Charcoal ecology: Its function as a hub for plant succession and soil nutrient cycling in boreal forests

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Abstract
We summarize current knowledge about the ecosystem functions of fire-produced charcoal in boreal forests with a special focus on its effects on soil carbon, nitrogen and phosphorous dynamics as well as on plant succession. Charcoal is a carbon-enriched material with a highly aromatic and porous structure. Charcoal is highly resistant to microbial decomposition and thus remains in soil for thousands of years, providing recalcitrant carbon to boreal forest soils. The abundant pores in and on charcoal surfaces have powerful adsorption abilities that can influence biogeochemical cycles and plant succession after fire. Our review details the influence of charcoal on plant and soil systems and explains the complex direct and indirect pathways of these influences that occur during succession after fires in boreal ecosystems. Among these pathways, the most important pathway through which charcoal influences plant and soil systems relates to the element composition and nutrient availability in soils and to the abundance of phenolics released from Ericaceae plants in the understory of boreal forests. We found a strong bias in the studied processes towards nutrient mineralization rather than immobilization, which suggests that it is risky to draw general conclusions about the influence of charcoal on soil nutrient dynamics. Last, the latest studies shed light on the enhancement of litter and humus decomposition by charcoal, given the possibility that charcoal accelerates CO2 release in a postfire forest. This review suggests comparative studies that are necessary to test the context-dependency of charcoal functions across a variety of boreal forest ecosystems.

KEYWORDS
above- and belowground linkages, black carbon, climate change, forest fire, succession

1 | INTRODUCTION

Forest disturbances, especially fires, are sensitive to climate conditions; thus, disturbance regimes are predicted to change due to accelerated warming and drying
climates in boreal forests (Johnstone et al., 2016; Seidl et al., 2020). Boreal forests are high-latitude forests in which the length of the season with subzero temperatures is 6–8 months and in which trees are 5 m in height at a minimum and the canopy cover is 10% (Gauthier, Bernier, Kuuluvainen, Shvidenko, & Schepaschenko, 2015). This biome constitutes at most 30% of the global forest area, ranging across high-latitude regions of Scandinavia, Canada, Alaska, Russia and Japan (Gauthier et al., 2015). Boreal forests possess a large amount of carbon (C); the biomass, detritus and soil of these forest ecosystems (including approximately 419 pg peat) contain approximately 709 pg C and sequester an estimated 0.7 pg C/year, which is the largest stock of all forested biomes (Dixon et al., 1994). Globally, this amount represents approximately 49% of the global total of forest C stocks (Dixon et al., 1994). In boreal forests, fire is the major disturbance agent (Seidl et al., 2020). Historically, severe crown fire was the most common form of fire in North America, while surface fire was the dominant form in Scandinavia and Russia (Gauthier et al., 2015; Makoto, Nemilostiv, et al., 2007). The mean annual percentage of burned area in boreal forests between 1997 and 2014 ranged from almost zero to more than 5% in the southern part of the Russian Far East, where the climate is relatively dry and human activity is high (Gauthier et al., 2015; Makoto, Nemilostiv, et al., 2007). Therefore, the relationship between C dynamics and fire disturbance in boreal forests needs to be understood to generate more accurate and precise predictions of global CO₂ dynamics in the future.

In terrestrial ecosystems, C sequestration occurs with plant succession and the associated inputs of plant litter (both above- and belowground litter) into humus and mineral soil. After a catastrophic disturbance, revegetation is first catalyzed by the dispersal of propagules, and the extent of this dispersal limits long-term succession (Makoto & Wilson, 2019). Therefore, C sequestration at the ecosystem level is regulated by the primary-succession dispersal limitations of plant propagules (Makoto & Wilson, 2016). On the other hand, given a lack of dispersal limitation, soil weathering and/or nutrient limitation in soil regulate plant succession after a disturbance (Walker & del Moral, 2003).

In this review, we summarize the current knowledge about the ecosystem functions mediated by fire-derived charcoal with a particular focus on the effects of charcoal on soil C, nitrogen (N) and phosphorous (P) dynamics as well as plant succession in boreal forests. A fire disturbance not only alters the structure of ecosystems but also creates pyrogenic substances such as charcoal, which is a unique characteristic of this type of disturbance. Therefore, an enhanced understanding of the influence of charcoal on plant and soil systems will provide insight into the mechanism of how forest fires influence plant succession in boreal forests. With the growing interest in the ecosystem function of biochar, several reviews have been published in this decade (e.g., El-naggar et al., 2019). Meanwhile, to our knowledge, the ecosystem functions of wildfire-derived charcoal have not been comprehensively synthesized by considering the characteristics peculiar to boreal forests. Because of the limited knowledge about charcoal functions in boreal forests, we also occasionally review data from cool-temperate coniferous forests.

2 | CHARCOAL AS A FORM OF RECALCITRANT C

Charcoal is one of the major byproducts of forest fires and is produced from the incomplete combustion of biomass and detrital materials (Preston & Schmidt, 2006). Charcoal has a highly porous structure with a high adsorption capacity but also has residual ash (calcium, magnesium) on its surfaces (Figure 1). The porous structure increases the surface area of charcoal, where the adsorption of substances occurs. The combustion and pyrolysis temperatures of biomass during forest fires vary significantly depending on the amount of fuel, the wind speed, the air temperature, the air humidity and the topography of the forests (Rothermel, 1983). Together with the characteristics of the source materials, the combustion conditions can influence the physical (notably the porosity) and chemical (notably the ash contents and pH) properties of charcoal. In general, charcoal produced in boreal forests is 6–8 months and in which trees are 5 m in height at a minimum and the canopy cover is 10% (Gauthier, Bernier, Kuuluvainen, Shvidenko, & Schepaschenko, 2015). This biome constitutes at most 30% of the global forest area, ranging across high-latitude regions of Scandinavia, Canada, Alaska, Russia and Japan (Gauthier et al., 2015). Boreal forests possess a large amount of carbon (C); the biomass, detritus and soil of these forest ecosystems (including approximately 419 pg peat) contain approximately 709 pg C and sequester an estimated 0.7 pg C/year, which is the largest stock of all forested biomes (Dixon et al., 1994). Globally, this amount represents approximately 49% of the global total of forest C stocks (Dixon et al., 1994). In boreal forests, fire is the major disturbance agent (Seidl et al., 2020). Historically, severe crown fire was the most common form of fire in North America, while surface fire was the dominant form in Scandinavia and Russia (Gauthier et al., 2015; Makoto, Nemilostiv, et al., 2007). The mean annual percentage of burned area in boreal forests between 1997 and 2014 ranged from almost zero to more than 5% in the southern part of the Russian Far East, where the climate is relatively dry and human activity is high (Gauthier et al., 2015; Makoto, Nemilostiv, et al., 2007). Therefore, the relationship between C dynamics and fire disturbance in boreal forests needs to be understood to generate more accurate and precise predictions of global CO₂ dynamics in the future.

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![Charcoal in the rhizosphere of trees. (a) Larch seedling develops the fine roots into the macro-pores of charcoal in East Siberia. (b) Tightly connected extraradical mycelium of ectomycorrhizal root of Betula platyphylla and charcoal particle and its detailed view (c) in northern Hokkaido. (d) The image of scanning electron microscope image of highly porous charcoal made of Quercus mongolica var. crispula (taken by Dr Yoko Watanabe). The visible pores are those of macro pores, while the abundant micropores are not visible in this photo but have significant functions for biogeochemical cycles [Color figure can be viewed at wileyonlinelibrary.com]](image-url)
at higher temperatures tends to be more porous than charcoal produced at lower temperatures. Furthermore, the surface area of charcoal from tree species with low-mineral ash wood tends to be higher than that from trees with high-mineral ash wood (e.g., alder). Fire-produced charcoal is a C-enriched, nitrogen-depleted pyrogenic material with a highly aromatic molecular structure (please see the details on the physiochemical properties of charcoal in Lehmann & Joseph, 2015).

In boreal forests across Scandinavia, the landscape-level amount of soil C stored as charcoal ranges from 0 to 2.2 mg C/ha, with an average of 0.7 mg C/ha (Ohlson, Dahlberg, Ökland, Brown, & Halvorsen, 2009). An experimental study triggered crown fire in a jack pine (Pinus banksiana) forest in Canada (Santin, Doerr, Preston, & González-Rodriguez, 2015). The study determined that 27.6% of the C affected by fire was retained as charcoal (4.8 ± 0.8 mg C/ha), while 12.6 ± 4.5 mg C/ha was emitted to the atmosphere after the experimental fire (Santin et al., 2015). A recent meta-analysis across temperate and boreal forests calculated that charcoal (in downed wood, humus and mineral soil) was produced, on average, at a rate of 5.2 ± 2.5% of the biomass exposed to fire in forest ecosystems, and a single wildfire event generated approximately 2.3 ± 1.7 mg C/ha in the form of charcoal (DeLuca, Gundale, Brimmer, & Gao, 2020). Interestingly, the amount of charcoal produced during fires is reported to increase in combination with beetle outbreaks in Alaskan boreal forests (Makoto, Kamata, Kamibayashi, Koike, & Tani, 2012), which are spreading in boreal forests probably due to climate warming (Kurz et al., 2008).

Due to its aromatic structure, charcoal is highly recalcitrant to soil microbial decomposition and thus remains in the soil ecosystem for hundreds to thousands of years (Liang et al., 2008). This characteristic separates it from other forest C pools in the ecosystem. For instance, the mean residence time of charcoal in soil has the potential to reach over 7,000 years, while those of pine log, pine branches and pine litter are approximately a few hundred years, 80 years and 10 years, respectively, in temperate coniferous forests (DeLuca & Aplet, 2008). Considering the substantial amount of charcoal produced and its long-term residence in soil, charcoal is expected to act as an important C pool in the soil of forest ecosystems (DeLuca et al., 2020).

Charcoal is also known to influence saprotrophic microbes. Findings from Wardle, Nilsson, and Zackrisson (2008) reported that charcoal accelerated humus decomposition in a Scandinavian boreal forest over 10 years. Furthermore, in a larch-dominant boreal forest in Far East Russia, Bryียนin, Abramova, and Makoto (2018) found that charcoal accelerated the decomposition of fine roots by 30% compared with the decomposition of fine roots without charcoal. Fine roots are a large source of C input to the soil in cold biomes (Mokany et al., 2006). This interaction between charcoal and litter and humus decomposition is important to consider in the prediction of global forest fire C dynamics and the potential for charcoal-C storage in boreal forest soils (Dixon et al., 1994). However, despite its importance, only a few studies have investigated the influence of charcoal on litter decomposition in boreal forests.

### 3 CHARCOAL AS A POROUS ADSORBENT AND SOIL N

N is a limiting nutrient in most forest ecosystems (e.g., Vitousek & Howarth, 1991) and is certainly limiting at earlier stages of primary succession in boreal forest ecosystems (DeLuca, Zackrisson, Gentili, Sellstedt, & Nilsson, 2007). Disturbances generally stimulate N mineralization and increase N availability in forest soils because they open the canopy, increase solar radiation and soil temperature and increase organic matter inputs (dead tree litter) to the forest floor (e.g., Vitousek & Matson, 1985). Meanwhile, in the case of a fire disturbance, fire-produced charcoal also acts as an enhancer of N mineralization and N availability in forest soil after the disturbance. In a laboratory experiment, charcoal made of bark and wood from mature Douglas fir and ponderosa pine trees in temperate forests produced at 350°C had more nitrate and less ammonium N (NH4+-N) than that produced at 800°C (Gundale & DeLuca, 2006). In their study, the concentration of NH4+-N in the charcoal produced at low temperature was likely low because the volatilization temperatures of organic nitrogen are lower than 800°C. The amine bonds of organic N begin cleaving at relatively low temperatures (Neary, Klopatek, DeBano, & Ffolliott, 1999), producing NH4+ molecules on the surface of charcoal. On the other hand, at least some of this NH4+ appears to oxidize into NO3−, as suggested by the higher NO3− concentrations on high-temperature charcoals (Gundale & DeLuca, 2006). Charcoal produced at a low temperature possessed more total inorganic N than that produced at a high temperature in a laboratory experiment (Makoto, Choi, Hashidoko, & Koike, 2011), partly due to the low volatilization temperature of N (Neary et al., 1999). The absorption of inorganic N as ash to the charcoal pores may contribute to the retention of inorganic N after forest fires (Makoto et al., 2012). Although NH4+ is positively charged and can be electrically bound to soil particles, a substantial amount of NH4+ is leached by rainfall (Bormann & Likens 1979) in the absence of charcoal after fire. Makoto et al. (2012) conducted a field burning experiment.
together with charcoal removal in a sub-boreal forest (Figure 2). Their study clearly showed a drastic decrease in \( \text{NH}_4^+ \) after several rainfall events, especially when charcoal was removed from the forest floor after fire in sub-boreal forests.

On the other hand, the adsorption capacity of charcoal contributes to N dynamics differently depending on the context. The adsorption capacity of charcoal is sometimes measured by using phenol as a standard material. In field observations, Pingree, DeLuca, Schwartz, and DeLuca (2016) measured the average adsorption capacity of fire-derived charcoal in several temperate pine forests as 29.7 \( \mu \text{g} \) phenol/mg charcoal. The abundant pores act as a powerful adsorbent for organic compounds such as phenolics (Keech, Carcailllet, & Nilsson, 2005), which are particularly released from the green leaves and litter of \textit{Ericaceae} species (e.g., \textit{Vaccinium} and \textit{Empetrum} spp.), and suppress N mineralization and nitrification in the forest floor in boreal regions (Figure 3). In such systems, charcoal adsorbs and removes phenolic compounds from soil and stimulates the activity of nitrifiers (Berglund, DeLuca, & Zackrisson, 2004; DeLuca, MacKenzie, Gundale, & Holben, 2006). It should be noted that although charcoal has the potential to remain in soil for thousands of years, the function of charcoal as an adsorbent is relatively short-lived, as the pores become clogged. In Scandinavia, the sorptive power of wildfire-produced charcoal decreases with time after the fire and persists for up to approximately 100 years in boreal forests (Zackrisson, Nilsson, & Wardle, 1996).

Charcoal can also have a negative influence on soil nitrate availability in postfire forests. In sub-boreal forests, Makoto, Shibata, et al. (2012) found that the removal of charcoal resulted in an increase in nitrate N (\( \text{NO}_3^- - \text{N} \)) after an experimental burn, which implies that charcoal may suppress the availability of \( \text{NO}_3^- - \text{N} \) after fire. Charcoal is recalcitrant but is slowly decomposable by soil microbes as a kind of litter (De La Rosa, Miller, & Knicker, 2018; Kuzyakov, Subbotina, Chen, Bogomolova, & Xu, 2009). If the litter C:N ratio is >30:1, N immobilization may occur (Liu & Sun, 2013), which decreases the levels of inorganic N in soil. In the experimental system studied by Makoto, Shibata, et al. (2012), the understory vegetation was not \textit{Ericaceae} sp. and phenolics were not abundant in the forest floor. The C:N ratio of the charcoal produced in the study system was 72:1, and the charcoal likely accelerated N immobilization. N immobilization can exceed N mineralization and may have also resulted in the
reduction of the soil nitrate concentration in the subboreal forests (Makoto, Shibata, et al., 2012).

4 | CHARCOAL AND SOIL P

The long-term absence of catastrophic disturbances may also cause P limitation for boreal vegetation in the later stage of primary succession, which may even trigger retrogression (Wardle, Walker, & Bardgett, 2004). In such P-limited ecosystems, charcoal produced by a low- to moderate-intensity fire can improve soil P availability. In field experiments, Makoto et al. (2012) showed that the presence of charcoal increases the P availability in soil, possibly due to the physical absorption of \( \text{PO}_4^{3-} \) to \( \text{Ca}^{2+} \) or \( \text{Mg}^{2+} \), which are abundant cations in charcoal pores.

For instance, the concentrations of inorganic nutrients and cations in the charcoal produced by experimental burning in a sub-boreal forest were as follows: available P, 4.9 g/kg; exchangeable Ca, 1.5 g/kg; and exchangeable Mg, 497 mg/kg. In North American temperate forests, charcoal produced at a low temperature (350°C) had more inorganic P than charcoal produced at a high temperature (800°C) (Gundale & DeLuca, 2006). On the other hand, despite the similar concentrations of inorganic P in charcoals produced at different temperatures (400°C and 800°C, Figure 4), the addition of charcoal produced at a low temperature resulted in more significantly increased soil P availability than the charcoal produced at a high temperature, especially when the charcoal content was abundant in the soil of sub-boreal forests (Makoto, Choi, et al., 2011). This contrasting influence of the charcoal formation temperature could be due to the difference in charcoal pH. At pH >7.0, inorganic P is fixed to \( \text{Ca}^{2+} \), which results in decreased mobility in inorganic P in soil (Brady & Weil, 2002). In fact, the pH of charcoal produced at a high temperature was 9.6, while that of charcoal produced at a low temperature was 6.0, likely due to changes in charcoal structure and chemistry (Makoto, Choi, et al., 2011).

Soil P availability can also be altered by charcoal in combination with soil faunal activity. Among soil fauna, earthworms are abundantly distributed in the southern parts of some boreal forests (Makoto & Kawakami, 2019; Phillips et al., 2019). Earthworms return to forest soils as time passes after fires (Bhaduria, Ramakrishnan, & Srivastava, 2000) and can incorporate charcoal into mineral soils via bioturbation (Carcaullet, 2001), thus changing nutrient availability. In sub-boreal forest soils, Pingree, Makoto, and DeLuca (2017) reported that charcoal and earthworms cooperatively increase soil P availability to specialized plant and microbial acquisition processes. Their findings suggest that charcoal, as a legacy of wildfire, and earthworm activity may stimulate the cycling of recalcitrant inorganic P pools. The influence of charcoal on soil fauna has attracted growing interest in the field of agriculture, but this topic has not been substantially investigated in forest ecosystems.

5 | CHARCOAL AND PLANTS

The influence of charcoal on soil N and P availability inevitably interacts with plant growth and regeneration in boreal forests (Figure 3). In a laboratory experiment, Makoto, Tamai, Kim, and Koike (2010) and Makoto, Choi, et al. (2011) showed that charcoal addition increased P uptake by boreal tree species and that the growth of these trees also increased at the same time. In the laboratory experiment, the charcoal produced at a low temperature (400°C) had a more positive effect on the growth of boreal tree species than the charcoal produced at a higher temperature (800°C) despite the similar concentrations of P within the charcoal types (43–44 mg P/kg charcoal) (Makoto et al., 2011). This may be due to the extremely high pH of charcoal produced at high temperatures (pH = 9.6). Charcoal not only directly influences soil P availability but also influences plant P uptake by activating symbiotic mycorrhizal fungi (Figure 3; Warnock, Lehmann, Kuyper, & Rillig, 2007). Warnock et al. (2007) suggested that the major mechanism through which charcoal benefits mycorrhizal fungi is by providing preferential habitats for mycorrhizal fungi with moderate moisture and oxygen availability. Another pathway through which charcoal increases P uptake by plants is to activate mycorrhizal helper bacteria by changing the signaling pathway between mycorrhizae and mycorrhizal helper bacteria (Warnock et al., 2007). In a laboratory experiment using woody boreal species, Makoto et al. (2010) reported that charcoal amendments produced...
by a low-intensity surface fire resulted in an increase in the ectomycorrhizal infection rate and the promotion of larch seedling growth, likely via a change in P uptake.

Interestingly, charcoal deposited on the soil surface did not have a positive influence on seedling growth in a larch species (Makoto et al., 2010). Instead, the charcoal buried in the subsurface soil had a positive influence on rhizosphere and seedling growth, suggesting that buried charcoal has a more positive influence on boreal trees than charcoal on the ground surface. These contrasting influences of charcoal on plants might be due to the black color of charcoal; when dry, charcoal is exposed to sunlight on the surface soil and thus reradiates heat. Despite the high concentration of P in charcoal, the P is difficult for plant roots to utilize due to the risk of drought stress (Makoto et al., 2010). For instance, in a permafrost area of boreal forests, the root depth is shallow (40 cm deep, Kajimoto et al., 2003) and trees frequently tip over (Figure 5). The root uplift can result in the burial of charcoal in a deeper soil profile (Figure 6). Furthermore, the vertical movement of earthworms (bioturbation) and the soil freeze–thaw cycle (cryoturbation) can translocate charcoal into deeper parts of the soil profile (Carcaillet, 2001). All these studies indicate that charcoal is not beneficial for plants directly after the fire, when it is still on the soil surface; over time, the charcoal is buried and thus becomes beneficial for plant growth in boreal forests.

Pluchon, Gundale, Nilsson, Kardol, and Wardle (2014) compared the influences of charcoal produced from various woody species in sub-boreal forests. In their study, the charcoal with the highest concentration of P had the greatest positive influence on seedling growth. Furthermore, this influence was most significant when the soil P existed at low concentrations. The effects of charcoal on tree growth via P availability are context-dependent and could be strongest when P is also limited, such as in a late stage of succession after the long-term absence of catastrophic forest fire in boreal forests (Wardle et al., 2004).

In Scandinavian boreal forests, Wardle et al. (1998) demonstrated that charcoal enhanced seedling growth by stimulating N mineralization after removing phenolics from soil. Interestingly, the improvement in growth in the presence of charcoal was species-specific for trees (more predominant for Pinus sylvestris than for Betula pendula), although the underlying mechanism of the species-specific response was not determined in the study. The beneficial effect of charcoal was revealed not only for growth but also for plant demography in an actual postfire forest, where multiple environmental factors can mask the influence of charcoal on plants. In a boreal forest in the Russian Far East, the number of seedlings of Pinus sylvestris was positively correlated with the presence of charcoal as well as with soil moisture and available P (Makoto, Hirobe, et al., 2011).

Considering seed germination, wood-derived charcoal often has a positive influence on the enhancement of soil moisture, soil temperature and physical properties that assist in oxygen absorption by seeds (Choi, Makoto, Quoreshi, & Qu, 2009). On the other hand, the charring of leaf litter can have a variety of influences on its function as a seedbed. For instance, for larch leaf litter, charring increased its function as a seedbed (germination rate increased by 30%), while charring diminished this
function in birch litter by 10–30% in Russian boreal forests (Makoto, Bryanin, Naumenko, et al., 2007).

6  FUTURE PERSPECTIVE

In summarizing previous studies in boreal forests, it becomes clear that biological activity may be a major limiting factor in boreal ecosystems. Charcoal has been shown to influence plant succession, and the mechanism by which charcoal influences plant growth and succession varies even within boreal forest ecosystems. The plant–soil system introduces unique pathways that create major limiting influences either from phenolics as inhibitors of microbial activity or from N and P as nutrients in boreal forests (e.g., Berglund et al., 2004; Makoto, Hirobe, et al., 2011; Wardle, Zackrisson, & Nilsson, 1998). Understanding these pathways allows us to predict the potential influence of charcoal on plant–soil systems, which is greatly context-dependent across boreal forests and should be tested with appropriate combinations of field and laboratory experiments. Furthermore, it is also notable that, compared its influence on N mineralization, the influence of charcoal on P mineralization, P immobilization and N immobilization has rarely been tested (see Pingree et al., 2017). These dynamics are especially important given the importance of P for boreal vegetation specifically (Giesler, Petersson, & Högberg, 2002), and more effort and experimentation are needed to elucidate the influence of charcoal on soil P dynamics.

As presented by Pluchon et al. (2014) and Keech et al. (2005), the influence of charcoal on plant regeneration differs depending on the material species of charcoal in boreal forests. Furthermore, Pluchon et al. (2014, 2015) demonstrated that the effect of charcoal on plants is habitat dependent in boreal forests. These studies point to an optimal combination of charcoal type and soil type for the amelioration of plant productivity in boreal forest soils. Charcoal, as a type of “biochar,” continues to attract interest for its suggested beneficial use in agriculture and environmental protection (Pujita et al., 2020; Woolf, Amonette, Street-perrott, Lehmann, & Joseph, 2010; Yuan, Wang, Pan, Shen, & Wu, 2019), though its acceleration of CO2 release from humus (Wardle et al., 2008), root litter (Bryanin et al., 2018) and leaf litter (Minamino et al., 2019) should also be considered as integral feedbacks to climate warming. Comparative studies are necessary in the future to test the effects of various charcoals on plant succession and related C dynamics in a wide range of contexts, to extrapolate the beneficial use of charcoal in managed environments and to intimately understand the functions of charcoal across fire-prone ecosystems.

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