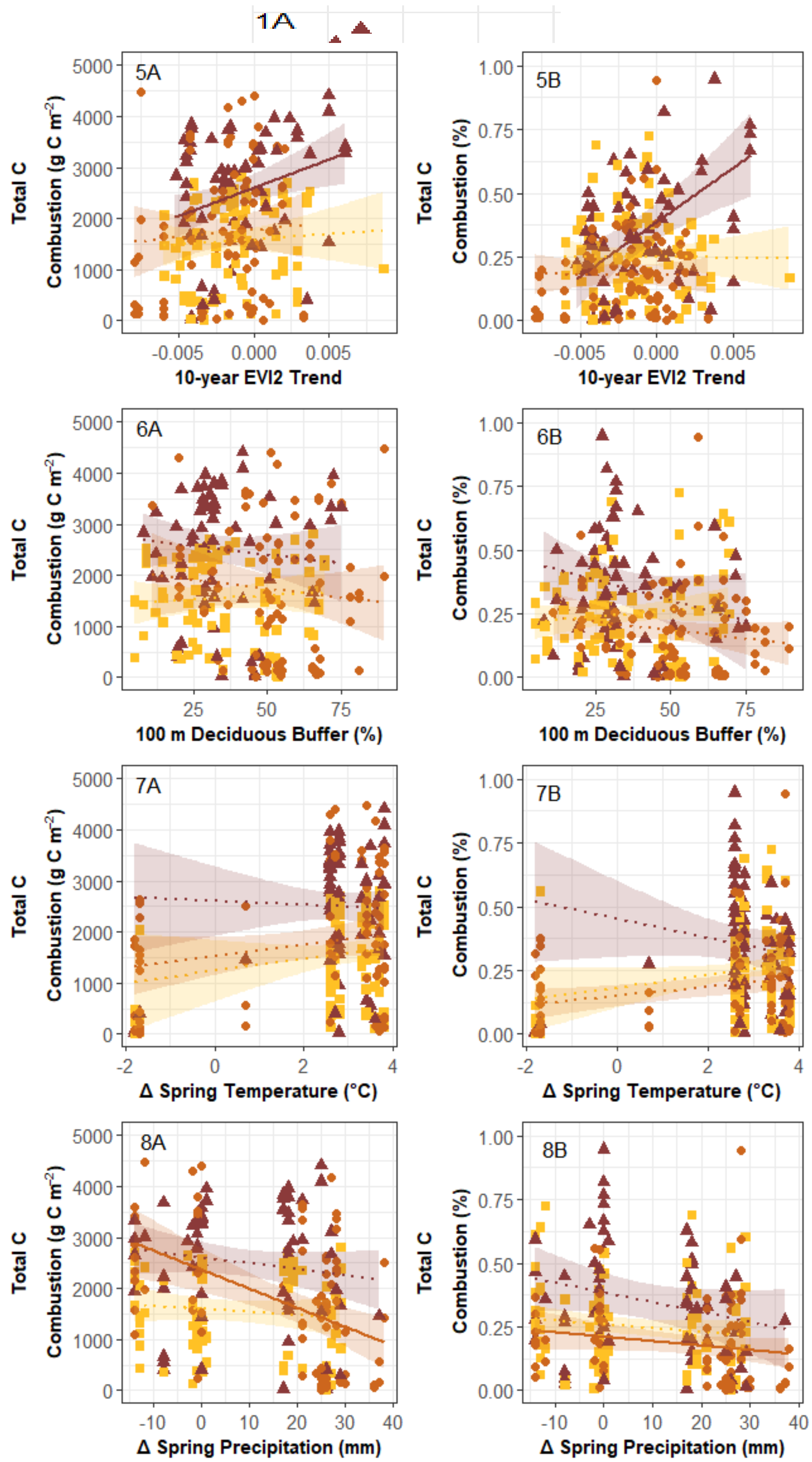
C pool Combusted	**Canker Present in Plot?**	
	Yes (n = 80)	No (n = 65)
Mean Total C Combusted (g C m^{-2})	1705 ± 188	1705 ± 197
Mean % Total C Combusted	28.0 ± 2.6	30.1 ± 2.8
Mean Tree C Combusted (g C m^{-2})	173 ± 20	158 ± 22
Mean % Tree C Combusted (%)	3.9 ± 0.4	4.1 ± 0.5

Drivers of Total C Combustion

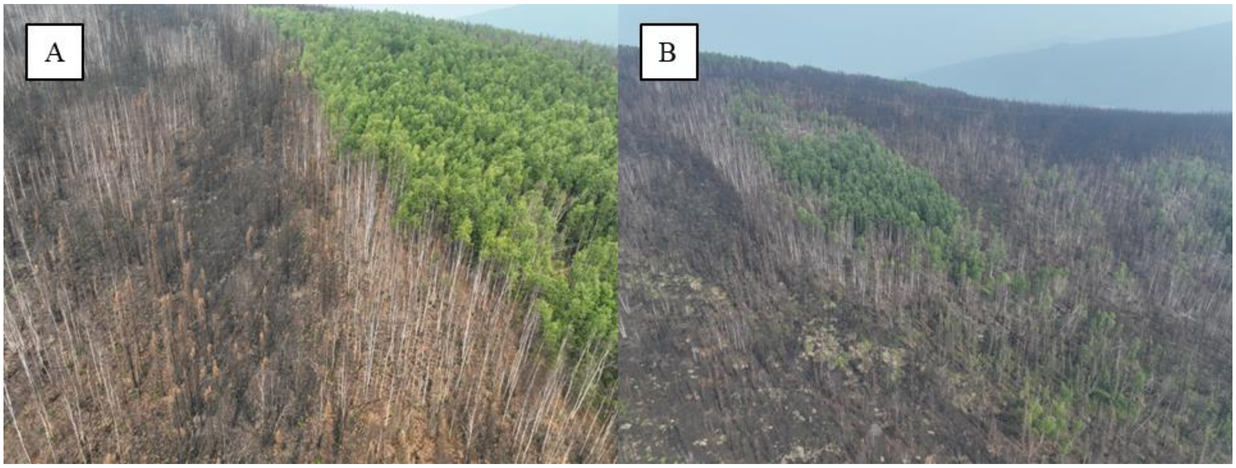
Counter to our expectations, absolute total C combustion was significantly greater in mixed and aspen stands with greater pre-fire aboveground C (Figure E: 1A, Table 2). In line with our expectations, proportional total C combustion significantly decreased with greater aboveground pre-fire C in mixed and aspen stands (Figure E: 1B, Table 3). In all stands, absolute and proportional total combustion were significantly lower with greater pre-fire belowground C (Figure E: 2A & 2B, Tables 2 & 3). This result was counter to our hypotheses for absolute total combustion, but agreed with our hypotheses for proportional total combustion. Proportional total combustion tended to be lower in older mixed stands, as expected (Figure E: 3B, Table 3). Additionally, if mixed stands trended greener in the years preceding fire, they experienced significantly greater absolute and proportional total combustion, counter to our hypotheses (Figure F: 5A & 5B, Tables 2 & 3). In birch stands, absolute and proportional total combustion were greater if less precipitation accumulated in the spring than normal. Spring precipitation had the largest effect on birch total combustion of any predictor we tested (Figure F: 8A & 8B, Tables 2 & 3). None of the other predictor variables were significant in our total C combustion driver models (Figures E & F, Tables 2 & 3).



Supplemental Figure E: Drivers of Total C Combustion. Relationship between total C combustion and hypothetical fire severity predictor variables in mixed, aspen, and birch stands. Trend lines are solid lines if the variable was a significant predictor (P < 0.05) of the combustion response metric in full model, otherwise trend lines are dotted (Tables 2 & 3). Line slopes are extracted from each stand type's full model.



Supplemental Figure F: Additional Drivers of Total C Combustion. Relationship between total C combustion and hypothetical fire severity predictor variables in mixed, aspen, and birch stands. Trend lines are solid lines if the variable was a significant predictor (P < 0.05) of the combustion response metric in full model, otherwise trend lines are dotted (Tables 2 & 3). Line slopes are extracted from each stand type's full model.



Supplemental Figure G: Unburned Deciduous Stand within a Fire Scar. Photographs were taken in the summer of 2022 with a DJI Mavic 3 unmanned aerial vehicle (UAV) at the Munson Creek 2021 fire scar in Chena Hot Springs, AK. Image A shows a transition from a severely burned (complete mortality) area composed of small patches of deciduous trees (white stems) in a black spruce matrix to a large, continuous deciduous stand that is severely burned at the edge adjacent to a black spruce forest, but unburned in the center. Image B is a zoomed-out view of the same patch and shows how the large, mostly unburned deciduous patch is surrounded on all sides by severely burned black spruce-dominated forest.

Supplemental Figure H: Burn Scar on a Possible Palsa Mire. A photograph taken in the summer of 2022 with a DJI Mavic 3 unmanned aerial vehicle (UAV) at the 2019BC005 fire scar in Snag Junction, YT, Canada. The image depicts the possible presence of palsas. Palsas are small hills with permafrost cores that remain insulated by the thermo-regulating effects of surrounding high water tables. At this particular fire scar, we noted many small hills topped with deciduous stands that were surrounded by small lakes.

Supplemental Figure I: Aspen Leaf Miner on Post-fire Regrowth. This photograph was taken in the summer of 2022 at the Shovel Creek 2019 fire scar near Fairbanks, AK. The image depicts a resprouting aspen tree afflicted with aspen leaf miner.

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