Edge effects of linear disturbances on plant functional traits in boreal fens of northern Alberta, Canada.

Authors: Brooklyn Bolstad[a,1*], Kellina L. Higgins[b], Ellie Goud[c,d], Maria Strack[d], Anna Dabros[b]
[a] Natural Resources Canada, Canadian Forest Service, 5320 122 Street NW, Edmonton, AB, T6H 3S5, Canada.
[b] Natural Resources Canada, Canadian Forest Service, 580 Booth Street, Ottawa, ON, K1A 0E4, Canada.
[c] Saint Mary's University, Department of Biology, 923 Robie St, Halifax, NS, B3H 3C3, Canada.
[d] University of Waterloo, Department of Geography and Environmental Management, 200 University Ave. West, Waterloo, ON, N2L 3G1, Canada.

[1] Present address: Memorial University of Newfoundland: Ocean Sciences Center, 0 Marine Lab Road, St. John's, NL, A1C 5S7, Canada

*Corresponding author: Brooklyn Bolstad: bbolstad@ualberta.ca, +1 (587) 830-1345. Memorial University of Newfoundland: Ocean Sciences Center, 0 Marine Lab Road, St. John's, NL, A1C 5S7, Canada

Abstract

Global resource development has resulted in numerous disturbances that have a myriad of consequences on peatlands. We examined edge effects from one such linear disturbance, seismic lines, on plant community composition and select functional traits in Alberta, Canada. We tested the hypothesis that these disturbances influence community composition and functional traits for eight dominant fen plant species: *Larix laricina, Picea mariana, Betula glandulosa*, *Salix pedicellaris, Andromeda polifolia, Menyanthes trifoliata, Carex aquatilis*, and *Sphagnum warnstorfii*. We analyzed species percent cover, plant height, leaf dry matter content, and tissue nitrogen, phosphorus, potassium, and carbon content on the seismic lines and at various distances from the line edge. The influence of these disturbances was most evident on species cover; *P. mariana, M. trifoliata, C. aquatilis,* and *S. warnstorfii* showed significant and unique responses across measured distances, with generally decreased plant cover on seismic lines. Leaf dry matter content did not show significant species-level changes. Plant height was significantly different across measured distances for *B. glandulosa* and *C. aquatilis*. Generally, tissue nitrogen, phosphorus, potassium, and carbon increased on the seismic line, consistent with a release of nutrients during disturbance. *Carex aquatilis, M. trifoliata*, and *S. warnstorfii* contained remarkably different levels of these nutrients in their tissues compared to our other study species. Connecting community composition to functional traits provided insight into why recovery is lacking on seismic lines. We show that functional trait variation in response to linear disturbances signals a pathway of stress resilience that must be considered in ongoing forest management practices.

Keywords: plant functional traits, edge effects, linear disturbances, plant nutrient content, community composition, boreal peatlands.

1. Introduction

In the boreal forest of Alberta, Canada, oil and gas development has been, and continues to be, extensive (Dabros et al., 2018). The exploration phase alone requires the creation of numerous linear clearings, known as seismic lines, which can exist in densities of up to 40 km/km^2 (Filicetti et al., 2019). Characterized as 5-10 m wide linear disturbances usually placed 100-500 m apart in a parallel fashion, conventional seismic lines can extend for many kilometres (Lee & Boutin, 2006; Dabros et al., 2018; Strack et al., 2019). Seismic line construction removes a significant portion of the vegetation and disturbs the soil (Lee & Boutin, 2006; Dabros et al., 2018; AHFMP, 2021). Following the construction phase, seismic lines can have profound impacts on ecosystems, such as reducing the quality of habitat for species at risk through fragmentation and changing wildlife dynamics, including predator-prey interactions (Dyer et al., 2001; Filicetti et al., 2019).

Peatlands, which cover up to 50% of Alberta's oilsands region, are significantly fragmented by seismic lines (Strack et al., 2019; Vitt et al., 2000). These unique forested ecosystems provide many services such as groundwater purification and storage, and carbon sequestration (Bonn et al., 2014). Given the high density of seismic lines in northern Alberta, there is a concerted effort to identify their direct impact on peatlands, as well as any radiating ecological impacts, known as edge effects. These are changes to an ecosystem that extend outwards beyond the visible disturbance, potentially increasing the disturbance footprint (Murcia 1995; Harper et al., 2005). Due to the linear nature of seismic lines, the ratio of edge to unit area can be much higher than for nonlinear disturbances such as well pads, thus increasing the area impacted by edge effects relative to the area which is directly disturbed (Jordaan et al., 2009).

Previous studies have shown that environmental conditions can be influenced by linear disturbances, thus altering growing conditions for plants. For example, Dabros et al. (2021) found that seismic lines are wetter, with more light reaching the ground, than adjacent interior treed bogs. Often in tandem, drying effects from peat piling and dense tree and shrub growth at line edges can counteract the wet conditions found directly on the line (van Rensen et al., 2015; Davidson et al., 2020). However, wet conditions can still prevail past the immediate edges of seismic lines (van Rensen et al., 2015; Davidson et al., 2020). Plants can adapt to this environmental variation through functional trait expression, allowing them to persist in, or further contribute to, these conditions. Knowing this, our study sought to understand potential patterns of plant functional traits and leaf nutrient content resulting from seismic lines and their associated edge effects.

Plant functional traits are widely defined to include any morphological and physiological plant attribute that influences a trade-off between survival, growth, and reproduction (Violle et al., 2007). Here, we compare functional traits of dominant species found on and off conventional seismic lines in a boreal fen to explore if and how they influence ecological regeneration and potential edge effects. By including representatives of major plant types, from bryophyte to angiosperm, we covered a range of functions in our study ecosystem (Table 1). We measured plant height and leaf dry matter content (LDMC) for seven dominant vascular plant species, as well as tissue nutrient content (nitrogen [N], phosphorus [P], potassium [K], carbon [C]) for those same vascular species and one bryophyte species (Table 1).

Plant height is a measure of overall plant size and growth that is highly responsive to growing conditions (Westoby, 1998; Westoby et al. 2002; Dabros et al., 2022), which might reflect changes in environmental conditions found on seismic lines and near the edges. While species-specific, plant height can be a function of water, light, and nutrient availability (Pandey et al., 2018; Joswig et al., 2022). Leaf dry matter content (LDMC), which is the ratio of dry to fresh leaf mass, is used to assess tissue density (Shipley & Vu, 2002; Goud & Roddy, 2022). LDMC can decrease with increased water availability and increase in tandem with solar radiation (Niinemets, 2001; Laine et al., 2021; Goud & Roddy, 2022). As LDMC decreases due to the redundancy of maintaining long-lasting photosynthetic organs under elevated nutrient conditions, plant height can increase for some plants (Ryser, 1996; Vaieretti et al., 2007; Polley et al., 2022). Measuring both plant height and LDMC can provide information on what trade-offs are occurring due to disturbances.

Plant functional traits, including height and LDMC, can also be influenced by available nutrients (Mengel et al., 2001a; Ramage & Williams, 2002). Included in the essential elements for plant growth are N, P, K, and C, each of which make up a critical portion of plant biomass (Mengel et al., 2001a; Ramage & Williams, 2002; Polley et al., 2022). In this study we focused on these four macronutrients, recognizing their potentially crucial role in plant survival and adaptation to the disturbed conditions created by seismic lines, both on the lines and near their edges in the peatland. N and P are both responsible for a wide array of plant functions; plant height, leaf growth, and leaf longevity are all regulated by the ability of these macronutrients to form photosynthetic enzymes (Mengel et al., 2001b; Brady & Weil, 2008; Malhotra et al., 2018; Pandey, 2018). K is integral in managing plant responses to stress conditions, which may be present on seismic lines due to the alteration of environmental factors such as soil moisture and light availability. For example, excessively wet conditions can reduce soil oxygen content, leading to the leaching of K from plants via their roots and their inability to acquire aqueous K from the soil (Rosen & Carlson, 1984). C is an essential constituent of all organic compounds including carbohydrates, which are a critical source of energy for plant metabolism (Smith & Stitt, 2007; Yaseen et al., 2013). Assessing C content within the growing tissues of the plant species we focused on may reflect a change in tissue composition to favour other nutrients, as well as highlight a continued decrease in C storage due to growth and community composition changes (Goud et al., 2017). From a perspective of global significance, reducing C storage within peatlands through linear disturbances may have an impact on climate change through greenhouse gas fluxes (Goud et al., 2017). Additional influence imparted by these disturbances beyond their direct footprint (edge effects) may further reduce this capacity.

Natural regeneration of seismic lines in boreal ecosystems throughout Alberta is often arrested, or slower than anticipated, based on known successional trajectories (van Rensen et al., 2015; Dabros et al., 2022; Goud et al., 2024). Fens (peatlands that receive groundwater inputs in addition to precipitation) are known to be less likely to regenerate to a pre-disturbance state than drier upland ecosystems (van Rensen et al., 2015). It is imperative to increase our understanding of the underlying mechanisms of ecosystem regeneration to guide future peatland forest management practices. We sought to do so through an examination of functional traits, as differences to these traits along the gradient from the seismic line, through the edge, and to the undisturbed fen can lead to higher level changes in overall ecosystem functioning which limit regeneration. For example, plant litter decomposition rate is correlated with growing-period nutrient content (Cornwell et al., 2008), so changes to these nutrients can affect peatland turnover rate. This turnover rate plays an important role in ecosystem regeneration, as well as the likelihood of these peatland ecosystems persisting through continued disturbances, thus shaping management decisions. The objective of our study was to determine to what extent plant functional traits are influenced by seismic line disturbances, how they are related to changes in species composition on the lines, and through potential edge effects, in the adjacent fen. If edge effects are present in the fen adjacent to seismic lines, then plant functional traits may show differences on the seismic lines and along the distance gradient from the line edge into the interior treed fen. Furthermore, we expect community composition to be different between the seismic line, its edges, and the interior peatland.

2. Materials and methods

2.1 *Site description*

Our study is located within the larger Boreal Ecosystem Recovery and Assessment (BERA) Project (BERA, 2024). This project is a multi-sectoral alliance of industry, academic, and not-for-profit organizations that aims to understand the effects of disturbance in the boreal forest, and the subsequent restoration and forest management strategies available (BERA, 2024). The study area is approximately 85 km northeast of Lac La Biche and 40 km south of Conklin, Alberta, Canada, within the Athabasca oil sands deposits (55°22’37.2” N, 111°10’3” W). This site is in the Boreal Forest Natural Region and Central Mixedwood Natural Subregion (Natural Regions Committee, 2006). The Central Mixedwood subregion supports deciduous, mixedwood, and coniferous upland forests, as well as fens and bogs of varying nutrient regimes in the lowland areas (Natural Regions Committee, 2006).

2.2 *Plant community*

Our research site was placed within a treed moderate-rich fen. *Picea mariana, Larix laricina*, *Salix pedicellaris*, *Betula glandulosa*, *Andromeda polifolia*, *Menyanthes trifoliata,* and *Carex aquatilis* were the dominant vascular species at our research site and therefore the focal species in this study (Table 1) (A. Dabros, personal observations, July 2018). *Sphagnum warnstorfii* was chosen as the representative bryophyte because of its relative ease of field identification and high abundance. Other prevalent species in this fen included *Vaccinium vitis-idaea*, *Rhododendron groenlandicum*, *Maianthemum trifolium*, *Carex gynocrates*, *Aulacomnium palustre*, and *Sphagnum angustifolium*.

Table 1. List of dominant plant species within the study site included in plant functional trait measurement. Full names are followed by the two-letter abbreviation used in this paper. Measurements include plant height, percent cover, leaf dry matter content, and leaf nitrogen (N), carbon (C), phosphorus (P), and potassium (K) content.

Species	**Abbreviation**	**Lifeform**
Larix laricina	LL	Overstory tree
Picea mariana	PM	Overstory tree
Betula glandulosa	BP	Deciduous shrub
Salix pedicellaris	SP	Deciduous shrub
Andromeda polifolia	AP	Evergreen shrub
Menyanthes trifoliata	MT	Forb
Carex aquatilis	CA	Graminoid
Sphagnum warnstorfii	SW	Bryophyte

2.3 *Plot selection and establishment*

The seismic lines in our study were oriented North-South and cut in 1996, 26 years before our study took place (P. Kip, personal communication, September 12, 2023). Five replicate lines were chosen for this study. We sampled three 1 m x 1 m quadrats distributed systematically across a 20 m x 5 m plot across each seismic line (Figs. 1, 2). Each quadrat was placed approximately 6 m away from the others such that the three quadrats spanned a 20 m length along the line (Fig. 1). The same procedure was followed at three additional distances: edge (0 – 1 m from the edge of the seismic line) near-edge (5 – 6 m), and interior fen (50 – 51 m, considered to be the undisturbed reference site) (Fig. 1). We consistently sampled to the east of each seismic line to standardize the amount of sunlight reaching the ground (Fig. 1). The edge and near-edge distances were chosen to detect if seismic line edge effects are present in the adjacent fen, assuming that if they are present, they would be most evident close to the line edge.

2.4 *Measuring species composition and plant functional traits*

Species composition was measured by taking percent cover estimates (to the nearest 1% when less than 10%, otherwise to the nearest 5%) of the eight species in this study within each quadrat. For trees and tall shrubs, percent cover was measured by estimating the summed cover of all stems and branches for each species that fell within the quadrat boundaries, up to 1.5 m above the ground substrate.

Regarding plant height, one individual was sampled in each quadrat, except if a species was not present in the quadrat, then the closest individual to the quadrat was sampled. Height (cm) was measured for three individuals per species per distance (line, 0 m, 5 m, 50 m), from the top of the ground substrate to the top of the growing photosynthetic tissues.

Depending on the size of the leaves for each species, 3 to 30 leaves were collected per vascular plant species at each distance for lab analysis of LDMC and chemical composition. *Sphagnum warnstorfii* was also collected for lab analysis of chemical composition, but due to its morphology not being comparable to vascular plants, height and LDMC were not measured. Once collected, specimens were stored in plastic zipper bags in coolers to maintain fresh mass and water content, and then brought to the lab for immediate weighing. Leaf fresh mass (g) was measured and recorded for a standard number of leaves for each species at every distance. Leaf dry mass was obtained by oven-drying the samples until they achieved a constant weight, then LDMC (mg/g) was calculated as the ratio between dry mass and fresh mass (Pérez-Harguindeguy et al., 2016).

Leaf N and C concentrations were determined using a CN828 Combustion Analyzer (LECO Corporation, 2020). Within this analyzer, N was detected using a thermal conductivity (TC) cell, and C was detected using a non-dispersive infrared (NDIR) cell (LECO Corporation, 2020). Leaf P and K were determined using HNO_3 digestion by a Microwave Accelerated Reaction System (MARS) (CEM Corporation, 2012), followed by Inductively Coupled Plasma Optical Emission Spectrometer (ICP-OES) detection.

2.5 *Statistical analysis*

All statistical analyses were conducted using the R software version 4.3.0 (R Core Team, 2022). For all analyses, the three quadrat values were averaged within each distance (n = 5), and a significance level of $\alpha = 0.05$ was used. As observations within the five replicate sites are not independent, sites were treated as a random factor. Results were analyzed and presented using the R packages detailed below.

An Aligned-Rank Transform ANOVA (ART ANOVA) using the ARTool package (Kay et al., 2021), followed by pairwise post-hoc tests using the emmeans package (Lenth et al., 2023) and the multcomp package (Hothorn et al, 2008), were performed to test for differences in plant percent cover, height, and LDMC (response variables) based on distance (explanatory variable, fixed factor) relative to the seismic line. This was done separately for each species and each response variable. ART ANOVA was chosen because the data did not meet the assumptions of parametric tests and could not be addressed with transformations (Harrar et al., 2019). An analysis of variance based on type III Wald F tests with Kenward-Roger degrees of freedom was used to assess which effects were significant. Post hoc tests using the ART-C procedure with Holm's adjustment for multiple comparisons were used to identify specific differences for significant fixed factors (Elkin et al., 2021).

A Principal Coordinate Analysis (PCoA) ordination was used as an exploratory analysis to understand how nutrient content (N, P, K, and C) changed between species by distance using the vegan package (Oksanen et al., 2022). This provided a visual analysis of the complex relationship between N, P, K, and C content within species and across distances. Following the PCoA, an ART ANOVA and post-hoc tests were used to test for intraspecific (within-species) differences in each nutrient based on distance, following the same procedures as above.

3. Results

3.1 *Percent cover*

In general, there was evidence that tree cover increased at the edge of the seismic line, while herbaceous species cover declined in tandem. There was little change in the cover of the dominant shrub species in response to the seismic line. Regarding *P. mariana*, percent cover was significantly lower on the line than the edge (0 m), but no distance was significantly different than the interior at 50 m (Table 2, Fig. 3). Percent cover of both *C. aquatilis* and *M. trifoliata* was significantly higher on the line compared to 0 m and 5 m, but not 50 m (Table 2, Fig. 3). Percent cover for *S. warnstorfii* was significantly lower at the line and 5 m compared to 50 m, but the edge (0 m) was not significantly different from any distance (Table 2, Fig. 3). The ART ANOVA test showed no significant differences in percent cover by distance for *L. laricina*, *B. glandulosa*, *S. pedicellaris*, and *A. polifolia*. (Table 2, Fig. 3).

3.2 *Plant height*

Betula glandulosa was taller on the seismic lines, though this was minimally significant (Table 2, Fig. 4). *Carex aquatilis* was significantly shorter on the line compared to 5 m, though edge (0 m) and 50 m distances were not significantly different from the former two (Table 2, Fig. 4). *Andromeda polifolia, B. glandulosa, L. laricina, M. trifoliata, P. mariana*, and *S. pedicellaris* showed no significant height differences between any distances (Table 2, Fig. 4).

3.3 *Leaf dry matter content*

An ART ANOVA for leaf dry matter content did not show significant intraspecific differences for any species with regards to distance from the seismic line (Table 2, Fig. 5). While we did not statistically examine interspecific (between-species) changes, LDMC for *M. trifoliata* was visibly lower than for the other six species, highlighting the unique properties of this species' growth form (Fig. 5).

Table 2. *F* and *p* values shown for ART ANOVA statistical tests on individual species for percent cover, height, and leaf dry matter content. Significant *p* values denoted with an asterisk. Degrees of freedom = 3 for each test. (See Table 1 for plant species list and abbreviations).

Species	**Percent Cover (%)**		**Height (cm)**		**Leaf Dry Matter Content (mg/g)**	
	F	*p*	*F*	*p*	*F*	*p*
LL	1.14	0.373	1.46	0.274	0.578	0.640
PM	1.91	0.0546*	2.30	0.138	1.54	0.255
BG	0.250	0.860	3.53	0.0484*	0.510	0.683
SP	1.13	0.375	0.112	0.951	0.155	0.925
AP	1.91	0.181	0.258	0.854	0.523	0.675
MT	1.91	0.00139*	0.700	0.587	2.39	0.120
CA	6.52	0.00727*	5.92	0.0102*	0.902	0.469
SW	1.913	0.02415*	NA	NA	NA	NA

3.4 *Leaf nutrients*

A Principal Coordinate Analysis ordination (PCoA) showed that *M. trifoliata* had the highest dissimilarity in leaf N, P, K, and C concentrations when compared to the other species, followed by *C. aquatilis*, and *S. warnstorfii* (Fig. 6). The other five species were more similar to each other (Fig. 6). In addition, the variation in nutrient values was much larger for *M. trifoliata*, *C. aquatilis* and *S. warnstorfii*. The first axis of the PCoA explained 72.6% of the variation in our data, while the second axis explained 22.2% of the variation (Fig. 6).

The percentage of total leaf N did not show any significant intraspecific changes for our eight species (Table 3, Fig. 7). While not examined statistically, N content of *M. trifoliata* was visually higher than the other seven species, which supports the high degree of dissimilarity in our PCoA (Figs. 6, 7).

Salix pedicellaris had significantly more P content in its leaves on the line than the edge distances and interior fen (Table 3, Fig. 8). *Sphagnum warnstorfii* showed significantly higher leaf P content on the line than at 5 m, but neither of these distances were significantly different against 0 m and 50 m (Table 3, Fig. 8). While the overall ART ANOVA was marginally significant for *C. aquatilis,* no pairwise differences were significant (Table 3, Fig. 8). *Menyanthes trifoliata* showed higher P content than the other seven species, supporting the high dissimilarity seen in the PCoA (Figs. 6, 8).

Larix laricina and *P. mariana* both had significantly higher K content on the line than at 50 m, though this difference was only seen for *L. laricina* when comparing the line and both edge distances (Table 3, Fig. 9). *Menyanthes trifoliata* had significantly lower K content on the line than at 50 m, though neither edge distance was significantly different from the line nor the interior fen (Table 3, Fig. 9). However, K content within *M. trifoliata* was much higher than the other seven species (Fig. 9). *Carex aquatilis* also presented higher K content than the six remaining species (Fig. 9). These two results support our PCoA where both species were visibly different from the others (Fig. 6).

No species showed significant intraspecific differences in the percentage of total carbon present across distances (Table 3, Fig. 10). However, *M. trifoliata, C. aquatilis,* and *S. warnstorfii* all contained marginally lower levels of C compared to the other plants, supporting our PCoA where these three species showed high dissimilarity (Figs. 6, 10). When examined together, ART ANOVA results for nutrients are consistent with the PCoA results, with *M. trifoliata* being the least similar due to its differences across all four nutrients, followed by *C. aquatilis* for P and C, and *S. warnstorfii* for C. (Figs. 6-10).

Table 3. *F* and *p* values shown for ART ANOVA statistical tests performed on individual species for leaf N, P, K, and C. Significant *p* values denoted with an asterisk. Degrees of freedom = 3 for each test. (See Table 1 for plant species list and abbreviations).

Species	Leaf Nitrogen		Leaf Phosphorus		Leaf Potassium		Leaf Carbon	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
LL	4.22	0.0297	2.57	0.103	8.55	0.00262*	2.38	0.120
PM	0.813	0.511	2.03	0.163	5.37	0.0141*	0.408	0.750
BG	1.14	0.371	0.614	0.619	0.319	0.811	0.505	0.686
SP	0.479	0.703	6.48	0.00742*	1.66	0.229	0.400	0.757
AP	1.48	0.269	1.10	0.385	0.687	0.577	1.02	0.416
MT	2.52	0.107	0.520	0.676	5.09	0.0168*	2.26	0.133
CA	0.996	0.428	3.54	0.0482*	2.76	0.0882	1.10	0.389
SW	2.40	0.119	4.12	0.0317*	1.54	0.256	2.79	0.0859

4. Discussion

Our study aimed to examine the extent to which species percent cover and plant functional traits (height, LDMC, and N, P, K, and C content) are influenced by seismic lines both within the linear footprint itself and near its edges. Fens are known to be less likely to regenerate to a pre-disturbance state than bogs, which do not receive groundwater inputs (van Rensen et al, 2015). These environmental changes can lead to shifts in species composition on the seismic lines and may also be reflected in changes to plant functional trait values, providing insight into how seismic lines affect peatlands and the plants growing within them (Dabros et al., 2022; Goud et al., 2024).

Higher light and moisture levels are generally observed on seismic lines within forested peatlands due to a reduction in tree cover (Dabros et al., 2022; Davidson et al., 2020; Deane et al., 2020). At the edges of seismic lines, moisture and light levels can both decrease markedly, with a gradual increase back to levels seen in the interior peatland moving away from the line edge (Dabros et al., 2022). However, because our study took place in a relatively open fen, changes to soil moisture and sunlight resulting from seismic line construction may have been less drastic than similar studies, such as Dabros et al. (2021), which took place in a drier, heavily treed bog. This could have influenced the smaller magnitude of significance seen in this study and is beneficial to account for when assessing the impacts of seismic lines in similar fens throughout Alberta.

4.1 *Species composition*

Species composition was influenced by edge effects, with both tree species being almost absent on the line and much higher at both edge distances, whereas *M. trifoliata, C. aquatilis,* and *S. warnstorfii* showed the opposite pattern. This suggests that the latter three species were filling spatial gaps left by decreased tree cover on the line.

Picea mariana is a late-stage successional species with a slow growth rate (Fryer, 2014; Filicetti et al., 2019). While it is generally well adapted to saturated growing conditions (Fryer, 2014), Krause & Lemay (2022) observed that *P. mariana* grew up to twice as much above-ground biomass in well-drained conditions compared to saturated conditions. Additionally, Deane et al. (2020) found canopy gap fractions (the amount of open canopy as compared to closed) were up to 95% greater on seismic lines as compared to adjacent treed peatlands. Given this, the significant reduction in percent cover on the line for *P. mariana* was expected. Furthermore, the high percent cover for *P. mariana* at 0 m reinforces that edge effects are creating more optimal environmental niche requirements (drier growing conditions) for this species, as compared to the wetter conditions in the fen further away from the edge.

Though not significant, the pattern of noticeably reduced growth on the seismic line for *L. laricina* and subsequent dramatic increase at 0 m suggests that growing conditions are more favourable on seismic line edges than the line itself for this species. This supports previous research that found high canopy gap fractions (Deane et al., 2020) and low tree recovery (Dabros et al., 2021; Goud et al., 2024; van Rensen et al., 2015) on seismic lines which traverse peatlands. Further, *L. laricina* was found by Islam et al. (2003) to sustain less tissue injury under saturated growing conditions than *P. mariana*, thus supporting the lack of significance seen for this species across measured distances. This species can also reestablish after disturbance earlier than forbs, herbaceous species, and other tree species (Filicetti et al., 2019). While our findings do not suggest that *L. laricina* has regenerated on the line, we do propose that the lack of significant differences when compared to *P. mariana* could be due in part to the quick growth rate and lesser sensitivity to disturbances of *L. laricina* (Filicetti et al., 2019; Islam et al., 2003).

Percent cover for herbaceous species *C. aquatilis* (a graminoid) and *M. trifoliata* (a forb) was similar between the seismic line and the undisturbed fen 50 m away from the edge, but was much reduced at 0 m and 5 m. This is a clear indication of edge effects acting on *C. aquatilis* and *M. trifoliata.* The reduction in graminoid and forb cover might be explained by the aforementioned increase in tree density at 0 m, which decreases the amount of sunlight reaching the understory layer (Dabros et al., 2021), and therefore the available light for graminoid and forb growth. In addition, Alignier & Deconchat (2013) found drier substrate conditions at seismic line edges, which might be attributed to increased tree growth, and therefore water consumption, by *P. mariana* and *L. laricina.* The drier conditions on seismic line edges may have further extended to 5 m, proving unfavourable to *C. aquatilis* and *M. trifoliata,* which both prefer wetter conditions (Hewett, 1964; Hauser, 2006). Interestingly, Hewett (1964) also showed a correlation between the removal of peat and increased populations of *M. trifoliata.* This could potentially explain the high abundance of *M. trifoliata* on the seismic line (as compared to the edges), since the peat layer was disturbed during line construction. Thus, the seismic line itself may be favourable in comparison to the edges for *M. trifoliata*, though not more so than the interior fen. In the case of *C. aquatilis,* drier edge conditions as shown in previous studies (Alignier & Deconchat, 2013; Davidson et al., 2020) might have limited its growth on the edges, while the seismic line itself did not affect this species as severely. Our findings suggest that the conditions on the edges are unfavourable for *C. aquatilis* and *M. trifoliata*, representing a shift in plant community composition as a result of seismic line development and persistence.

Sphagnum warnstorfii, like *C. aquatilis* and *M. trifoliata,* prefers wet conditions (Vicherová et al., 2017) and lacks a competitive advantage against other bryophytes in shaded conditions (Deane et al., 2020). This might explain why its growth was reduced at line edges, where tree cover was higher than on the lines and other measured distances. Like other *Sphagnum* species, its propensity for growing in dense mats usually leads to relatively high percent cover (Laing et al., 2014; Bengtsson et al., 2016). However, the disturbance to the peat layer during seismic line construction is a likely cause as to why percent cover of *S. warnstorfii* cover was significantly reduced on the line as compared to the undisturbed fen. Where Dabros et al. (2021) found that wetter conditions on the line corresponded with high percent cover of *Sphagnum* species, the studied disturbances in this paper were considerably younger (around 26 years old in this study versus up to around 70 years in Dabros et al., 2021), therefore allowing for less recovery time for *S. warnstorfii* after it had been disturbed during line construction.

Overall, the significant changes to percent cover across the aforementioned vascular and nonvascular species, alongside further visual changes expressed in our data, support our hypothesis that seismic line disturbances are notably altering species composition in boreal peatlands, not only on the lines themselves, but also near the line edges. This finding strongly supports edge effects – influences from disturbances spreading beyond their boundaries. In consideration of forest management practices, understanding how recovery is hindered can help in planning strategic restoration actions of existing seismic lines in boreal peatlands. For instance, reducing line compaction through mounding may generate more suitable habitat for *P. mariana* and *L. laricina* by reducing moisture levels (Filicetti et al., 2019). However, it may also result in a decrease of *S. warnstorfii* and other *Sphagnum* species' cover by means of a second disturbance (Filicetti et al., 2019; Kleinke et al., 2022).

4.2 *Plant height*

The significant height differences seen for *C. aquatilis* across measured distances are consistent with its known height plasticity across its circumboreal distribution, based on available growing conditions (Hauser, 2006; Betway-May et al., 2021). Generally, this species grows tallest in very wet, open conditions (Hauser, 2006; Betway-May et al., 2021), though this has not been the case in our study, where *C. aquatilis* was shorter on the lines, despite seismic lines generally presenting more open and wet conditions (Dabros et al., 2022; Davidson et al., 2020; Deane et al., 2020). However, in addition to creating wetter and more open conditions, seismic line construction is known to compact the soil (Davidson et al., 2020), which may reduce the capacity for growth on the lines, counterbalancing the advantages of greater soil moisture and increased light. Furthermore, despite the conditions on the line being visibly more open than the adjacent fen, the fen at our research site was sparsely treed (see Fig. 2), with the canopy reaching a maximum recorded height of just 3 m tall (B. Bolstad, personal observations, July 2022). As such, the light advantage on the lines might have only been substantial enough to provide a trade off between plant abundance and height for *C. aquatilis,* thus inhibiting significant increases on the line for both parameters.

Larix laricina and *P. mariana* showed a larger variability in height in the adjacent fen (edges and interior) than on the seismic lines, as compared to *C. aquatilis*. This is likely due to the trees on the edges and interior fen having a larger range of ages, and thus larger differences in height, than the ones of relatively uniform age on the seismic line. In comparison, *C. aquatilis* grows new photosynthetic tissue every year, and thus it is less likely to have substantial differences in height at any measured distance. Additionally, the persistence of hummocks and hollows may provide a greater range of environmental conditions in the adjacent fen than on seismic lines, which are known to have reduced microtopography (Lovitt et al. 2018; Stevenson et al. 2018). This may provide a higher diversity of suitable microsites for tree seedlings to establish and grow in the adjacent fen, which could be reflected by higher variability in tree heights, as our results showed.

Some variability in height was observed for deciduous shrubs *B. glandulosa* and *S. pedicellaris*, with both species growing taller on the seismic line. Increased shrub growth is supported by greater light availability on the lines as compared to the interior fen (Dabros et al., 2021). However, for *A. polifolia* and *M. trifoliata,* height varied very little across our measured distances. These two species are generally short statured, and their overall height plasticity is not large to begin with (Hewett, 1964; Taylor, 2007). It can be concluded that the altered environmental conditions on the lines impacted the height response of *B. glandulosa* and *S. pedicellaris,* though not *A. polifolia* and *M. trifoliata*.

4.3 *Leaf dry matter content*

Leaf dry matter content reflects variation in leaf tissue density which can indirectly influence plant growth, rates of litter decomposition, and ecosystem nutrient cycling (Pakeman et al., 2010; Smart et al., 2017; Tao et al., 2019). Variation in LDMC can highlight important trade-offs in resource use and structural allocation in response to disturbances to an ecosystem. For instance, increases in soil water, nutrient, and light availability often correspond with decreasing LDMC (Candeias & Fraterrigo, 2020; Niinemets, 2001). However, Laine et al. (2021), challenged this theory by finding that LDMC decreased for vascular plants experiencing water level drawdown and therefore, decreased soil moisture, in a rich fen. Despite seismic lines being generally wetter with more light availability, LDMC was not significantly altered in any of our species along the seismic line to interior fen gradient.

Although most species had similar average LDMC values relative to each other, LDMC values for *M. trifoliata* were about half as high as any other species, indicating leaves that are much less dense relative to the other species. *Menyanthes trifoliata* is quite distinct from the other six vascular species, with the first distinction being its classification as a forb. As such, it does not have woody tissues like the shrub and tree species we studied. Possessing broad, fleshy leaves in a tri-leaflet arrangement, *M. trifoliata's* mean leaflet size is 32.2 cm^2 (Hewett, 1964). This sets it apart from our other non-woody species, *C. aquatilis* (graminoid), which has long, grass-like leaves. Large, fleshy leaves are usually correlated with smaller LDMC, as plants with this feature are equipped for wet conditions where water conservation is not strictly necessary (Goud & Roddy, 2022). With these uniquely fleshy leaves, LDMC for *M. trifoliata* is then expectedly lower than our other species of interest.

4.4 *Tissue nutrient content*

Existing studies show that available soil N decreases under saturated conditions due to denitrification and leaching, thus providing less plant-available N (Mengel et al., 2001b; Nguyen et al., 2018). While we did not assess soil nutrient levels, given this knowledge, foliar levels of N may be reasonably expected to decrease on the line under saturated conditions and increase on the edges where it is drier. However, our results did not show significant changes to foliar N content for any species. One reason may be that N is not limiting in this fen and thus, even when N content in the soil is lowered due to saturated conditions, it is still available in sufficient quantities for plants to acquire. Furthermore, while the conditions in other, drier boreal ecosystems like uplands and bogs are known to be significantly wetter on the lines than the surrounding area (Dabros et al., 2017, 2021; Davidson et al., 2020), this difference may be less pronounced in wet fens. Our study site was no exception. Saturated soil conditions generally prevailed across our fen, regardless of distance from seismic line. Consequently, if denitrification under saturated conditions occurs in this fen, it would be of similar magnitude on and off the seismic lines (Nguyen et al., 2018). Overall, when considering foliar N content, we suggest that edge effects are not present.

Similar to N, plant-available P in soil can be reduced due to waterlogging, leaching, and soil erosion processes (Huang et al., 2003). However, the general trend for foliar P content showed an increase within our species on the line compared to the edges or the interior fen, particularly for *S. pedicellaris* and *S. warnstorfii*. This may suggest that wetter conditions on the seismic line did not limit the acquisition of P for these species, especially *S. warnstorfii,* which prefers very wet conditions (Vicherová et al., 2017). While increased plant-available P can influence leaf growth and longevity (Mengel et al., 2001a; Malhotra et al., 2018), this was not reflected in a change to LDMC for *S. pedicellaris*, nor was its percent cover affected, potentially due to previously discussed opposing environmental factors negatively affecting the growth of this species.

Many enzymes responsible for photosynthesis and stomatal closure require K for activation, making it an important chemical for plant growth and water retention (Brady & Weil, 2008; Tighe-Neira et al., 2018). In higher light environments such as exposed seismic lines, sufficient levels of K become increasingly important to prevent water loss (Brady & Weil, 2008; Tighe-Neira et al., 2018). It was unsurprising then that K content significantly increased for *L. laricina* and *P. mariana* on the line as compared to the adjacent fen, both of which may have been required to adapt to these conditions with increased foliar K levels. It is plausible that increased levels of foliar K on the seismic line for these species could further explain the lack of differences in height and LDMC, as K does not seem to be limiting as a result of seismic lines and edge effects. Interestingly, the opposite trend was seen for *M. trifoliata,* where foliar K content was significantly lower on the line than the undisturbed adjacent fen. This may be because, by possessing low LDMC and adaptations to wet conditions, *M. trifoliata* does not need as much foliar K to prevent water loss on the seismic line as compared to other distances (Wang et al., 2022). Further, *M. trifoliata* stood out as most dissimilar to other species with regards to N, P, and K. It contained higher levels of these three macronutrients than the other species, supporting findings from Wang et al. (2022), which show a correlation between low LDMC and increased ease of nutrient acquisition.

There were no significant intraspecific changes to C concentration, suggesting that environmental alterations on the seismic lines compared to the adjacent fen were not substantial enough to affect C content within our studied species. However, the observed shifts in species composition resulting from these disturbances may be compromising the amount of long-term C storage possible within Alberta's peatlands through biomass reductions (Goud et al., 2017). This is especially prevalent when considering the near removal of *P. mariana, L. laricina,* and the peat layer on seismic lines, all of which store C for longer periods of time than annual or biannual forbs and herbaceous species. To build on the foundational results of our work, future studies should assess nutrient content and species composition immediately following seismic line creation, further monitoring changes over time. This would lead to a greater understanding of the temporal effect of seismic lines on peatland plant communities, influencing a more sustainable process and outcome for future forest management globally.

4.5 *Conclusions*

Seismic lines and their associated edge effects influence relative abundance and functional trait values for notable peatland plant species, even after almost three decades since line construction. These findings explain one mechanism by which natural regeneration is lacking on seismic lines. Our results are supported by existing literature showing that regeneration is severely delayed, or even entirely lacking, within peatland ecosystems (van Rensen et al., 2015; Dabros et al., 2022; Goud et al., 2024). The visible network of seismic lines throughout Alberta's boreal forest further corroborates these findings by providing clear visual evidence of a lack of regeneration. Our findings also affirm global concerns surrounding reduced peatland C storage resulting from resource development in a time of increased atmospheric CO_2 levels. By connecting changes in plant community composition to select functional traits, our results signal a pathway of plant stress resilience that must be considered in ongoing forest management practices.

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Author contributions

Brooklyn Bolstad: Methodology, Formal Analysis, Investigation, Data Curation, Writing – Original Draft, Writing – Review & Editing, Visualization. **Kellina L. Higgins:** Conceptualization, Methodology, Validation, Formal Analysis, Data Curation, Writing – Review & Editing, Visualization. **Ellie Goud:** Conceptualization, Methodology, Validation, Investigation, Writing – Review & Editing, Supervision. **Maria Strack:** Conceptualization, Methodology, Validation, Investigation, Writing – Review & Editing, Supervision, Funding Acquisition. **Anna Dabros:** Conceptualization, Methodology, Validation, Investigation, Writing – Review & Editing, Supervision, Project Administration, Funding Acquisition.

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Fig. 1. Study design showing larger plot (white rectangle) placed on the seismic line to delineate the line precisely, with sampled quadrats (dark grey squares) placed where data was collected during the 2022 field season. Sampled edge distances are depicted by a distance bar representing the transect which was placed perpendicular to the larger plots.

Fig. 2. Aerial drone photograph of our study site: a moderate rich fen fragmented by conventional seismic lines south of Conklin, Alberta, Canada. Plots established for our study were marked with white flagging tape, visible on the seismic line. Photo credit: X.Y Chan, 2022.

Fig. 3. Variation in percent cover for eight peatland plant species at four positions relative to seismic line disturbance (line, edge [0 m], 5 m, and 50 m), assessed using an ART ANOVA (See Table 1 for plant species list and abbreviations). Values are medians (bars) with individual data points overlain at each distance. Bars with different letters are statistically significant based on a post-hoc test using the ART-C procedure with Holm's adjustment for multiple comparisons for tests with overall significant results.

Fig. 4. Variation in plant height for seven vascular peatland plant species at four positions relative to seismic line disturbance (line, edge [0 m], 5 m, and 50 m), assessed using an ART ANOVA (See Table 1 for plant species list and abbreviations). Values are medians (bars) with individual data points overlain at each distance. Bars with different letters are statistically significant based on a post-hoc test using the ART-C procedure with Holm's adjustment for multiple comparisons for tests with overall significant results.

Fig. 5. Variation in leaf dry matter content for seven vascular peatland plant species at four positions relative to seismic line disturbance (line, edge [0 m], 5 m, and 50 m), assessed using an ART ANOVA (See Table 1 for plant species list and abbreviations). Values are medians (bars) with individual data points overlain at each distance.

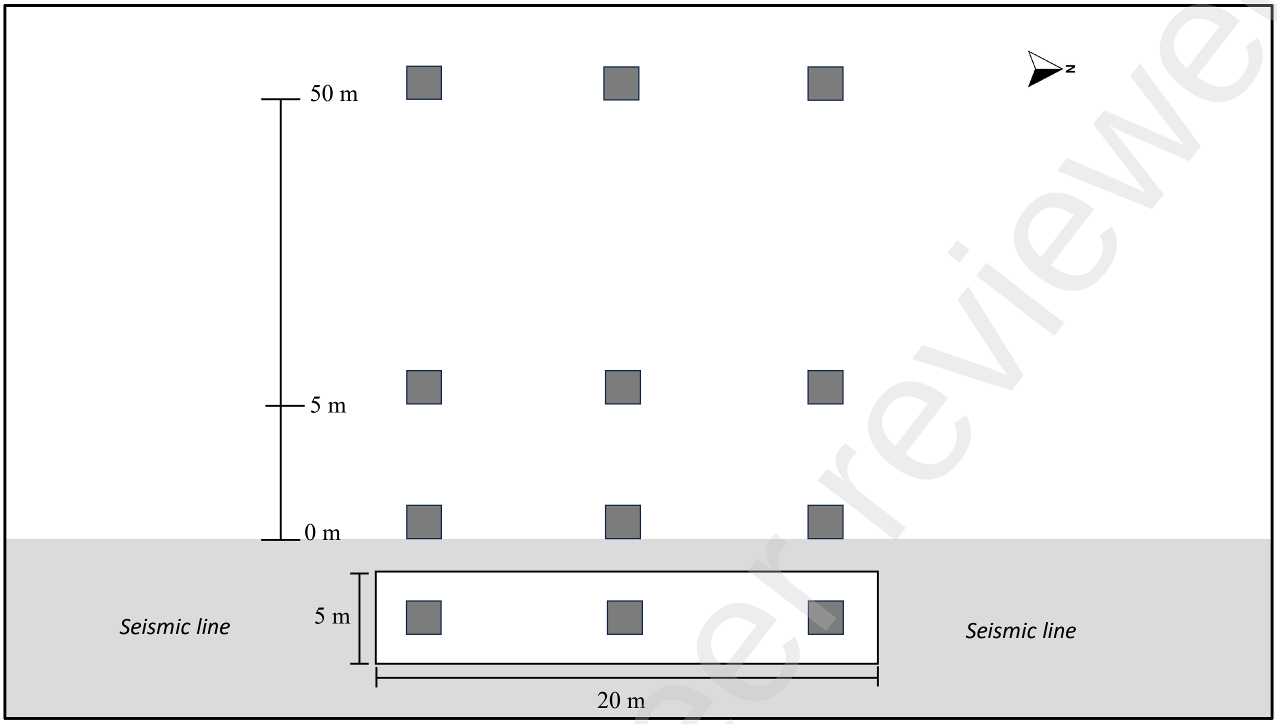
Fig. 6. Principal Coordinate Analysis (PCoA) of leaf N, P, K and C contents by individual plants at all positions relative to seismic line disturbance, combined (See Table 1 for plant species list and abbreviations). Ellipses show 95% confidence intervals around group centre points. The percentage of variation explained is depicted on each axis, as calculated from relevant eigenvalues.

Fig. 7. Variation in total leaf nitrogen (%) for eight peatland plant species at four positions relative to seismic line disturbance (line, edge [0 m], 5 m, and 50 m), assessed using an ART ANOVA (See Table 1 for plant species list and abbreviations). Values are medians (bars) with individual data points overlain at each distance.

Fig. 8. Variation in leaf phosphorus (mg/kg) for eight peatland plant species at four positions relative to seismic line disturbance (line, edge [0 m], 5 m, and 50 m), assessed using an ART ANOVA (See Table 1 for plant species list and abbreviations). Values are medians (bars) with individual data points overlain at each distance. Bars with different letters are statistically significant based on a post-hoc test using the ART-C procedure with Holm's adjustment for multiple comparisons for tests with overall significant results.

Fig. 9. Variation in leaf potassium (mg/kg) for eight peatland plant species at four positions relative to seismic line disturbance (line, edge [0 m], 5 m, and 50 m), assessed using an ART ANOVA (See Table 1 for plant species list and abbreviations). Values are medians (bars) with individual data points overlain at each distance. Bars with different letters are statistically significant based on a post-hoc test using the ART-C procedure with Holm's adjustment for multiple comparisons for tests with overall significant results.

Fig. 10. Variation in total leaf carbon (%) for eight peatland plant species at four positions relative to seismic line disturbance (line, edge [0 m], 5 m, and 50 m), assessed using an ART ANOVA (See Table 1 for plant species list and abbreviations). Values are medians (bars) with individual data points overlain at each distance.


50 m
5 m
0 m
Seismic line
5 m
Seismic line
20 m
N