Abiotic and native vegetation species associations of an invasive tree species in the Central Kootenays BC: Implications for invasion risks and opportunities for native vegetation recovery

By

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Declaration of Committee

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Title:	Abiotic and native vegetation species associations of an invasive tree species in the Central Kootenays BC: Implications for invasion risks and opportunities for native species recovery
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Abstract

I studied an invasive tree species black locust (*Robinia pseudoacacia* L.), in BC's Lower Columba Valley (LCV). Black locust has invaded forests and open lands since its introduction to revegetate disturbed slopes in the 1940's. I conducted research to help my partners Teck Metals Ltd. achieve three goals: (1) assess the ability of aerial imagery to support visual identification of black locust stands and recommend strategies for improving black locust identification, (2) identify abiotic conditions and native vegetation species associated with risks of black locust invasion, and (3) develop strategies to contain new black locust invasions in the LCV and remediate sites invaded by black locust. Aerial imagery successfully helped identify flowering black locust trees but did not help identify non-flowering trees and black locust shrubs and recruits. Black locust cover increased in association with increasing temperature, light availability, moisture availability, and soil disturbance, but black locust did not occur on sites with permanently saturated soils. Black locust was associated with early-seral deciduous tree species including black cottonwood and trembling aspen and the native conifer species western white pine and Douglas-fir. Black locust was not associated with later-seral coniferous species associated with either hot and dry conditions (including ponderosa pine) or cool conditions (including western hemlock). Black locust invasions may be able to be contained and restored by physically remediating disturbed sites, removing black locust on disturbed sites, and planting native tree and shrub species to stabilize soils and reduce black locust seedbank and rootstock establishment and maturation success by outcompeting black locust for light, space, and moisture. Native forests may be able to be re-established on sites invaded by mature black locust stands by protecting sites from further disturbances, restoring native tree species throughout the region to increase propagule availability and re-colonization success, and planting native tree and shrub species to replace maturing black locust stands with native mid- and later-seral forest species.

Keywords: black locust; forest ecology; invasive species; ecosystem succession; image validation; ecological restoration

Dedication

Dedicated to my Dad Robert Fuller, my Mom Peggy Evans, and my sister Natalie Fuller. Thank you for your caring, intelligent, and always loving support, your challenging questions, your patience, and your love through my Master's degree. Dad, thank you for your advice on study design and your time helping me understand where tree species grow. Mom, thank you for encouraging me to take risks, not worry overmuch, and follow through with this commitment. Natalie, thank you for chatting science at the dinner table and over the phone. It has been a pleasure completing our Master's degrees together. Thank you! Much love.

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I respectfully acknowledge SFU and BCIT are on the unceded territories of the Coast Salish peoples including the Tsleil-Waututh, Kwikwetlem, Squamish, and Musqueam Nations. This research was conducted in Trail BC on the territories of the Ktunaxa Nation and the Okanagan Nation.

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List of Acronyms

SFU	Simon Fraser University
BCIT	British Columbia Institute of Technology
LCV	Lower Columbia Valley
BL	Black locust
UAV	Unmanned Aerial Vehicle
DEM	Digital Elevation Model
BEC	Biogeoclimatic Ecosystem Classification
TEM	Terrestrial Ecosystem Mapping
VIF	Variance inflation Factor
NMDS	Non-Parametric Multi-Dimensional Scaling
GLMM	Generalized Linear Mixed-Effects Modelling
AIC	Akaike Information Criterion
LRT	Likelihood Ratio Test
USGS	United States Geological Survey
NDMI	Normalized Difference Moisture Index

Tree Species Acronyms and Notation

Species Code	Common Name	Scientific Name
BL	Black locust	Robinia pseudoacacia
AT	Trembling aspen	Populus tremuloides
ACT	Black cottonwood	Populus trichocarpa
CW	Western redcedar	Thuja plicata
EP	Paper birch	Betula papyrifera
FD	Interior Douglas fir	Pseudotsuga menziesii
FG	Grand fir	Abies grandis
FS	Subalpine fir	Abies lasiocarpa
FB	Balsam fir	Abies balsamea
HW	Western hemlock	Tsuga heterophylla
LT	Larch spp.	Larix spp.
MS	Silver maple	Acer saccharinum
Picea	Spruce spp.	Picea spp.
PL	Lodgepole pine	Pinus contorta
PW	Western white pine	Pinus monticola
PP	Ponderosa pine	Pinus ponderosa
YP	Pacific yew	Taxus brevifolia

Shrub Species Acronyms and Notation

Species Code	Common Name	Scientific Name
Acerglab	Douglas maple	Acer glabrum var. douglasii
Berbaqu	Oregon grape	Berberis aquifolium
Cornser	Red-osier dogwood	Cornus stolonifera
Corycor	Beaked hazelnut	Corylus cornuta
Elder	Black elderbery	Sambucus nigra
Phillew	Mock orange	Philadelphus lewisii
Prunvir	Chokecherry	Prunus virginiana
Rosa.spp	Rose species	Rosa spp.
Rubuparv	Thimbleberry	Rubus parviflorus
Salix	Willow species	Salix spp.
Spirea	Western spirea	Spiraea douglasii
Sympalb	Common snowberry	Symphoricarpos albus

Executive Summary

I studied an invasive tree species black locust (*Robinia pseudoacacia* L.), in BC's Lower Columba River Valley (LCV). Black locust has invaded forests and open lands since its introduction in the 1940's to revegetate disturbed sites in the LCV. I conducted research to help my research partners Teck Metals Ltd. achieve three goals: (1) assess the ability of aerial imagery to support visual identification of mature and invading black locust stands and recommend strategies for improving black locust identification, (2) identify abiotic conditions and native vegetation species associated with risks of black locust invasion, and (3) develop strategies to contain new black locust invasions in the LCV and remediate sites invaded by black locust.

I used 6 cm^2 resolution imagery collected from an unmanned aerial vehicle (UAV) survey in June 2022 to identify black locust stands within a 600 ha study area in the Lower Columbia Valley (LCV), approximately 5 km north of Trail BC. I recorded black locust cover, abiotic conditions, and native tree and shrub species cover within the study area on 151 circular ground plots of 11.28 m radius (400 m^2 area). I used a 1 m^2 resolution digital elevation model (DEM) to generate total incoming solar radiation (insolation), an indicator of light availability and temperature, at plot centers. I used Sentinel-2 satellite imagery collected in summer 2021 and 2022 to generate Normalized Difference in Moisture Index (NDMI), an indicator of moisture availability in soils and vegetation. I visually estimated black locust and native tree species cover on ground plots across three different height classes: tree (> 10 m), shrub (2 – 10 m), and recruit (< 2 m).

I assessed the ability of aerial imagery to support visual identification of black locust invasions by comparing identification success of black locust within plot boundaries on aerial imagery to true presences and absences on ground plots. Aerial imagery successfully helped identify flowering black locust trees but did not help identify non-flowering trees and black locust shrubs and recruits. Identification of flowering black locust trees on aerial imagery had a 61 % true positive identification rate, a 98 % true negative identification rate, a 38 % false negative identification rate, and a 3 % false positive identification rate. Black locust and native trees were occasionally misidentified – black locust flowers looked like the bright, reflective undersides of black cottonwood leaves blown in gusts of wind. Collecting imagery on calm days will reduce mistaken identification between black cottonwood and

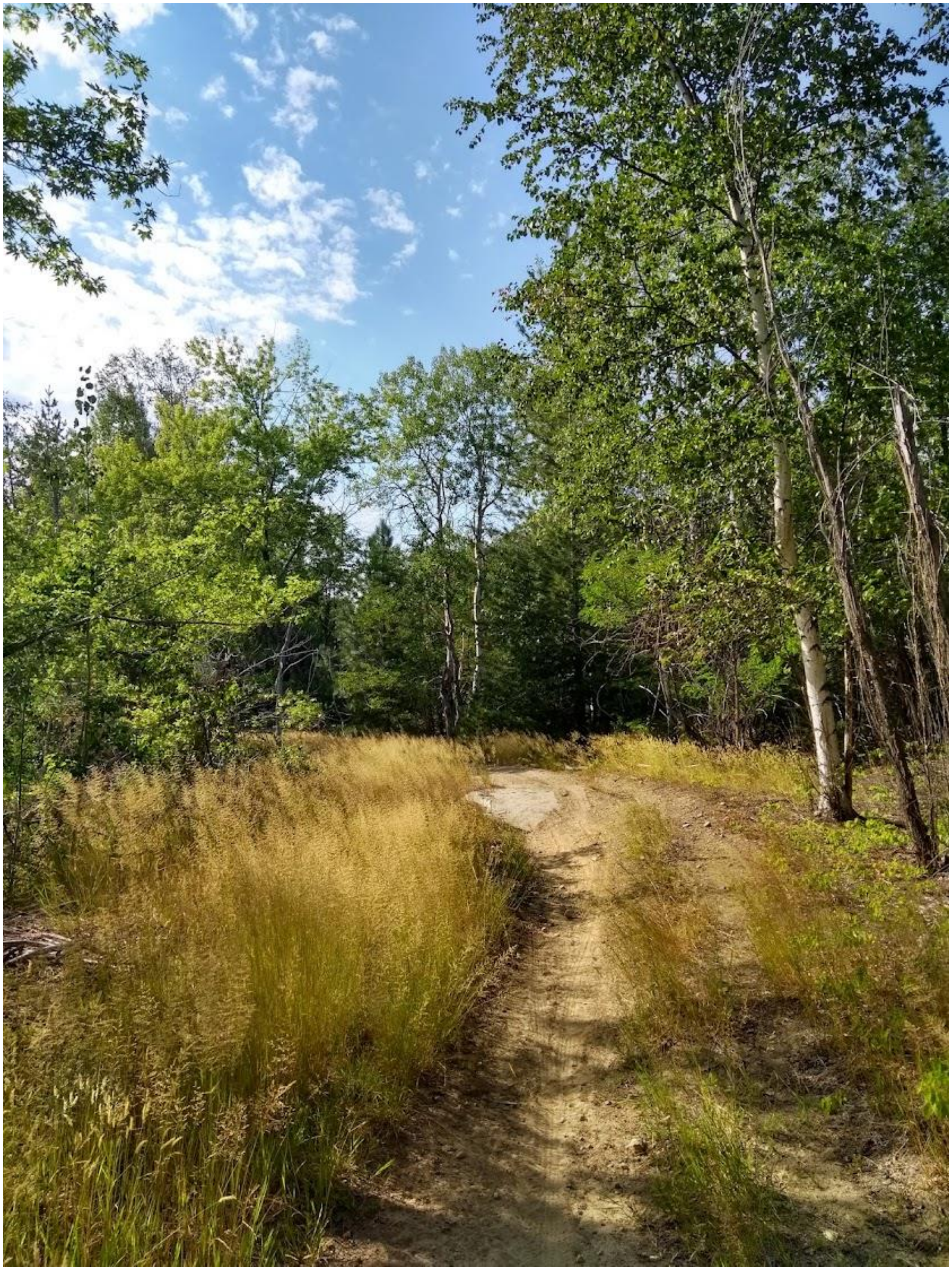
black locust. Black locust was also difficult to differentiate from surrounding native tree canopies on forested sites on 2-dimensional imagery – collecting stereoscopic imagery from overlapping drone flights or draping imagery over a LIDAR point cloud will help identify tree species in different forest layers. Aerial imagery did not allow shorter non-flowering black locust shrubs and recruits to be identified in either open areas or forest understories. To identify areas where black locust invasions are likely to occur around visible flowering tree-height black locust visible on aerial imagery, I assessed black locust recruit and shrub cover associations with abiotic conditions including light and moisture availability and native tree and shrub species cover.

I ran correlation analysis, multi-variable generalized linear models, and non-parametric multi-dimensional scaling to assess associations between black locust cover, abiotic conditions, and native tree and shrub species cover. I used observations from field plots and findings in the scientific and technical literature to support recommendations for containing new black locust invasions and remediating mature black locust stands in the LCV.

Black locust tree, shrub, and recruit cover increased with increasing temperature and light availability, represented by insolation, and increasing soil and vegetation moisture availability represented by NDMI. Black locust grew on warm (exposed) and dry areas where increased moisture was available at slope bases, within gullies, and surface and sub-surface seeps. It grew on cool (shaded) and moist areas where mass wasting, roads, and historic rural and industrial disturbances had loosened soils, created canopy gaps, and increased understory light availability. Black locust also grew abundantly along active and legacy roads and trails and along warm creek and river edges. Black locust's plot cover increased in association with early-seral deciduous tree species including black cottonwood and trembling aspen, especially on warm and well-lit aspects. Black locust was not associated with undisturbed coniferous tree stands growing on cool conditions (including western redcedar and western hemlock) or very dry conditions (including ponderosa pine). Active and legacy roads and trails, creek edges, moist micro-sites including gullies, seeps and slope breaks on dry areas, warm-aspect deciduous forests, and canopy gaps and soil disturbances in cool coniferous forests are invasion vectors allowing black locust to access and colonize native forests.

Several strategies may be employed to contain and treat new black locust invasions and recover native forests on sites occupied by mature black locust stands. Soil disturbances and canopy gaps on invasion vectors should be remediated by planting native tree and shrub species. Planting dense thicket-forming deciduous tree and shrub species will help contain initial invasions by outcompeting black locust for light and moisture and planting mid and later-seral conifer species will help establish long-term shade to discourage black locust growth. Existing black locust invasions on active and legacy disturbed sites including roads, trails, and rural and resource use areas may be removed with mechanical treatments and herbicide as long as these treatments are limited to the footprints of already disturbed sites and avoid disturbing surrounding vegetation. Reducing soil disturbance within the seed dispersal area around black locust will avoid breaking the dormancy of seeds dispersed by reproductive trees into surrounding intact forests (Morimoto et al. 2010) and reduce the likelihood of black locust germinating outside the footprint of already disturbed sites after treatment. Removing these trees or stands will reduce propagule pressure into surrounding native forests. New black locust invasions often occurred in the understories of mature native deciduous trees and alongside native deciduous shrub species, especially on warm and moist sites. Recruit and shrub height black locust individuals in the understories of native forests should be selectively removed with methods that minimize soil disturbances and avoid creating early seral conditions and loose soils that benefit black locust recruitment. Where black locust invasions appear to be benefiting from understory light availability due to senescing native tree canopy cover or bare soil due to low understory vegetation cover, native tree and shrub species should be planted to outcompete black locust recruitment. Dense plantings of native conifers and thicket-forming deciduous tree and shrub species may be able to outcompete black locust root suckers and seedlings. The best locations for dense vegetation plantings to outcompete black locust are at the outer edges of invasions and around mature black locust trees exerting propagule pressure into surrounding native forests. Established black locust stands in the study area showed evidence of native deciduous species (including trembling aspen and black cottonwood) and coniferous species (including western white pine and Douglas-fir) beginning to establish in their understories. If protected from further disturbances these native tree species should continue maturing as black locust stands increase in height and die and understory light availability increases. Succession from mature black locust stands to native forests can be supported by planting native mid- and later-seral tree and shrub species in the understories of black locust stands and protecting these stands from disturbances that would re-create early seral conditions favoured by black locust. By removing black locust and remediating disturbances on legacy anthropogenic invasion vectors, planting native species on natural invasion vectors, selectively removing new recruit and shrub invasions into native forests and slowing invasion speed with native plantings, planting native tree and shrub species in the understories of maturing stands, and protecting sites from further disturbances, black locust invasions can be successfully contained and remediated in the LCV.

Suggestions for future research related to black locust establishment and containment in the LCV are presented. There is a need for future research (1) identifying abiotic factors that support the establishment and maturation of black locust, (2) assessing the impacts of black locust invasions on different abiotic site types and native vegetation species communities (3) testing methods of containing and restoring black locust invasions on disturbed sites and natural areas by modifying site conditions and planting native species to stabilize sites and inhibit colonization, and (4) monitoring native species replacement under black locust stands on disturbed and undisturbed conditions and testing methods of replacing black locust stands with native species by manual removal, site modifications, and native species planting.



1. Introduction

Invasive species pose a global threat to biodiversity through their ability to out-compete native species and modify ecosystem trajectories towards alternate and degraded stable ecosystem states (Ghazoul et al. 2015). While many invasive shrub, herb, and grass species are common in BC, there are few invasive tree species in BC (British Columbia Ministry of Forests 2023). Studying invasive tree species' invasion and effects on ecosystems takes a longer time to complete than studying invasive shrub and herb species. I studied black locust (*Robinia pseudoacacia* L.), an invasive tree species in BC (British Columbia Ministry of Forests 2023; CKISS 2023) in the Lower Columba Valley. Black locust was introduced to assist site revegetation in the 1940s (Hodson 1971) and has become invasive in forests and open lands in the Lower Columbia Valley and the surrounding Central Kootenay region (Wikeem 2007). In the Central Kootenays, black locust has been recorded between 2013 and 2022 in or near Kaslo, Nakusp, the Slocan Valley, Nelson, Trail, and Creston (Figure 1.1). Insufficient information has been available on black locust in the Lower Columbia Valley to adequately assess its invasion risks and impacts, but its increase in abundance had become a concern for land managers by the mid 2000's (Wikeem 2007). Teck Metals Ltd. Trail Operations (Teck) is currently developing a program to restore historically impacted vegetation communities in the Lower Columbia Valley. The current distribution and risk for further dispersal and establishment of black locust must be understood to inform the restoration program. In this study I (1) assess the ability of aerial imagery to help visually identify black locust invasions and offer recommendations for improving the detection of new black locust invasions, (2) characterize black locust's associations with abiotic conditions and native tree and shrub species to identify areas with high and low invasion risks in the Lower Columbia Valley, and (3) suggest strategies for treating and containing new black locust invasions and restoring established black locust stands.

1.1. Ecosystems and Invasion

Exotic and invasive species are species originating outside locations where they are observed occurring and reproducing (Grace College 2021). Exotic species, also called introduced or non-native species, may be recently introduced and not well established in their new locations, or they may be well established in new locations and not observed impacting abiotic conditions, plant or animal communities, or human health. Invasive species are non-native species that have established and begun reproducing in new areas, and have been observed damaging their new ecosystems, human health, and the ability to use or interact with local places and resources (Grace College 2021). Invasive species can out-compete native species and change community composition on sites. In doing so they can modify ecosystem trajectories towards permanently disturbed early or mid seral species assemblages or lead to the formation of stable later-seral species assemblages that may not resemble native species communities (Ghazoul et al. 2015).

Species have different impacts in different areas they are introduced: a species may be native in certain locations, non-native with minimal impacts on local ecosystems in some locations, and non-native and invasive in other locations (Sitzia 2014; Deneau 2013; Theoharides & Dukes 2007). Factors affecting invasive species impacts can include the time an invasive species has been present on a landscape (Motta et al. 2009), interactions (including competition, predation or parasitism, and facilitation) between invasive and native species or between multiple invasive species, and abiotic conditions including light availability and temperature, moisture, nutrient, and disturbance regimes (Hofle et al. 2014; Holzmueller & Jose 2009; Theoharides & Dukes 2007). Many invasive species are also associated with anthropogenic disturbances (Vitková et al. 2015; Kercher & Zedler 2004). The differing invasiveness of non-native species across landscapes (depending on local biogeoclimatic and anthropogenic contexts) challenges land managers to assess exotic species' risks to ecosystem structure, composition, and function, and to identify their involvement in successional trajectories towards or away from native species communities (Lazzaro et al. 2018; Vitková et al. 2017; Motta et al. 2009).

Non-native and introduced invasive species contribute to global biodiversity homogenization and the loss of local specialist species in favour of global generalist species alongside human disturbance and natural landscape changes (Finderup Nielsen et al. 2019; Vellend et al. 2013). Many invasive species have the greatest impacts on native communities in disturbed areas where native species' health is already lessened due to acute and chronic stresses (Kercher & Zedler 2004). They may outcompete other early-seral or disturbance-tolerant native species and alter successional pathways recovering from disturbance, leading to novel mid and later-seral community composition (Pyšek et al. 2020;

Bellard et al. 2016). For example, both native and exotic tree species exposed to harsh conditions on disturbed sites can grow and persist in stunted shrub and tree forms capable of arresting native tree species establishment at early and mid-successional stages. These altered tree forms can encourage herb and grass species cover capable of outcompeting tree seedlings, and these altered early-successional stages prevent the regrowth of disturbed sites to later-successional native forests (Groninger et al. 2007).

Many plant species that are currently invasive have escaped into native habitats from agricultural and forestry systems (Palit & DeKeyser 2022). These invasive plant species have been bred from native populations over generations and have no identical native species they can be compared with to understand their environmental tolerances or ecological roles within ecosystems (Palit and DeKeyser 2022, Pysek et al. 2020). Specific cultivars of agronomic invasive plant species are often selected when breeding and planting for the environmental conditions of the sites where they are out-planted (Williams et al. 2016; Colautti & Lau 2015; Stockwell et al. 2003). This leads to large genetic variation in traits between sub-populations in different locations: for instance, drought-tolerant cultivars of a plant species may be selected and planted in dry areas, and particularly cold-tolerant cultivars of the same species may be selected and planted at the northern end of a range (Williams et al. 2016; Colautti & Lau 2015; Stockwell et al. 2003). Once a sub-population has established and begun dispersing across a new landscape, exposure to abiotic, biotic, and anthropogenic stresses can produce contemporary evolution, differentiating the exotic species from its source population (Szűcs et al. 2017; Williams et al. 2016; Colautti & Lau 2015; Stockwell et al. 2003). Black locust in the Lower Columbia Valley is an exotic deciduous tree species native to Southeastern North America bred for forestry across North America and Europe (Kellezi & Kortoci 2022; Nicolescu et al. 2020). Black locust was introduced to revegetate disturbed sites in the 1940s (Archibold 1978; Hodson 1971). Since its introduction it has begun colonizing and maturing on both disturbed and natural sites outside its introduction sites in the Lower Columbia Valley and is now classified as an invasive species in BC (British Columbia Ministry of Forests 2023; CKISS 2023).

1.2. Black Locust Information

Black locust (*Robinia pseudoacacia* L.) is a pioneer early-successional deciduous tree species native to deciduous woodland forests (Stone 2009) in the Appalachian mountain ranges of southeastern North America (Bouteiller et al. 2019; Huntley 1990). Black locust is useful for agricultural windbreaks and rural hedgerows, fuel, and building materials due to its dense wood, rapid growth, tolerance to a wide range of natural and anthropogenic disturbances, and its aesthetic beauty during flowering season (Commonwealth Agricultural Bureau International (CABI) 2019; Gabriel 2018). Its usefulness and beauty in forestry, agricultural, rural, urban, and industrially modified settings encouraged black locust to be planted across North America in the 1800's and 1900's. (Commonwealth Agricultural Bureau International (CABI) 2019). Black locust has now naturalized across all lower 48 American states and personal observations on iNaturalist.org show it is found across Canada in BC, Ontario, Quebec, and the Maritime provinces. Black locust has been observed in the Kootenays from the United States border to Kaslo, BC (Figure 1.1) (CKISS 2023).

Black locust is listed as an invasive species in British Columbia (British Columbia Ministry of Forests 2023; BC Inter-Ministry Invasive Species Working Group 2023). Black locust is listed in the "Management" priority category, the lowest level assigned to invasive species. This category is assigned to invasive species that are widespread but may be of concern in specific high value sites including conservation lands. The management objective for these species is to reduce impacts locally or regionally where resources are available (BC Inter-Ministry Invasive Species Working Group 2023). BC has not released any management regulations or policy for controlling black locust: no regulations limit sales or planting of black locust, and landowners are not responsible for controlling plants on their properties (BC Nature 2022). As of 2022, black locust is on CKISS' priority list for treatment, but insufficient information exists to determine its management priority relative to other invasive vegetation species (CKISS n.d). Black locust is not listed as a pest registered in Canada (Warn 2016). Black locust is listed as an invasive alien plant species of primary concern to pink milkwort (*Polygala incarnata*), a species designated nationally at risk known only in Canada in Ontario (COSEWIC 2009). Ecosystems most threatened by black locust in Ontario are similar to those invaded by black locust in BC and the Central Kootenays, including dry and sand prairies, savannahs, and upland forest edges (Canadian Food Inspection Agency 2008). Black locust is not listed in the Canadian Food Inspection Agency's

Weed Seeds Order, an order made under the *Seeds Act* restricting the presence of weed species in commercially sold seeds to prevent the introduction and spread of new weeds (Warne 2016). In summary, while black locust is known to invade disturbed sites and is treated as a species of management concern in ecosystem types common in the Central Kootenays, no legal or regulatory requirements exist limiting its sales and planting or requiring its control on invaded sites within BC.

In its native range, black locust is primarily an early-successional tree species that thrives in nutrient-poor, sandy soils in sites with high sun exposure and moderate moisture (Stone 2009). It cannot tolerate full shade and is not found in closed-canopy forests (Stone 2009). As an early-successional tree species, black locust rapidly colonizes disturbed sites with a clonal suckering root system, stabilizing disturbed soils and establishing canopy cover that shelters open sites and allows other species to grow (Commonwealth Agricultural Bureau International (CABI) 2019; Motta et al. 2009; Stone 2009). As a species in the legume family, black locust fixes atmospheric nitrogen in soils with symbiotic bacteria on its root nodules and increases soil nitrogen and soil acidity from leaf litter deposition (Poblador et al. 2019; Lazzaro et al. 2018). In its native range black locust stabilizes disturbed sites with shallow, aggressive rhizomatous root growth and builds and enriches soils with leaf litter and nitrogen from nitrogen-fixing bacteria in its roots. This facilitates native later-seral tree and shrub species colonizing black locust's understory (Commonwealth Agricultural Bureau International (CABI) 2019; Motta et al. 2009; Stone 2009). Black locust is a short-lived tree with an average lifespan of 80 to 90 years (Warne 2016). Within its native range, clonal stands of black locust begin declining in growth rate 20 to 30 years after establishment. This allows codominant tree species that recruited alongside black locust and shade-tolerant native tree and shrub species that established in its understory to mature and outcompete black locust as stands age (Boring and Swank 1984). Maturation and succession can be delayed temporarily or for decades if sites are severely disturbed and revert to early seral conditions that allow black locust to regenerate and exclude co-occurring species (Commonwealth Agricultural Bureau International (CABI) 2019; Benesperi et al. 2012; Stone 2009; Huntley 1990) Black locust's rapid colonization of disturbed sites, above and below-ground soil stabilization and soil building properties through leaf litter deposition and nitrogen fixation, and short lifespan allow it to colonize, stabilize, and remediate disturbed sites. Within black locust's native range, these properties allow black locust to facilitate the succession of later-seral native shrub and tree species that help return disturbed sites to native mid and later-seral forests (Commonwealth Agricultural Bureau International (CABI) 2019; Benesperi et al. 2012; Stone 2009; Huntley 1990).

Black locust can tolerate diverse soil acidity, moisture, and parent-material conditions (Vitková et al. 2015). Outside its native range it can be a major colonizer of openings in coniferous and deciduous forests, intact prairies, pine barrens, and savannah habitats (Sadlo et al. 2017; Stone 2009), and high-moisture sites including floodplains and riparian forests (Poblador et al. 2019; Medina-Villar et al. 2015; Staska et al. 2014). Black locust's root system is typically shallow and wide-spreading, but colonies can develop deep vertical roots to access deep water-tables and expand into dry landscapes (Warne 2016). Black locust is tolerant of a range of environmental disturbances including drought, fire, soil disturbance, and soil and air pollutants (Commonwealth Agricultural Bureau International (CABI) 2019; Vitková et al. 2017).

Black locust is a clonal species, sprouting vigorously from underground root systems and above-ground stumps in disturbed areas with high resource availability (Commonwealth Agricultural Bureau International (CABI) 2019; Warne 2016; Stone 2009). Physical disturbances to roots and stems from fire and mechanical disturbance stimulate vigorous resprouting while scarification of seeds from disturbances stimulates germination (Bouteiller et al. 2021). Disturbance to surrounding vegetation provides light required for seeds and shoots to germinate and establish (Stone 2009). Black locust seeds are large, heavy, and gravity dispersed, and can disperse up to 100 m from mature trees (Warne 2016; Stone 2009; Morimoto et al. 2010). Black locust produces seeds from approximately 6 to 60 years age, with the greatest productivity from 15 to 40 years age. Mature trees deposit large volumes of seed. Seeds have a highly impermeable seed coat and can remain viable in the soil for decades until stimulated by light and soil disturbances including fire and physical scarification (Warne 2016; Stone 2009). Vegetative regeneration (suckering from roots) is more important for reproduction and colonization of new habitats than seed production (Warne, 2016; Vitková et al. 2015; Cierjacks et al. 2013; Stone 2009). Black locust reproduces vigorously in disturbed areas including old pastures and fields, forest edges, second-growth forests, floodplains, and transport and utility rights-of-way (Stone 2009; Huntley 1990), and it appears to have an exclusionary rather than facilitative role in novel areas compared to its native range (Nicolescu et al. 2020; Commonwealth Agricultural Bureau International (CABI) 2019; Stone 2009).

Black locust does not occupy the same successional role in its introduced range as it does in its native range (Deneau 2013; Benesperi et al. 2012). Instead of facilitating later-seral native tree species growth in its understory as it ages and decays, it appears to establish dominance and exclude other vegetation species, halting or changing natural succession towards later-seral native vegetation communities (Deneau 2013). Black locust invasion can homogenize species composition by eliminating spatial heterogeneity in soil nitrogen, light, and microclimate conditions (Sadlo et al. 2017; Sitzia et al. 2016; Vitková et al. 2015; Cierjacks et al. 2013; Von Holle et al. 2006). Some authors have found native plant diversity in black locust stands is reduced compared to forests of similar successional stage (Benesperi et al. 2012; Von Holle et al. 2006). Black locust leaf litter contains allelopathic compounds which may inhibit weeds and crop species (Nasir et al. 2005). Because its allelopathic effect has not been demonstrated under natural conditions, it is more likely vegetation change in black locust stands is caused by changes in soil nutrient availability and the physical effects of leaf-litter mulching and shading from tree canopies than it is from allelopathic influences (Nicolescu et al. 2020; Vitková et al. 2017). Nitrogen fixation by black locust may hinder native vegetation species establishment and maturation in ecosystems not adapted to high nitrogen levels (Nicolescu et al. 2020). Exotic plant species that benefit from high nitrogen concentrations can overwhelm native species, leading to alternative species assemblages and successional trajectories (Vitková et al. 2015; Cierjacks et al. 2013; Michigan Department of Natural Resources 2012). The combined effect of soil shading and nutrient inputs from roots and leaf litter can supress native vegetation species and facilitate exotic species, especially in naturally low-nutrient open vegetation communities including sandy areas (Deneau 2013), savannahs, and pine-oak forests (Cierjacks et al. 2013; Rice et al. 2004). Direct human impacts, changing abiotic drivers and disturbance cycles, and the impacts of additional plant and animal invasive species may slow or alter the dispersal, recruitment, and growth of native vegetation occurring alongside black locust stands (Fei et al. 2008). This can allow the tree species to behave invasively in areas it would otherwise avoid or occur in but not dominate (Sadlo et al. 2017; Ghazoul et al. 2015; Groninger et al. 2007).

Black locust has weedy-species characteristics that make it difficult to remove and control (Commonwealth Agricultural Bureau International (CABI) 2019; Michigan Department of Natural Resources 2012; Stone 2009; Huntley 1990). Disturbance stimulates black locust growth and can revert maturing and thinning black locust stands to earlier-successional stages with dense root and seed sprouts (Commonwealth Agricultural Bureau International (CABI) 2019; Sadlo et al. 2017; Motta et al. 2009). Cutting, girdling, grazing, root digging, windthrow, disease, fire, and even moderate herbicide application all stimulate the production of new stems from any remaining stems and roots of the tree (Commonwealth Agricultural Bureau International (CABI) 2019; Michigan Department of Natural Resources 2012). This resprouting ability means control and restoration efforts can make treated black locust stands more vigorously productive than untreated stands if control actions do not persist until all of the stems and roots are removed (Warne 2016; Skowronek et al. 2014; Stone 2009). Lateral root growth and sprouting from runners allows black locust to quickly spread across both disturbed and intact vegetation communities (Stone 2009; Huntley 1990). Sprouting begins after plants are 4 to 5 years old and is highest in full sun and sandy soils (Stone 2009; Huntley 1990). Sprouts need significant sun to survive (Stone 2009), so natural or artificial heavy shade at the boundaries of black locust stands is a prospective approach to species containment. Once established, black locust stems live fewer than 100 years and growth rates begin to decrease after 20-30 years for colonies belonging to its native range. However, it is unclear how long clonal stands from the same root-mass persist outside of their native range (Stone 2009).

Black locust in the Lower Columbia Valley is an exotic species selectively bred for forestry traits in North America, Europe, and Asia (Bouteiller et al. 2021; Nicolescu et al. 2020; Bouteiller et al. 2019), with sub-populations differentiated based on both their current geographic locations and the locations from which their source material originated (Yaegashi et al. 2020; Guo et al. 2018). Black locust was introduced to the Lower Columbia Valley to revegetate disturbed and eroded slopes in the 1940s (Hodson 1971): in the course of being planted in BC, specific stock would have been selected from source populations. Black locust stock may have been intentionally selected for the hot and dry growing conditions in the Valley or it may have been randomly selected based on availability.

The selection of certain black locust plant stock represents a population founder event, where a small sample of a populations' genetic variability from sources of unknown genetic provenance is the source for the entire genetic variability of a new sub-population (Berkley Evolution 2021). The founding of a new black locust sub-population from one or many unknown propagule sources indicates the Lower Columbia Valley black locust sub-population may have distinct traits from other sub-populations in North America based on the observation of distinct traits in other black locust sub-populations in its introduced range (Bouteiller et al. 2021). These traits may impact black locust's invasiveness in the Lower Columbia Valley including its selection of abiotic habitat conditions and its interactions with native species (Bouteiller et al. 2021; Granata et al. 2020; Dreiss & Volin 2013). The Lower Columbia Valley is hotter and drier than climatic conditions in the Southeastern United States where black locust is native (Bouteiller et al. 2019; Szűcs et al. 2017). After its founding, sub-population of black locust in the Lower Columbia Valley will have been exposed to selective pressure to adapt to its new growing conditions as it dispersed across the landscape (Szűcs et al. 2017; Williams et al. 2016).

Genetic and trait variation is observed between natural black locust sub-populations and nursery cultivated stock (Abri et al. 2022). Black locust has been bred for high photosynthetic assimilation and water-use efficiency for forestry in Europe (Abri et al. 2022). In natural areas, black locust has been found to have a high phenotypic plasticity index at the leaf level, allowing it to maximize light harvesting and grow in closed-canopy forest understories (Granata et al. 2020). Phenotypic variation amongst life-history traits has been observed between black locust sub-populations in their introduced European ranges and their native ranges in North America. Introduced black locust has a higher germination rate in its invasive European range than in its native range (Bouteiller et al. 2021). This differentiation has a genetic basis, which was theorized to have been caused by a combination of human selection and propagation of nursery stock with a high germination rate and by natural selection and phenotypic plasticity in response to environmental conditions (Bouteiller et al. 2021). Eighty years after black locust was planted in the Lower Columbia Valley, assessing the abiotic conditions and native vegetation species communities associated with this sub-population of black locust will help determine if it is invading similar sites and having similar impacts as invasive sub-populations in other regions. This will help determine if management conclusions drawn in other regions will be useful for managing black locust in the Lower Columbia Valley and will help target restoration treatments in the area.

1.3. Study Region

I studied black locust in the Lower Columbia Valley, within the Kootenay Boundary region of British Columbia. The Lower Columbia Valley is oriented north-south along the Lower Columbia River, from Castlegar in the north to the United States border in the south. The City of Trail is located along this corridor, approximately 25 km south of Castlegar and 10 km north of the US border. The Teck Trail Operations smelter is located at the north end of the City of Trail. The valley corridor around Trail is developed with urban, industrial, and utilities features, and some agriculture to the south and east. The sides of the Lower Columbia Valley remain comparatively undeveloped due to their steep slopes and unstable substrates (Teck Metals 2011).

The slopes of the Lower Columbia Valley at Trail consist of a series of narrow fluvial and glacio-fluvial terraces with coarse to sandy well-drained soils with low organic matter content (Jungen 1980). Terraces and plateaus of different heights are bordered by short, steep slopes bisected by valleys and creeks running into the Columbia River. Mass-wasting slope-failures and channels are common between terraces of different heights and along the steep edges of creeks and rivers. Soils on the valley terraces are Orthic Brunisols comprised of fluvial and glaciofluvial deposits (Jungen 1980). The terrace escarpment slopes are steep and gravelly, with finer material accumulating on plateau tops and valley bottoms. They are loose, well-sorted, moderately coarse to sandy at the surface, and rapidly to excessively well drained (Jungen 1980). Organic content is low, and the soils have been eroded since settlement and development in the area began in the late 1800's (Hodson 1971). Logging since the late 1800's and large stand-replacing fires in the early 1900's cleared much of the Valley's original vegetation cover. Erosion of soil organic matter and mineral soils followed the loss of vegetation cover, making natural and assisted vegetation regeneration more difficult. Frequent summer drought, lack of water retention and high and low temperature extremes on bare soil, and sulphur dioxide and heavy metal smelter emissions reduced native species' revegetation success and maintained open conditions throughout the 1900's (Hodson 1971).

The climate in the Lower Columbia Valley at Trail is continental. Winters are cold, and summers are warm, with occasional cool periods. Precipitation is low. Winter precipitation is from snow, and summer rainfall can be heavy but sporadic due to thunderstorms (Hodson 1971). The complex topography of valley slopes and terraces means local factors including aspect and surrounding topographic features are important in determining heat and frost exposure intensity and duration. Because of local variation in temperature and moisture, different vegetation communities are observed on spatially close slopes with different aspects (Hodson 1971). Plateaus and valley bottoms generally have consistent vegetation communities due to uniform micro-climate conditions.

The Lower Columbia Valley is within the Interior Cedar Hemlock (ICH) Biogeoclimatic (BEC) zone (Banner & Ehman 2016; Meidinger & Pojar 1991). The ICH BEC zone is characterized by western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) forests receiving rainfall from orographic lift on the steep mountain ranges east of the Lower Columbia Valley (Banner & Ehman 2016; Meidinger & Pojar 1991). The study region around Trail BC is in the driest subzone of the ICH – the Very Dry Warm zone (ICHxw) – the subzone is so dry it was earlier classified as the Ponderosa Pine (PP) BEC zone (Hodson 1971). In the Very Dry Warm subzone, cedar and hemlock are limited to warm (cedar) and cool (hemlock) moist sites on cool aspects, moisture-receiving mid-slopes, and valley bottoms. Dominant deciduous trees in the ICH xw sub-zone are black cottonwood (*Populus trichocarpa*), paper birch (*Betula papyrifera*), and on the study region, trembling aspen (*Populus tremuloides*) (Banner & Ehman 2016). Trembling aspen is not listed as a dominant species in this area, but in the study area I observed mature trembling aspen stands on both warm and cool slopes and on upland plateaus (Fuller 2022, Field Data). Along with western redcedar and western hemlock, dominant conifer species are western white pine (Pinus monticola), Douglas-fir (*Pseudotsuga menziesii*), and ponderosa pine (*Pinus ponderosa*), with spruce (*Picea* spp.) and true fir (*Abies* spp.) species interspersed throughout mixedwood and coniferous stands, and western larch (*Larix* spp.) forming small stands on cool microsites (Banner & Ehman 2016; Meidinger & Pojar 1991).

The Lower Columbia Valley was impacted by historical sulphur dioxide (SO_2) and metal emissions from the Teck smelter (Teck Metals 2011), as well as other industrial, urban and rural disturbances. The smelter was established in 1896 at its present location in north Trail (Hodson 1971). The Lower Columbia Valley north and south of Trail was heavily logged beginning in the late 1800's for lumber to build Trail and the smelter and fuel for the community, smelter open roasting pans, railway, and river steamships (Hodson 1971). Following logging, natural forest regeneration success was slow and partial, leading to persistent open vegetation conditions and soil erosion in the Valley. The area was repeatedly burned over with natural and anthropogenic fires from the late 1800's to the mid 1900's (Hodson 1971). Multiple stand-replacing fires killed adult trees, reduced or eliminated soil seedbanks, and reduced or eliminated the soil organics (hummus) layer. Soil organic matter reduces evaporation from soils and retains moisture, allowing tree seedlings to germinate and survive in open conditions. Natural vegetation regeneration was further reduced by low tree survival due to exposure on open sites during the hot dry summers and cold winters in the region; subsequent soil erosion from rainfall reducing available nutrients, moisture, and substrate for tree establishment; and smelter emissions including sulphur dioxide and heavy metals (Hodson 1971). Emissions control management began in the 1930s when the Teck smelter began recovering sulphur emissions from the concentrate roasting process (Queneau 2010). Further significant emissions reductions were realized following the switch to KIVCET smelting technology (an acronym for "flash-cyclone-oxygen-electric smelting") (Goodwin & Ponikvar) in 1997 (Queneau 2010). There is evidence that elevated metal levels in soils and previous air pollution injury continued to influence plant communities in the Valley into the late 2000's (Teck Metals 2011). Wildfires, logging, mining, linear developments (including roads, power and gas line right of ways) and rural homestead development along with the over hundred year long history of smelter disturbance (Teck Metals 2011; Hodson 1971) impacted vegetation communities and lead to the re-planting of vegetation to restore the Valley in the mid 1900's.

Tree planting was conducted in the 1940's with two non-native deciduous tree species – black locust and silver maple (*Acer saccharinum*) – and in the 1960s with native conifer species to restore vegetation communities in the Lower Columbia Valley (Archibold 1978; Hodson 1971). Black locust, a native North American tree species outside its native range in BC, was deemed suitable for plantings in the 1940s due to its high disturbance tolerance and rapid establishment on degraded lands with acidic soils (Stone 2009). Revegetation with black locust succeeded in establishing closed-canopy stands 10-15 metres high by the 1960's. Black locust spreads quickly on degraded sites and now appears to be limiting the establishment of native vegetation species and changing natural succession trajectories, challenging further restoration and conservation objectives in the Valley (personal communication with Marlene Machmer, 2022). Teck is investigating black locust spread, competitiveness, and invasion risk in natural areas to guide containment and restoration of lands impacted by smelter emissions and containing black locust stands in the Valley.

Black locust stands planted in the 1940's on sites with histories of anthropogenic disturbances (Archibold 1978; Hodson 1971) have expanded to occupy adjacent lowland and occasional upland sites (on Teck, public and other private lands) in the Lower Columbia Valley. These locust-dominated sites are typically characterized by relatively open sandy slopes and benches, and many are alongside roads, powerlines and other linear corridors which have been subject to ongoing anthropogenic disturbance (e.g., mechanical cutting, pruning, brushing, piling, etc.) which tends to exacerbate tree resprouting, seeding, rhizomatous growth and overall spread of this invasive tree (Marlene Machmer, personal communication). Black locust's colonization from human disturbance footprints into native forests is affected by abiotic conditions including slope- and aspect-derived light and temperature availability, soil moisture, soil nutrients, natural soil disturbances, and natural disturbances including fire history (Stone 2009; Huntley 1990). Colonization into native forests is also affected by temperature, light, moisture, and nutrient-availability conditions caused by the structure and species composition of vegetation communities (Stone 2009; Huntley 1990). Black locust colonizes early seral shrublands, early seral deciduous forests, mid seral mixedwood forests, and early or late seral coniferous forests with different densities and invasion impacts (Stone 2009; Huntley 1990). With the assistance of Teck, I set up a research project to assess the distribution of black locust trees in a study area within the Lower Columbia Valley, and to assess abiotic and biotic conditions contributing to their invasion of native forests.

1.4. Research Goals and Objectives

Goal 1. Assess the effectiveness of aerial imagery as a tool for visually identifying mature black locust stands and new black locust invasions.

Objective 1.1. Compare the presence of black locust identified on aerial imagery to the true presence and absence of black locust in ground plots to assess the success rate of visually identifying black locust using aerial imagery.

Objective 1.2. Identify strategies to improve collection of aerial imagery to better identify black locust.

Objective 1.3. Identify black locust structural stages not visible on aerial imagery and suggest strategies for identifying areas at high and low risk of new invasions using aerial imagery, GIS data and field data.

Goal 2. Characterize the abiotic conditions and native tree and shrub species associated with black locust invasions in the study area using ground sampling plots, field observations, ecological modelling, and literature review.

Objective 2.1. Map black locust cover within the study area using ground sampling plots.

Objective 2.2. Characterize abiotic conditions associated with black locust tree, shrub, and recruit cover within the study area.

Objective 2.3. Characterize native tree and shrub species associated with black locust tree, shrub, and recruit cover within the study area.

Goal 3. Based on black locust tree, shrub, and recruit associations with abiotic conditions and native tree and shrub species, provide recommendations for containing black locust invasions and restoring established black locust stands in the study area and the Lower Columbia Valley.

Objective 3.1. Identify combinations of abiotic conditions, landscape features, and native vegetation species associated with high and low risks of black locust invasions.

Objective 3.2. Suggest strategies for containing and restoring black locust recruit and shrub invasions on both disturbed sites and natural areas.

Objective 3.3. Suggest strategies for restoring established black locust stands on both disturbed sites and natural areas.

1.5. Introduction – Figures

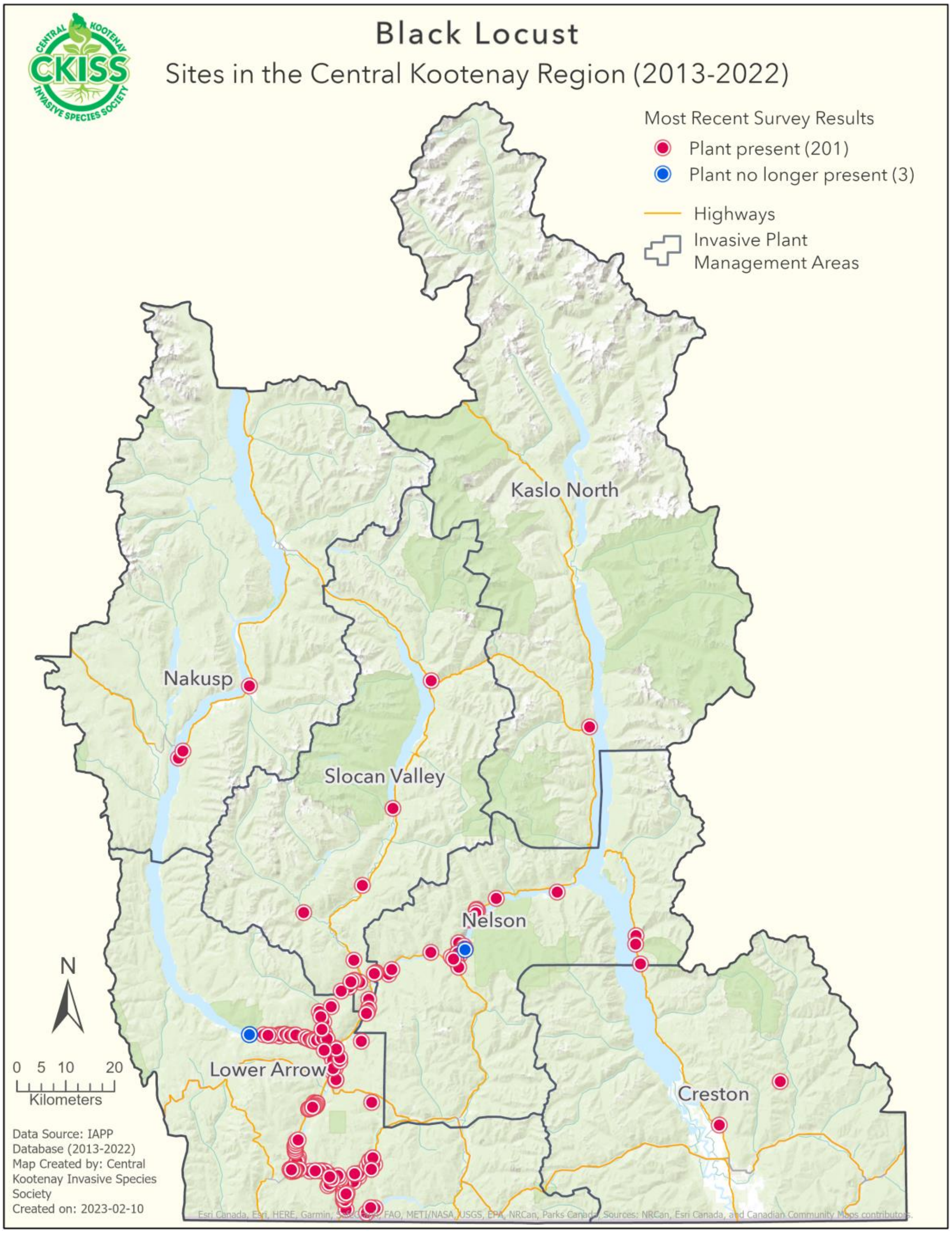


Figure 1.1: Black locust road survey observations in the Central Kootenay region between 2013 and 2022 by the Central Kootenay Invasive Species Society (CKISS 2023).

2. Methods

2.1. Study Area and Plot Layout Objectives

Study Area Preparation

Teck Metals identified a 600-ha study area within the Lower Columbia Valley as their focus area for this project (Figure 2.1). Teck used maps, former surveys, and professional judgment to choose the area. The area was selected to include a range of black locust densities including contiguous black locust stands, discontinuous patches, small clumps, single trees, and areas where black locust is absent. Criteria for selection of the study area also included accessibility (near the highway and access roads), an adequate proportion of lands owned by Teck to allow for site access, and for the study area to include a range of anthropogenic disturbance regimes, including roadsides and utility right of ways, rural land use areas, and intact natural areas set away from ongoing disturbances.

Teck classified the Lower Columbia Valley area into biophysical habitat unit polygons based on soil, terrain, and vegetation characteristics (Enns & Enns 2007). Enns and Enns (2007) created the polygons using terrain ecosystem mapping (TEM) based on visual classification of aerial imagery and digital elevation models with some ground-truthing, and Ehman and Machmer (2014) updated the polygons with new mapping and classification methods. The 600-ha black locust study area fully or partially included 43 unique ecosystem monitoring polygons (Figure 2.1). I used the TEM polygons as the base for vegetation plot stratification across the study area.

Plot Layout Objectives

To achieve Goal 1 and Goal 2 I used a study design combining visual identification of black locust on aerial imagery with data on abiotic site conditions, black locust cover, and native tree and shrub species cover collected on ground vegetation plots. I used high resolution UAV imagery taken of the 600-ha study area to identify possible locations of flowering black locust trees as starting regions to lay out ground sampling plots in black locust stands. I deployed one hundred and fifty-one (151) 400 m^2 (11.28 m radius) circular plots using the TEM polygons provided by Teck as initial strata to distribute plots across my study area. I used site series visually identified during ground sampling as internal boundaries within TEM polygons to stratify the locations of multi-plot arrays. These arrays sampled similar underlying abiotic conditions including elevation, slope, and aspect. Arrays contained plots where black locust was present and plots where black locust was absent. On ground vegetation plots I visually estimated black locust, native-tree species, and native shrub-species cover at different height-classes (structural-stages) following methods in (British Columbia Ministry of Forests and Range & British Columbia Ministry of Environment 2010) and derived abiotic conditions from desktop GIS analysis. I used the same plots and plot data to assess black locust identification success on aerial imagery for Goal 1 and to assess black locust's associations with abiotic conditions and vegetation species for Goal 2.

2.2. Aerial Imagery Validation

To achieve Goal 1, aerial imagery was collected by Harrier Aerial Surveys (Harrier Aerial Surveys 2023) from drone flights over the 600-ha study area between June 15 and June 25. Imagery was 2-dimensional 6 cm^2 resolution single-band colour imagery and was collected by flying over each portion of the site once in east-west oriented transects. Imagery was pre-processed by Harrier Aerial Surveys and sent for use in this study. The survey was chosen during the peak of black locust's flowering season to maximize visibility of its white flowers. Because of the cold and wet spring across BC in 2022, black locust flowered two to three weeks later than expected (Marlene Machmer, personal communication).

On the georeferenced aerial imagery, I attempted to visually detect black locust presence or absence in a 11.28 m radius (equal to the radius of my ground-vegetation plots) around the GPS center of each vegetation plot (Figure 2.2). To minimize observer bias based on recognizing plot names and recalling true black locust presence or absence on plots, I identified black locust on imagery plots in a random plot order and recorded image validation scores using the random numbers instead of plot names. I transitioned between plots automatically to avoid recognizing landscape contexts and I zoomed in to fill my computer screen fully with plot boundaries to avoid observing surrounding terrain that would allow me to recall plot names and locations.

I assessed the ability of aerial imagery to assist visual identification of black locust by comparing the presence of black locust identified on aerial imagery to true presence and absence of black locust in ground-vegetation plots (Goal 1, Objective 1.1). I summarized black locust identification success on aerial imagery using a confusion matrix (Objective 1.1) (Gustafsen 2022). The confusion matrix compares true positive detections and true negative detections in the imagery against false negative and false positive detections: this determines success at identifying black locust presence in the imagery where it is present on the ground and success at identifying black locust absence in the imagery where it is absent on the ground. True positives are where black locust is present on plots and is identified in the aerial imagery, and true negatives are where black locust is absent on plots and identified as absent in the aerial imagery. False positives are where black locust is absent on plots and is misidentified as being present on plots in the aerial imagery, and false negatives are where black locust is present on plots and is misidentified as absent in the aerial imagery. I used interpretation results to inform suggestions for using drone imagery to sample larger areas in the Lower Columbia Valley.

2.3. Abiotic Conditions and Vegetation Species Associations

Field Plot Study Design

I conducted all fieldwork between July 8 2022 and September 8 2022. To achieve all goals, I deployed circular monitoring plots of 400 m^2 area (11.28 m radius) and sampled abiotic conditions using GIS, black locust and native tree-species tree, shrub, and recruit stage cover, and native shrub-species cover in the study area. The methods are adapted from BC Terrestrial Ecosystem Monitoring Protocol (British Columbia Ministry of Forests and Range & British Columbia Ministry of Environment 2010), which Teck's existing ecosystem monitoring protocol also follows (Machmer et al. 2018). This consistency allows compatibility of these data with Teck's ecosystem monitoring program and will provide an opportunity for Teck to continue studying black locust using this study's data.

I targeted TEM polygons for plot sampling by identifying possible black locust stands in the aerial imagery. I visually identified black locust on aerial imagery using its white flowers to distinguish it from surrounding tree species. I marked individual trees and outlined polygons around possible black locust stands. I used TEM polygons identified by

Teck as my initial stratification guide to group and disperse ground-vegetation plots across the study area. I accessed every TEM polygon with possible black locust identified on aerial imagery to confirm black locust presence in the locations I had identified and to search for black locust stands I had not been able to identify. After confirming true black locust presence or absence in a polygon on foot sampling, I deployed at least one plot occupied by black locust and one plot unoccupied by black locust in every TEM polygon with black locust present. To provide plots with known true absences of black locust in imagery validation and to sample vegetation conditions in unoccupied plots I deployed plots in 9 polygons with no indication of black locust presence on the aerial imagery. Of the 43 TEM polygons fully or partially included in the 600-ha black locust study area (Figure 2.3) I deployed ground vegetation plots in 29 TEM polygons: 20 TEM polygons had black locust present and 9 polygons had no black locust present.

Following the plot layout methods above, I located at least one plot occupied by black locust and one plot unoccupied by black locust within every TEM polygon with possible black locust in the study area. To sample spatial variation across occupied and unoccupied sites within the boundaries of TEM polygon strata, I deployed arrays of two or more plots with centers separated by at least 45 metres (one full plot diameter, 22.6 m) between the edges of any two adjacent plots. To make sure all plots within an array were in similar conditions I used TEM polygon boundaries as the main boundaries for setting boundaries for prospective arrays. Habitat conditions within TEM polygons are not homogeneous: TEM polygon boundaries can include up to three ecosystem site series within their boundaries, representing mosaics of riparian, mid-slope, and plateau habitats with differences in light, temperature, moisture, substrate, and soil nutrient conditions creating differences in vegetation communities within polygons boundaries. Because of the presence of multiple unmarked site series within TEM polygons, I identified boundaries for arrays by visually assessing regions of similar abiotic and biotic site characteristics. These site characteristics included slope, aspect, surface moisture, and surface substrate characteristics, and dominant vegetation structure (e.g., herb, shrub, or tree covered) and species composition (e.g., native coniferous, native deciduous, or black locust dominant). I used TEM polygons for my initial array deployment strata, searched for black locust I had identified on aerial imagery for my starting regions for arrays, and identified similar habitat conditions around black locust for my plot array boundaries within TEM polygon boundaries.

Once I determined array boundaries, I determined the locations of occupied plots and unoccupied plots using a used/unused or presence/absence framework following resource and habitat selection studies (Boyce 2006; Boyce et al. 2002). I located occupied/presence plots randomly within mature black locust stands identified on the aerial imagery and in field visits, according to methods below. To sample unoccupied/absent sites where black locust was truly absent ("true species absences") – rather than unoccupied sites possibly suitable for invasion but outside the dispersal distance of existing black locust trees ("unoccupied but unavailable" sites) – I located most of my unoccupied plots within the approximately 100 m seed and root dispersal distance (Pyšek et al. 2020; Bellard et al. 2016; Morimoto et al. 2010) of stands of mature black locust trees. Sampling unoccupied plots near enough mature trees to be invaded but with the absence of mature trees on them allowed me to assume unoccupied plots represented areas of true species absences. These are locations where black locust had the opportunity to be observed after dispersing into an area over time from nearby propagule sources but was not observed in my study, indicating it had the opportunity to be truly present on a site and instead was truly absent (Boyce et al. 2002). Had I sampled unoccupied plots within any distance of mature black locust stands I would not have been able to assume true species absences on plots. Black locust absences would have been due to the absence of nearby propagule sources: unoccupied plots could have represented suitable habitat conditions but remained uninvaded due to time requirements for dispersal and colonization from mature stands. By locating unoccupied plots near enough to mature black locust stands representing areas of propagule pressure into surrounding habitats, I was able to assume true species absences on plots and infer conditions on unoccupied plots represented conditions of lower suitability for black locust than conditions on plots where they were established.

I accessed plot sites on foot. To maximize detection of black locust, I followed black locust invasion vectors – including roads and trails, slope edges, riparian edges, and gullies (Stone 2009; Huntley 1990) – towards marked possible black locust stands. To reduce sampling bias, I searched for black locust (1) outside the edges of invasion vectors (e.g., away from roads, gullies, and waterways), and (2) outside the areas I had marked on the imagery while walking into possible invasion sites. I recorded all locations of black locust tree, shrub, and recruit groups I found while accessing sites, and searched for their nearest possible source populations and invasion vectors. – either on-site plantings or dispersal along natural or anthropogenic habitat features.

After arriving at possible invasion sites identified on the aerial imagery, I recorded whether black locust was present or absent. When black locust was absent, I recorded the feature I had mis-identified as black locust. When black locust was present, I defined boundaries for my sampling array based on TEM polygon boundaries and similar habitat strata described above, and I generated a random location for the location of my first plot within the array. On narrow linear sampling regions (approximately less than three plot diameters wide) including riparian edges bounded by banks and water and road or trail edges, I sampled plots in the middle of these regions' widths and generated one random number, representing the distance in metres from the regions' edge (for example, along the creek edge) I travelled before laying out the first plot center. On wider polygonal sampling regions – including large slope edges or irregularly shaped black locust stands on plateaus – I generated two random numbers to locate my first plot center. The first number gave travel distance into the sampling region: for example, distance travelled into a forest stand. The second number gave travel direction (positive or negative number) and distance across the region perpendicular to the first direction I travelled: for example, leftward or rightward across the stand after walking a random distance into it based on my first number. I measured all travel distances into and across sampling regions using GPS. After sampling the first plot, I continued the array for at least one additional plot, 45 metres from the first, if black locust was still present. I stopped my survey of a site and moved to a new location when I encountered more than one unoccupied plot on an array. Once an array of 2 or more plots was complete in a TEM polygon, I moved on to a different region, gradually infilling the study array while sampling different underlying habitat types and forest stands.

I prioritized sampling occupied stands due to time constraints. I sampled 151 ground vegetation plots (Figure 2.3). Of these plots 102 were occupied by black locust and 49 were unoccupied. Unoccupied plots were used for two purposes in my analysis. First, unoccupied plots anywhere on the landscape were used to validate the ability of aerial imagery to identify plots containing no black locust. Second, unoccupied plots within the 100 m dispersal distance of mature black locust trees were used to evaluate habitat conditions adjacent to occupied black locust stands that have remained unoccupied in spite of propagule pressure from nearby mature trees, following the true presence/ true absence or occupied/unoccupied study design discussed earlier (Boyce 2006; Boyce et al. 2002). To validate aerial imagery, I used all 49 unoccupied plots. To evaluate habitat selection by black locust, I filtered my plots to include only unoccupied plots within dispersal distance (100 m) of black locust trees.

After filtering plots based on dispersal distance, I had 137 plots available for abiotic and vegetation community analysis (Figure 2.4), 35 of which were unoccupied by black locust. Other plots had low densities of black locust. By removing unoccupied plots outside of the 100 m dispersal distance of black locust I removed habitat conditions from my analysis that may have been suitable for black locust but remained uninvaded only due to absence of propagule pressure. This reduces the risk of associating certain conditions with low black locust cover when in the study area they are associated with areas black locust has not yet had time to invade along existing dispersal vectors since it has been introduced. The 35 unoccupied plots in the habitat selection analysis are within dispersal distance of mature black locust in the study area. As these plots have had time and propagule pressure to become invaded, they can be considered sites where nearby black locust has not yet been able to colonize. Conditions on these plots may indicate habitat conditions associated with resistance to black locust stands. I investigated these conditions to achieve Goal 3 and to suggest strategies for containing new black locust invasions and restoring established black locust stands for Teck Metals and other land stewards in the Lower Columbia Valley.

Data Collection

Abiotic Data

I used a 1 m^2 resolution digital elevation model (DEM) with a 1 m vertical resolution downloaded from the BC Data Catalogue (Government of British Columbia - GeoBC Branch 2014) and Sentinel-2 satellite imagery (European Space Agency 2023) to derive abiotic variables for my analysis (Table 2.1). I ran all abiotic data preparation in ArcMap 10.8 and R (R Core Team 2021). I calculated slope and aspect on the 1 m^2 DEM and ran 5.6 metre radius (half of my plot radius) focal statistics with a circular window on the slope and aspect DEMs to calculate the mean slope and aspect around every map pixel. Focal statistics on DEM pixels smoothed out metre-scale slope and aspect variations at half the radius of my plot radiuses, minimizing the impact of small elevation differences on the overall slope and aspect values given to my plots. I used the raw 1 m^2 DEM to calculate total incoming summer and winter solar radiation on plots using the Points Solar Radiation tool in ArcMap (ESRI 2022). Summer insolation was from May 1st to September 1st 2022, and winter insolation was from November 1st to March 1st. I calculated one insolation value per hour per day at plot centers and summed these values as total watt-hours per metre square for each plot center over each of the two seasons. Insolation is determined by slope angle, slope position, and aspect. I used insolation as an indicator of site light availability, temperature, and exposure in my analysis. High summer and winter insolation values indicate high amounts of solar radiation received by plots due to exposed positions and warm (south and west facing) aspects and low insolation values indicate low amounts of solar radiation received by plots due to enclosed or cool (north and east facing) aspects.

I used 20m Sentinel-2 imagery downloaded from the Copernicus Open Access Hub (European Space Agency 2023) to calculate Normalized Difference in Moisture Index (NDMI) at plot centers. NDMI is a soil and vegetation moisture index calculated by comparing using the near-infrared (NIR) and the short-wave infrared (SWIR) reflectance (EOS Data Analytics 2022; USGS n.d.). I used NDMI to represent site moisture in my analysis because it is a reliable indicator for moisture stress in vegetation (EOS Data Analytics 2022). High NDMI values indicate high moisture in vegetation and soils and low NDMI values indicate low moisture in vegetation and soils.

To calculate NDMI for my sites, I downloaded eight multi-band Sentinel-2 images with no cloud cover over the study area: one from July 2021 and seven from July 23 to September 26 2022. Because of the wet growing season in 2022, I had no entirely cloud-free Sentinel-2 images of the study area from May or June. I calculated NDMI for each of the eight Sentinel-2 images using standard methods described by the USGS (USGS n.d.) and averaged NDMI across each of the eight images to create one composite NDMI image representing average summer-season NDMI values for the study area. I extracted these values to plot centers.

Vegetation Data

<u>Overview</u>

I followed the BC Terrestrial Ecosystem Monitoring Protocol (British Columbia Ministry of Forests and Range & British Columbia Ministry of Environment 2010) and Teck's existing ecosystem monitoring protocol (Machmer et al. 2018) and deployed circular monitoring plots of 11.28 m radius (400 m^2 area) to characterize vegetation community structure and composition, including black locust invasions, in the study area. This consistency will help these data be compatible with Teck's existing ecosystem monitoring program and will provide an opportunity for Teck and other land managers to continue studying black locust in the future using this study's data. I recorded all tree species and visually estimated the percent cover for each species in each of three height class structural stages: tree (> 10 m), shrub (2 – 10 m), and recruit (< 2 m) (Table 2.2). I recorded all shrub species on plots and visually estimated total shrub species cover and percent cover by species using a modified Braun-Blanquet cover class system in the sense of Wikum & Shanholtzer (1978). I recorded total grass cover, total herbaceous layer cover, all herb species visible on plots, and all herb layer shrubs identified in the BC Terrestrial Ecosystem Monitoring Protocol (British Columbia Ministry of Forests and Range & British Columbia Ministry of Environment 2010) and visually estimated their percent cover using the same modified Braun-Blanquet cover class system (Table 2.2). These data form the key species diversity, composition, and structure component of the habitat suitability analysis.

Tree Species Cover

I followed the BC Terrestrial Ecosystem Monitoring Protocol to classify tree species and structural height-classes in the study area (British Columbia Ministry of Forests and Range & British Columbia Ministry of Environment 2010). I classified tree species into three structural stage height-classes: "Tree" (height > 10 m), "Shrub" (height 2-10 m) and "Recruit" (height <2 m). I used a digital rangefinder to classify tree species' heights as either in the shrub structural stage or the tree structural stage. I visually estimated tree cover for each species in each structural stages using the percent cover circles in BC Terrestrial Ecosystem Monitoring Protocol (British Columbia Ministry of Forests and Range & British Columbia Ministry of Environment 2010) (Figure 2.5) and the suggestions for estimating cover provided in the document. I completed the first round of canopy cover measurements with Marlene Machmer of Pandion Ecological Consulting to develop my sampling methods.

I classified the cover of trees into tree or shrub height classes based on stem height and stem attachment location. I classified all stems coming from the same tree root-crown as belonging to the height layer (structural stage) they terminated in – either greater than 10 m or 2 to 10 m. Conifers tend to have one stem or clusters of stems of similar height, so each conifer individual fell into the same height class. In contrast, some deciduous trees such as paper birch and black locust can coppice at their bases and have multiple stems of many heights coming off the same root-crown. Some individual trees were therefore represented in my cover measurements by both tree cover for their tallest stems and by shrub cover for lower stems originating from the root crown. I only classified tree individuals as "recruits" when they were separate individuals growing at least 0.5 metres way from the root crown of a shrub or a tree, and less than 2 m tall. I followed the same structure and cover estimations for both native tree species and black locust. I also collected three cumulative tree cover estimates: (1) the total non-overlapping canopy cover of all native and exotic trees greater than 10 m tall, (2) the total non-overlapping canopy cover of just native trees, excluding black locust, and (3) the total non-overlapping cover of all tree and shrub species in the shrub (2-10 m) vegetation layer. After recording tree cover data in the field, I generated composite vegetation-structure variables by adding together different vegetation structural stages (

Table 2.3). Tree species codes, common names, and scientific names are provided in (Table 2.4)

Shrub and Herb Cover

I recorded shrub and herb species and percent cover using a modified Braun-Blanquet cover-class system in the sense of Wikum & Shanholtzer (1978) (Table 2.5): I added an extra cover class of 6-10 percent to provide finer resolution in classifying vegetation cover than the standard cover classes of 0 to 5 percent and 15 to 25 percent. I visually estimated the total (cumulative) non-overlapping cover of all shrub species in the 2-10 m height class, and the total non-overlapping cover of all tree and shrub species in the 2-10 m height class. To use cover classes in correlation analysis and GLMMS I followed (McNellie et al. 2019) and converted each class to percent cover scores. McNellie et al. (2019) compared visual estimates of tree-, shrub-, and herb-species cover and cover classes and found mid-points for percent cover in cover classes were poorly suited to real cover distributions because true vegetation cover was often left-skewed within cover classes. This indicates percent-cover values assigned to cover classes should be slightly left of the median class value (McNellie et al. 2019). Given the extra cover class I added to the standard Braun-Blanquet system to increase data resolution at low percent-cover values, I used the midpoints provided by McNellie et al. (2019) as a starting point and modified the percent cover assigned based on my observations of species abundances during field sampling (Table 2.5).

Data Investigation and Statistical Analysis

Data Investigation and Statistical Modelling Framework

I investigated response variables (black locust cover and count) and predictor variables (abiotic and biotic plot data) according to the data investigation protocols and recommendations in Zuur et al. (2010). I ran correlation analysis and variance inflation factors (VIF) to look for co-linear (dependent) predictor variables with abiotic, vegetation-structure, tree-species, or shrub-species variables before including them in multi-variable models. Following Zuur et al (2010), when correlation coefficients were greater than 0.35 and VIF were greater than 3 I did not include predictor variables together in multi-variable models; instead, I modelled them separately as single variable models. I evaluated relationships between black locust cover across structural stages, abiotic variables, and vegetation species by running non parametric multi-dimensional scaling (NDMS), correlation analysis, single-variable models, and multi-variable models. I ran NMDS in R using the package vegan (Oksanen et al. 2020), I ran correlation analysis in R using spearman correlation coefficients and plotted relationships using the package ggcorplot (Alboukadel Kassambara 2022), and I ran single and multi-variable models using the package glmmTMB in R (Anders Nielsen et al. 2017).

Abiotic Predictors:

I investigated abiotic landscape predictors expected to drive vegetation community composition on plots. I built and ranked single variable models of black locust responses to abiotic predictor variables. I then ran NMDS on all tree-species cover, including black locust, across all structural stages to illustrate tree species' associations with the same abiotic variables.

Biotic Predictors:

I investigated the association of black locust with vegetation-structure variables and native tree and shrub species by testing correlation coefficients and by building single and multi-variable models associating black locust cover at all structural stages with native tree-species cover at all structural stages. Correlation coefficients describe the relationship between two covariates without modelling one as a predictor for the other. Single variable and multi-variable models require specifying a predictor and a response variable in model equations. I modeled black locust cover across structural stages as a response to native vegetation species' cover across structural stages. I also modeled native vegetation species' cover across structural stages as a response to black locust cover across structural stages.

I tested correlations and single and multi-variable models for the same structural stages (comparing black locust tree cover to other species tree cover, and black locust recruit cover to other species recruit cover) and between different structural stages. I modelled black locust shrub and recruit cover as a response native tree cover to determine tree species black locust was colonizing underneath. I also modelled native recruit and shrub cover with black tree cover to determine tree species colonizing underneath established black locust stands. I modelled relationships between different structural stages to help understand tree species black locust is replacing on the landscape, and tree species colonizing under black locust stands. These species may form the next forest stages as black locust stands mature and die back.

Use of Abiotic Conditions, Vegetation Structure, and Vegetation Species Associations in Management Recommendations

While achieving Goal 1, initial inspection of aerial imagery showed flowering black locust trees were able to be identified, but shrubs and recruits in open areas and under forest canopies were not able to be identified. Understanding black locust shrubs' and recruits' association with abiotic and vegetation species communities can help indicate areas at risk of having high undetected invasions. Following Objective 1.3, areas with suitable abiotic conditions and vegetation species communities for black locust recruit and shrub invasions can be identified using desktop aerial imagery, GIS data, and other field data. Results from this study can be combined with desktop and field data to indicate – on aerial imagery used to identify black locust – where visible black locust stands may be associated with higher or lower invisible invasions of shrubs and recruits into surrounding natural areas.

To achieve Goal 3 and provide recommendations containing black locust invasions and restoring established black locust stands I used abiotic, vegetation-structure, and vegetation-species modelling results from Goal 2 in combination with field observations and information from literature reviews to identify light, temperature, moisture, disturbance, and vegetation species associations with black locust tree, shrub, and recruit stage cover in the study area. Conditions associated with high amounts of colonization can be treated more thoroughly or avoided being created: for example, canopy gaps can be filled, and disturbances that create canopy gaps can be avoided. Conditions associated with low amounts of colonization can be applied across other sites and maintained where they are present: for example, coniferous tree cover can be planted to fill abandoned trail invasion vectors and maintained at the edges of black locust stands.

Statistical Analysis and Modelling:

I ran NMDS on abiotic variables representing abiotic conditions assessed in GIS (Table 2.1), black locust cover across structural stages, and native tree-species cover across structural stages. NMDS is a form of unconstrained non-parametric ordination suitable for indicating how response variables are grouped together and along a range of gradients in other variables. NMDS is not a statistical test – it is a graphing exercise suitable showing tree species' cover-values' associations with each-other and underlying abiotic gradients (insolation and NDMI) in my study area (Oksanen 2015). I ran NMDS in R using the package vegan (Oksanen 2015). I ran NMDS in 3 dimensions based on minimizing residual error in a stressplot and I used the Bray-Curtis dissimilarity measure to on species' cover values calculate the input distance matrix. Species with highly correlated cover-values have smaller distance-matrix values and are plotted close together on the NMDS graph, and species with less correlated cover-values have larger distance-matrix values and are plotted farther away on the NMDS graph. NMDS automatically plots the two dimensions representing the most variation on the graph when it is run in three or more dimensions (Oksanen 2015). I graphed tree-species total cover, and cover at the tree and recruit structural stages. I added contours representing variation in NDMI and insolation on the same graphing space as my species distance points. I visually compared black locust and native species positions relative to each-other and NMDI and insolation contours to evaluate the light, temperature, and moisture conditions black locust was associated with in my study area.

I compared black locust cover across structural stages with abiotic, vegetation-structure, and species-cover variables using Spearman correlation coefficients and Generalized Linear Mixed Effects Models (GLMMS). I ran Spearman correlation coefficients in base R and graphed them using the package ggcorrplot (Alboukadel Kassambara 2022). I found many outlying values in the distribution of species cover across plots and used Spearman correlation coefficients instead of Pearson correlation coefficients because Spearman correlation coefficients are more resilient to outliers (McDonald 2015). Correlation coefficients show the strength, direction, and statistical significance of the relationship between two covariates and do not make a distinction between predictor (independent) or response (dependent) variables the way linear modelling does (McDonald 2015).

To assess the relationship between specific abiotic, tree-species, and shrub-species cover variables as predictor variables and as response variables I ran single and multi-variable models using a generalized linear mixed effects modelling framework in the package glmmTMB (Bolker 2022). All species cover data is in percent cover form and follows a beta distribution. These data have true zeros where no black locust or other vegetation species were observed on plots. Beta distributions cannot model true zeros (Blasco-Moreno et al. 2019; Damgaard & Irvine 2019); because of this, I modeled all tree variables with a mixed-effects component added to beta distributions to account for true zeros in species cover on plots. I used a beta-binomial family with a logit link and added a single zero inflation parameter applying to all observations (Bolker 2022; Brooks et al. 2017). I checked this model performance against generalized additive models (GAMs) built in the package gamlss (Rigby et al. 2017) with a multi-part method of specifying zeros. Both model frameworks produced similar coefficients and AIC scores to 2 to 3 decimal places for most models. I used generalized linear mixed effects models (GLMM) instead of generalized additive models (GAM) because they make fewer assumptions about the causes of zero's and because they work within a familiar GLM modelling framework allowing interface with other packages I used to plot model outputs (Zuur et al. 2009; Bolker 2008).

To determine the predictor variables (abiotic, vegetation-structure, and vegetation species-cover) that best predicted a given response variable (black locust cover or other species cover), I built single variable GLMMS representing the relationship of predictor and response variables ranked their performance against each-other by comparing models' Akaike's Information Criterion (AIC) scores and Likelihood Ratio Tests (LRT) values (Shoemaker 2021). AIC scores assess the predictive capacity of models using two components: (1) a negative log-likelihood component representing the relationship between predictor and response variables, and (2) a penalty term for adding extra predictors variables in models to reduce the effect of biasing larger models over smaller more parsimonious models (Shoemaker 2021). Lower AIC scores represent the best supported models in a set of candidate models in terms of the fit of the predictor variable and response variable distributions and in terms of maximum parsimony, with the benefit in explanatory power of adding extra variables being balanced by the penalty of adding extra variables (Shoemaker 2021; Burnham et al. 2011; Burnham & Anderson 2002). AIC scores absolute value is not meaningful – model fit is assessed using the difference in AIC scores between models (Shoemaker 2021; Burnham et al. 2011; Burnham & Anderson 2002). Models with a difference in AIC scores (ΔAIC) of less than 2 have equivalent explanatory power and are equally well supported predictors (Burnham et al. 2011). Models with a difference in AIC scores of greater than 2 have different explanatory power: the greater the ΔAIC is between given models, the more the model with the lower ΔAIC is supported as best explaining the distribution of the response variable (Burnham et al. 2011).

Likelihood ratio Tests (LRT) are a statistical frequentist test comparing the goodness of fit of a null model of just the response variable distribution against the goodness of fit of a more complex model built with the response variable and at least one predictor variable (Shoemaker 2021). Models must be nested to be input into LRT (the smaller null model being a subset of the larger model), so I always compared null models (the smallest possible models) against models with one addition predictor variable – for example, comparing the null model for black locust tree cover with no predictor variables against the model for black locust trees as a response to NDMI. LRT provides p-values indicating if adding additional variables statistically significantly improves the goodness of fit of the alternate model over the null model (Shoemaker 2021). I used $p < 0.5$ as the critical value indicating statistical significance for LRT model comparisons.

Using AIC scores and LRT values as test criteria, I built single-variable GLMMs and determined which predictors in a set of models best explained the distribution of a response variable (AIC scores) or best contributed to the goodness of fit of modelled response variable and a predictor variable against a null model with just the response variable (LRT). To indicate the explanatory power of all variables in a set of predictors and to indicate whether certain single-variable models performed better than more complex models after AIC score penalization from adding extra variables, I built and ranked a "global" multi-variable model containing black locust cover modelled against all predictors in a set of single variable models – for example, a global model containing all tree species' cover compared against single variable models of specific tree species' cover and black locust cover. After building and ranking overall predictor variable importance using single-variable GLMMs, I built multi-variable GLMM's assessing the direction, strength, and significance of predictor variable coefficients when other predictor variables from the same set of variables were included alongside each-other. By including multiple predictor variables in a model for a given response variable, multi-variable models more closely represent the influence of predictor variables on the response variable by allowing variance in the response variable residuals not captured by a single predictor variable to be assigned to other predictor variables, rather than residual error as it would be in a single variable model (James and McCulloch 1990).

2.4. Methods – Tables and Figures

Tables

Table 2.1: Abiotic variables derived from GIS data used in analysis of black locust's (*Robinia pseudoacacia* L.) associations with abiotic site conditions. All variables represent values at the centers of 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. Slope and aspect represent consistent values across seasons. Summer and winter insolation were collected from May 1 to September 1 and November 1 to March 1 respectively.

Variable	Description	Input dataset	Operation	Data Source
Slope	Slope, derived from slope calculation on a 1 m^2 DEM raster, followed by focal statistics calculating the mean slope value in a 5.6 m radius window around every pixel	1 m^2 DEM	1. Slope on 1 m^2 DEM. 2. Focal statistics on 1 m^2 slope layer, with a 5.6 m circular window, calculating the mean slope value in the 5.6m radius window around every pixel	(British Columbia Ministry of Forests and Range & British Columbia Ministry of Environment 2010)
Aspect	Aspect, derived from aspect calculation on a 1 m^2 DEM raster, followed by focal statistics calculating the mean aspect value in a 5.6 m radius window around every pixel	1 m^2 DEM	1. Aspect on 1 m^2 DEM. 2. Focal statistics on 1 m^2 aspect layer, with a 5.6 m circular window, calculating the mean aspect value in the 5.6m radius window around every pixel	(British Columbia Ministry of Forests and Range & British Columbia Ministry of Environment 2010)
Summer Insolation	Total incoming solar radiation from May 1 to September 1 2022 on plots, in Watt Hours per meter square	1 m^2 DEM	2 Points Insolation One insolation value calculated per hour per day for the time period, summed for total summer insolation at plot centers	(British Columbia Ministry of Forests and Range & British Columbia Ministry of Environment 2010)
Winter Insolation	Total incoming solar radiation from November 1 2021 to March 1 2022 on plots, in Watt Hours per meter square	1 m^2 DEM	1. Points Insolation. One insolation value calculated per hour per day for the time period, summed for total winter insolation at plot centers	(British Columbia Ministry of Forests and Range & British Columbia Ministry of Environment 2010)
Mean NDMI	Normalized Difference Moisture Index	July 2021 & July-Sept 2022 Sentinel 2 multi-band images	1. NDMI calculation on each of eight multi-band Sentinel-2 images 2. Mean of pixel values across eight NDMI images	(European Space Agency 2023)
NDMI Difference	NDMI Difference	July 2021 & July-Sept 2022 Sentinel 2 multi-band images	Difference between highest recorded NDMI value and lowest recorded NDMI value for every pixel, calculated between the 8 Sentinel-2 images	(European Space Agency 2023)

Table 2.2: Vegetation plot data fields and descriptions. All variables represent cover values visually estimated across 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. Reference for all data fields is British Columbia Ministry of Forests and Range and British Columbia Ministry of Environment (2010).

Variable	Description	Unit, Scale
Tree species total cover	Summed tree, shrub, and recruit cover visual estimations across whole plot	Percent 0-100
Tree species tree-stage cover by species	Tree species tree height-class cover, visually estimated according to methods in Section 2.3	Percent 0-100
Tree species shrub-stage cover by species	Tree species shrub height-class cover, visually estimated according to methods in Section 2.3	Percent 0-100
Tree species recruit-stage cover by species	Tree species recruit height-class cover, visually estimated according to methods in Section 2.3	Percent 0-100
Total canopy cover	Visual estimate of total tree-species canopy cover across whole plot, including black locust (*Robinia pseudoacacia* L.)	Percent 0-100
Native canopy cover	Visual estimate of total tree-species canopy cover across whole plot, not including black locust	Percent 0-100
Total shrub species cover	Percent cover-class visual estimation of shrub species cover across the whole plot.	Cover class 0-7
Total shrub layer cover	Percent cover-class visual estimation of all shrub height-class cover (2 to 10m high) on plot including shrub species and tree species in the shrub structural stage	Cover class 0-7
Shrub species cover by species	Shrub species cover, visually estimated according to methods in Section 2.3	Cover class 0-7
Total herb species cover	Total percent cover-class visual estimation of herb species cover across the whole plot.	Cover class 0-7
Total grass cover	Total percent cover-class visual estimation of all grass cover across the whole plot.	Cover class 0-7

Table 2.3: Vegetation-structure variables derived by adding visually-estimated tree-species cover at specified structural stages observed on ground plots. All variables are in percent units from 0-100. All input tree species' cover values were visually estimated across 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. Species codes are given in (Table 2.4)

Variable Name in Modelling	Full Variable Name	Input visually-estimated tree-species cover values from vegetation plots
Tree Layer Cover	Total Tree-Stage Cover	ACT.Tr + AT.Tr + EP.Tr + MS.Tr + CW.Tr + FD.Tr + FG.Tr + FS.Tr + FB.Tr + HW.Tr + LT.Tr + Picea.Tr + PL.Tr + PW.Tr + PP.Tr + YP.Tr
Decid Total Cover	Deciduous Tree Species Total Cover	ACT.Tr + AT.Tr + EP.Tr + MS.Tr + ACT.Sh + AT.Sh + EP.Sh + MS.Sh + ACT.Rc + AT.Rc + EP.Rc + MS.Rc
Decid Tree Cover	Deciduous Tree Tree-Stage Cover	ACT.Tr + AT.Tr + EP.Tr + MS.Tr
Decid Shrub Cover	Deciduous Tree Shrub-Stage Cover	ACT.Sh + AT.Sh + EP.Sh + MS.Sh
Decid Recruit Cover	Deciduous Tree Recruit-Stage Cover	ACT.Rc + AT.Rc + EP.Rc + MS.Rc
Conif Total Cover	Coniferous Tree Total Cover	CW.Tr + FD.Tr + FG.Tr + FS.Tr + FB.Tr + HW.Tr + LT.Tr + Picea.Tr + PL.Tr + PW.Tr + PP.Tr + YP.Tr + CW.Sh + FD.Sh + FG.Sh + FS.Sh + FB.Sh + HW.Sh + LT.Sh + Picea.Sh + PL.Sh + PW.Sh + PP.Sh + YP.Sh + CW.Rc + FD.Rc + FG.Rc + FS.Rc + FB.Rc + HW.Rc + LT.Rc + Picea.Rc + PL.Rc + PW.Rc + PP.Rc + YP.Rc
Conif Tree Cover	Coniferous Tree Tree-Stage Cover	CW.Tr + FD.Tr + FG.Tr + FS.Tr + FB.Tr + HW.Tr + LT.Tr + Picea.Tr + PL.Tr + PW.Tr + PP.Tr + YP.Tr
Conif Shrub Cover	Coniferous Tree Shrub-Stage Cover	CW.Sh + FD.Sh + FG.Sh + FS.Sh + FB.Sh + HW.Sh + LT.Sh + Picea.Sh + PL.Sh + PW.Sh + PP.Sh + YP.Sh
Conif Recruit Cover	Coniferous Tree Recruit-Stage Cover	CW.Rc + FD.Rc + FG.Rc + FS.Rc + FB.Rc + HW.Rc + LT.Rc + Picea.Rc + PL.Rc + PW.Rc + PP.Rc + YP.Rc
Tree Recruit Cover	Tree Recruit Total Cover	ACT.Rc + AT.Rc + EP.Rc + MS.Rc + CW.Rc + FD.Rc + FG.Rc + FS.Rc + FB.Rc + HW.Rc + LT.Rc + Picea.Rc + PL.Rc + PW.Rc + PP.Rc + YP.Rc

Table 2.4: Tree species abbreviation codes, common names, and scientific names for tree species identified in 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022.

Species Code	Common Name	Scientific Name
BL	Black locust	Robinia pseudoacacia
AT	Trembling aspen	Populus tremuloides
ACT	Black cottonwood	Populus trichocarpa
CW	Western redcedar	Thuja plicata
EP	Paper birch	Betula papyrifera
FD	Interior Douglas fir	Pseudotsuga menziesii
FG	Grand fir	Abies grandis
FS	Subalpine fir	Abies lasiocarpa
FB	Balsam fir	Abies balsamea
HW	Western hemlock	Tsuga heterophylla
LT	Larch spp.	Larix spp.
MS	Silver maple	Acer saccharinum
Picea	Spruce spp.	Picea spp.
PL	Lodgepole pine	Pinus contorta
PW	Western white pine	Pinus monticola
PP	Ponderosa pine	Pinus ponderosa
YP	Pacific yew	Taxus brevifolia

Table 2.5: Cover classes and percent cover scores used for shrub cover data collection and analysis. Shrub species cover classes were visually estimated across 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022.

Modified Braun-Blanquet Cover Class	Percent Cover and Description	Percent Cover Assigned During Modelling
0	0% cover, no individuals	0
1	< 2 % cover, few individuals	1 %
2	2 – 5 % cover, many individuals	3 %
3	6 – 10 % cover	7 %
4	11 – 25 % cover	15 %
5	26-50 % cover	41 %
6	51 – 75 % cover	62 %
7	75 – 100 % cover	82 %

Figures

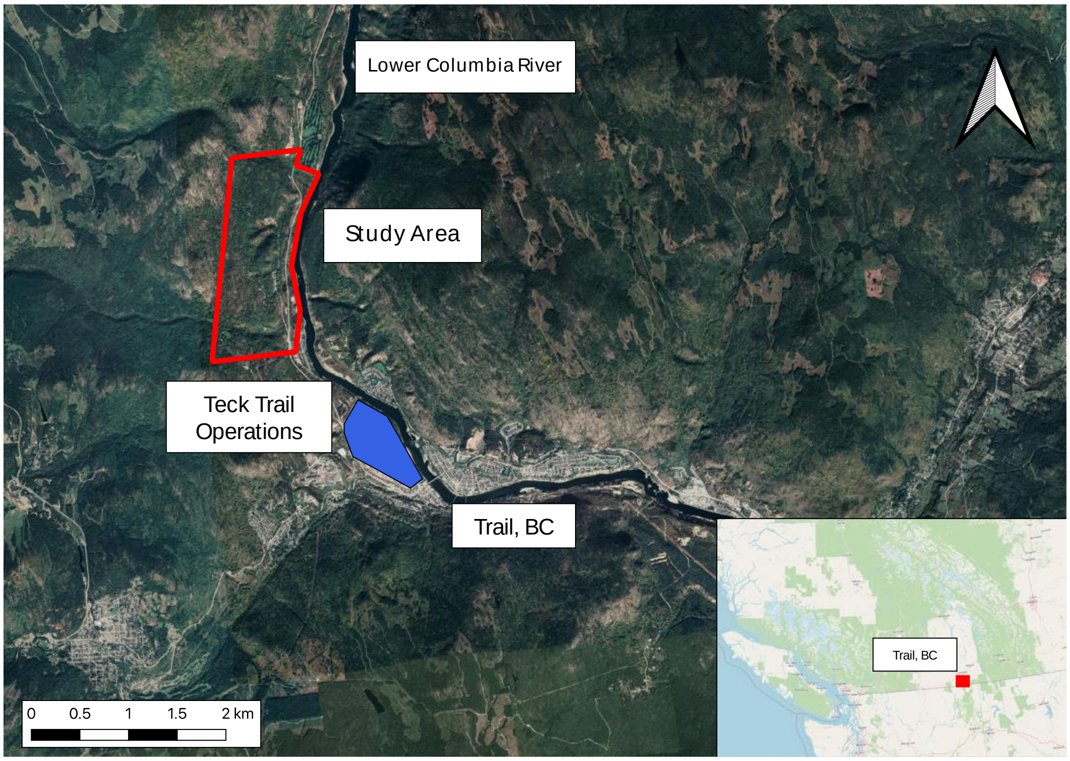


Figure 2.1: Study Region Map showing the Lower Columbia Valley, Trail BC, and Teck Trail Operations. The 600-ha study area for aerial imagery and vegetation plots surveyed from July to September 2022 is indicated by the red polygon north of Teck Trail Operations.

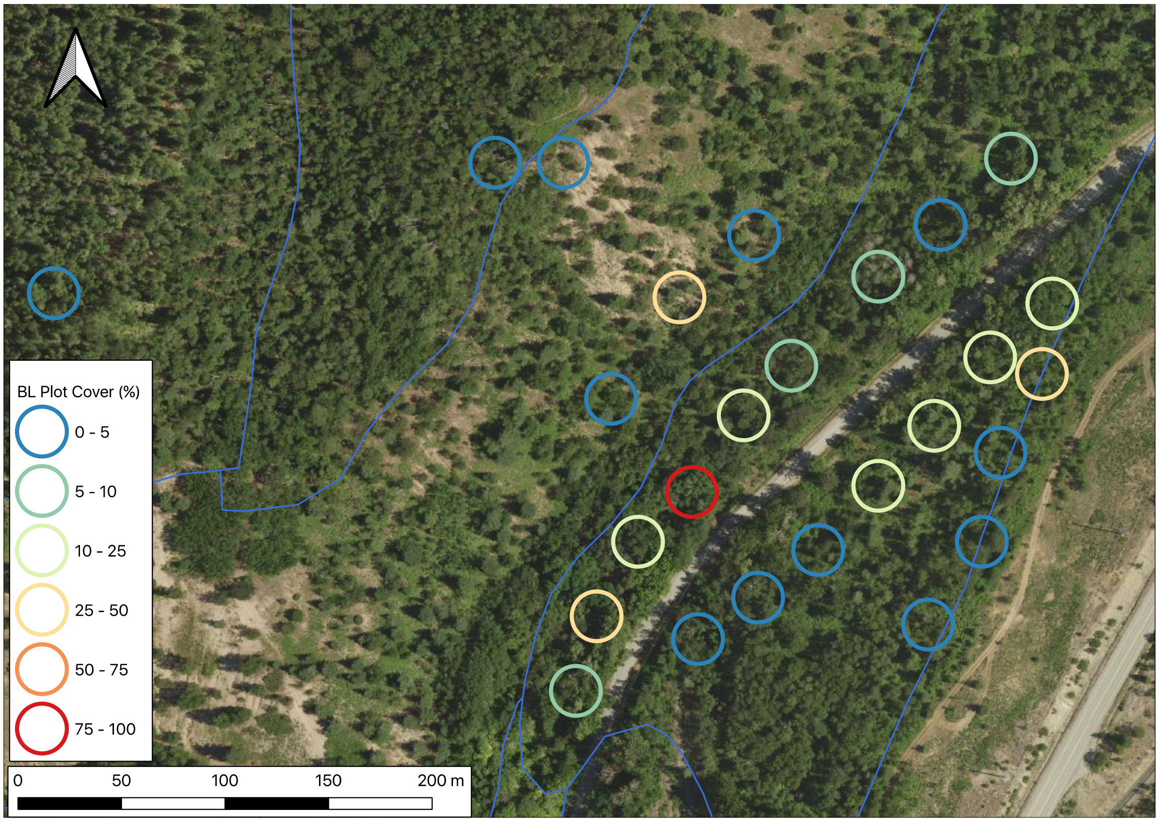


Figure 2.2: Image validation sample plots showing 11.28 m radius circles around plot centers representing plot boundary locations in the aerial imagery, coloured to represent the actual percent cover of black locust (*Robinia pseudoacacia* L.) identified during ground sampling within the plots. Black locust presence and absence was visually identified within the 11.28 m radius circles around plot centers and compared to actual values across corresponding plots to determine image validation success. All plots were deployed in a 600 ha study area north of Trail BC from July to September 2022.

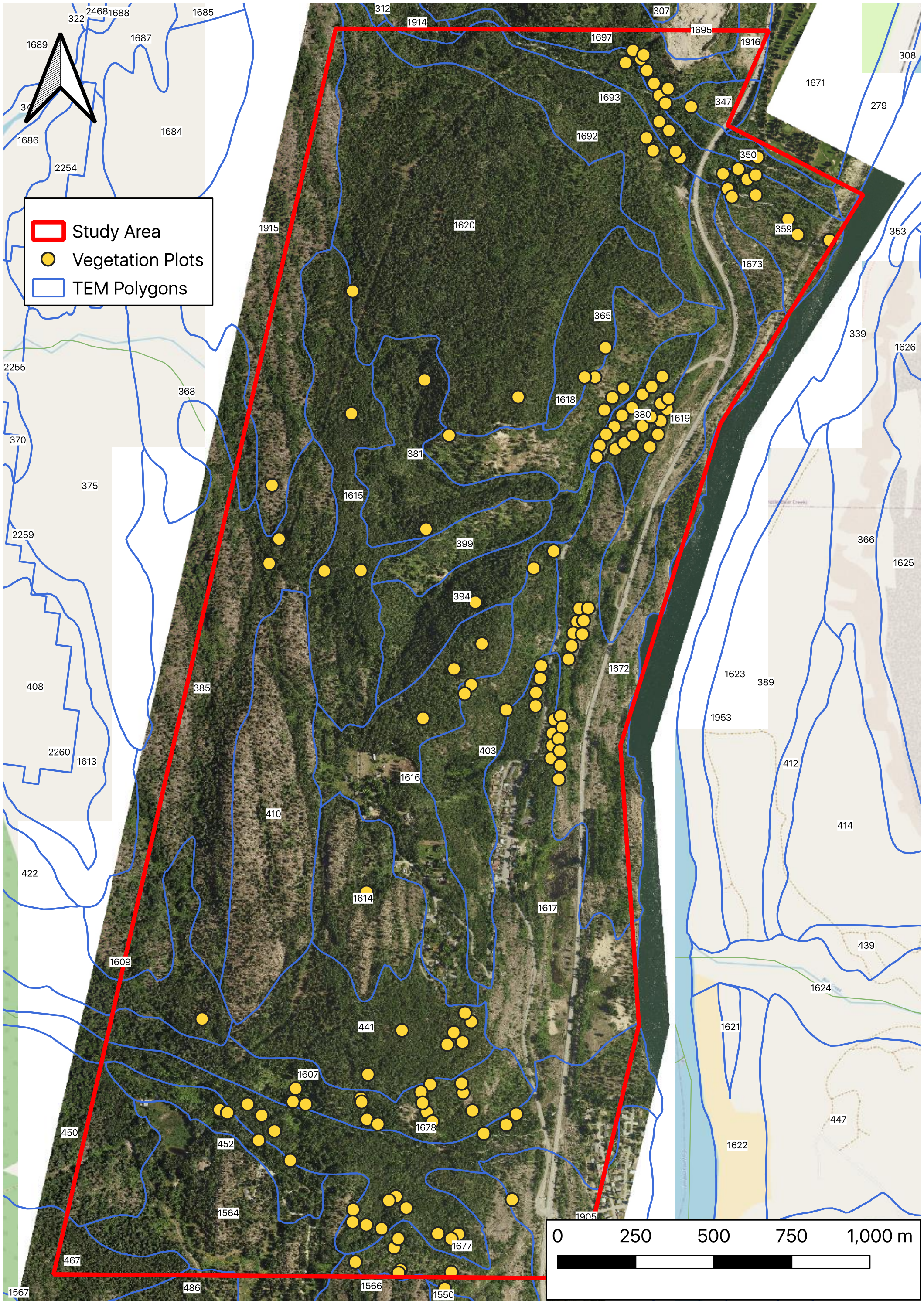


Figure 2.3: Study area for Unmanned Aerial Vehicle (UAV) imagery collection in July 2022, TEM polygons (blue), and black locust (*Robinia pseudoacacia* L.) abiotic conditions and vegetation community monitoring plots (yellow) completed from July to September 2022. The study area is 600 ha, and its boundaries were allocated to cover a range of natural habitats and anthropogenic disturbance conditions representative of areas occupied by black locust within the Lower Columbia Valley.

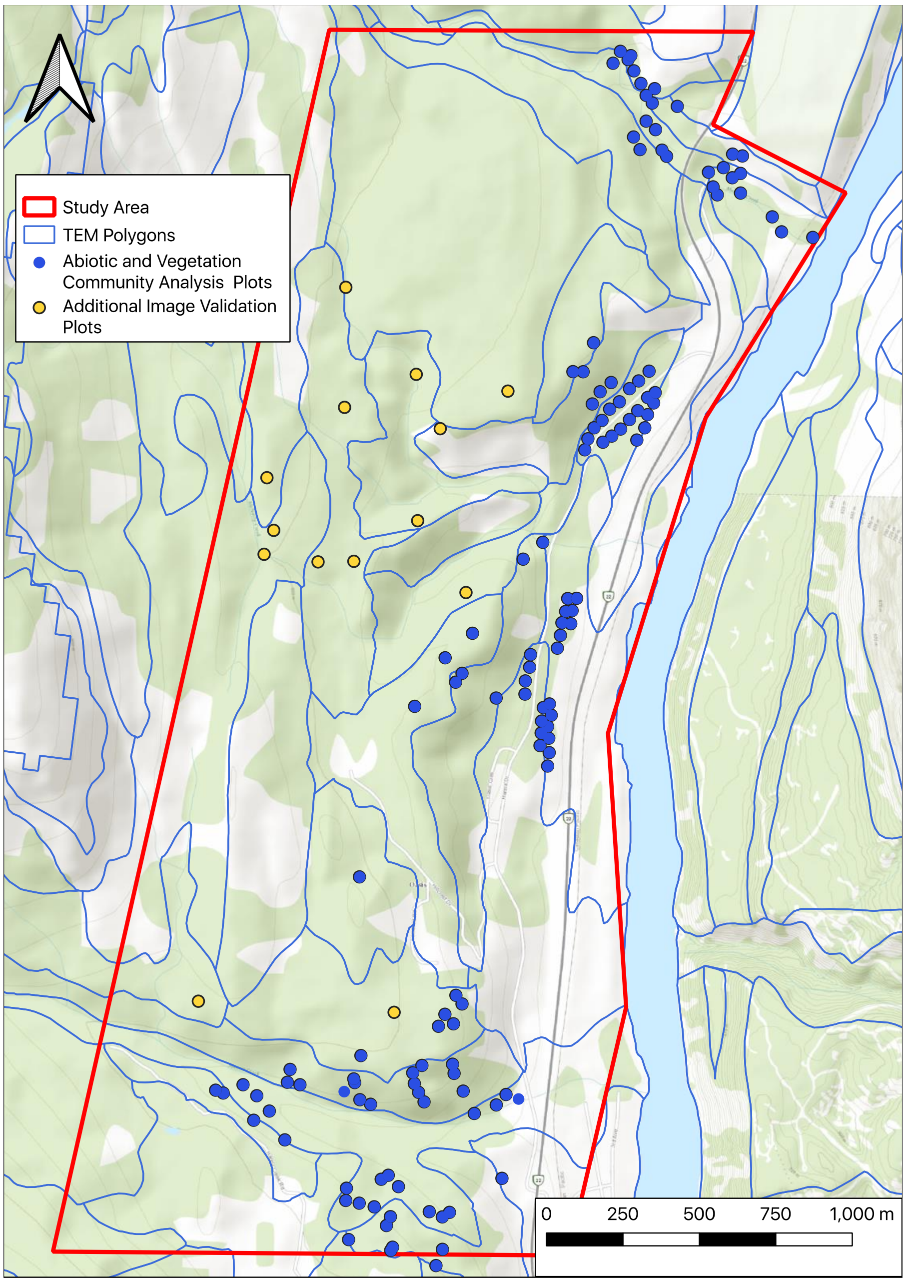


Figure 2.4: Map of the 151 plots used in aerial imagery analysis and the 137 plots used in analysis of black locust's (*Robinia pseudoacacia* L.) associations with abiotic conditions and native vegetation communities. All plots were 400 m^2 (11.28 m radius) and deployed in a 600 ha study area north of Trail BC from July to September 2022.

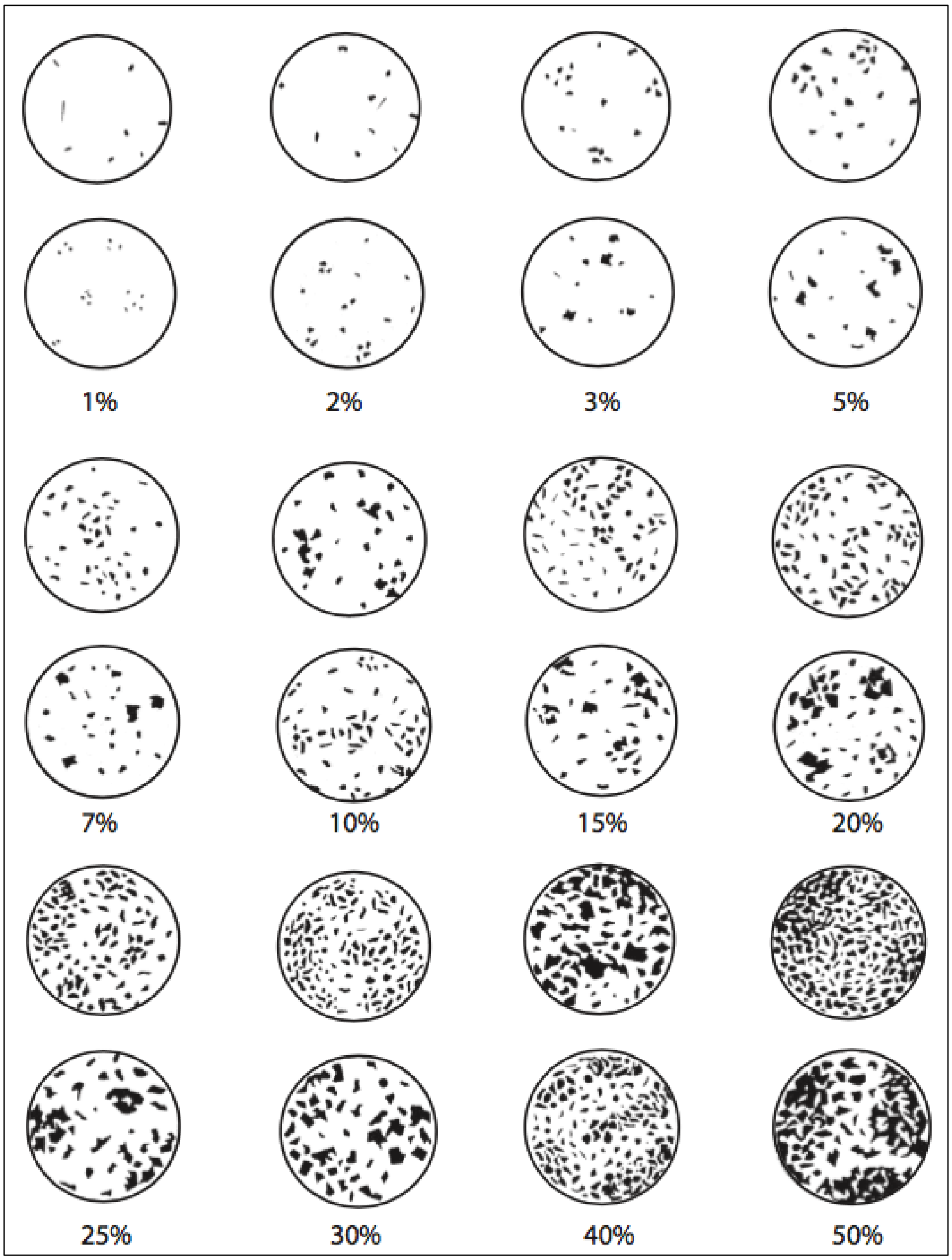


Figure 2.5: Comparison charts for visual estimation of vegetation cover on 400 m^2 (11.28m radius) plots deployed from June to September 2022 used in analysis of black locust's (*Robinia pseudoacacia* L.) associations with abiotic conditions and native vegetation communities, from the BC Terrestrial Ecosystem Monitoring Protocol (British Columbia Ministry of Forests and Range & British Columbia Ministry of Environment 2010).

3. Results

3.1. Aerial Image Validation

Following Goal 1 and Objective 1.1, I compared the presence of black locust identified on aerial imagery to the true presence and absence of black locust in ground plots and created a validation matrix showing effectiveness of aerial imagery as a tool for visually identifying black locust stands. Summer 2022 aerial imagery was able to help identify flowering black locust trees and was not able to help identify non-flowering black locust trees and new invasions of black locust shrubs and recruits. True positive identification rate (identified presence on aerial imagery and true presence on plots) was 61 percent. True negative identification rate (identified absence on aerial imagery and true absence on plots) was 98 percent. False negative identification rate (identified absence on aerial imagery and true *presence* on plots) was 38 percent. False positive identification rate (identified presence on aerial imagery and true *absence* on plots) was 3 percent. I created a confusion matrix to communicate the success and failure rate of visual identification of black locust trees (Table 3.1).

3.2. Abiotic Conditions and Vegetation Species Associations

3.2.1. Black Locust Mapping and Plot Cover Summaries

Following Goal 2 and Objective 2.1, I mapped black locust cover within the study area using ground sampling plots. Of the 137 plots suitable for use in the habitat suitability analysis 102 plots had black locust of any structural stage (tree, shrub, or recruit) and 35 had no black locust of any structural stage. Of the 102 plots with black locust present, 74 had trees, 98 had shrubs, and 77 had recruits. The distribution of black locust on plots was right skewed: a small number of plots (n = 9 of a total 102 plots with black locust present) had black locust total cover greater than 50 percent. Plots with highest black locust total cover and recruit cover were evenly distributed throughout the study area (Figure 3.1, Figure 3.2)

3.2.2. Abiotic Conditions

Following Goal 2 and Objective 2.2, I characterized black locust tree, shrub, and recruit cover associations with abiotic conditions in the study area using correlation analysis and multi-variable models. Black locust total cover was best supported by a positive response to three equivalent models (ΔAIC <2): summer insolation, winter insolation, and NDMI (Table 3.3). Black locust tree cover was not best supported by any abiotic variable. Black locust shrub cover was best supported by a positive response to summer insolation and winter insolation. Both models were strongly supported above other models (ΔAIC > 4) and had significant p values. Black locust recruit cover was best supported by a positive response to winter insolation, with a significant p value. Black locust cover across all structural stages increased with increasing insolation and moisture: the response of trees and recruits to increasing moisture was more pronounced than the response of shrubs to increasing moisture (Figure 3.3).

NMDS contour maps indicated abiotic conditions observed for black locust and native tree species on study plots (Figure 3.4). Black locust appeared to select moist, high light, and warm conditions represented by high NDMI and high insolation values. Black locust of any structural stage occurred on 43 of 55 plots with black cottonwood of any structural stage (Fuller 2022, Field Data) but was present on drier and more exposed sites than black cottonwood (Fuller 2022, Field Data). Field observations indicated black locust appeared to select warmer aspects than paper birch and trembling aspen. Compared to native conifer species, black locust's temperature and moisture conditions appeared similar to Douglas-fir, true firs, and western white pine. True firs and other pine species were not observed frequently enough to provide an accurate comparison of growing conditions. Black locust appeared to select similar moisture conditions to western hemlock and spruce species but on warmer aspects instead of cooler aspects. It often occurs in the study area on warm-aspect ridgeline and gully slopes opposite Douglas-fir, western hemlock, and spruce species on cooler-aspect slopes at the same elevations (Fuller 2022, Field Data).

3.2.3. Vegetation Structure

Vegetation Structure Correlation with Black Locust Cover

Following Goal 2 and Objective 2.3, I characterized the structural characteristics of native vegetation communities associated with black locust stands of different structural stages using correlation analysis and multi-variable models. Black locust total cover was positively correlated with total shrub-species cover (0.24) and total grass cover (0.36) and negatively correlated with tree-stage cover (-0.31), coniferous tree-stage cover (-0.25), tree shrub-stage cover (-0.31), herb cover (-0.28), and other variables (Table 3.4). Black locust tree cover was positively correlated with shrub-species cover (0.20), and negatively correlated with total coniferous cover (-0.22), coniferous tree-stage cover (-0.22), tree shrub-stage cover (-0.26), deciduous shrub-stage cover (-0.22), and herb cover (-0.23). Black locust shrub cover was positively correlated with shrub-species cover (0.23) and grass cover (0.41), and negatively correlated with native tree canopy cover (-0.27), tree-species shrub-stage cover (-0.25), and herb cover (-0.26). Black locust recruit cover was positively correlated with shrub-species cover (0.22) and grass cover (0.39), and negatively correlated with native tree canopy cover (-0.23) (Table 3.4).

Black locust total cover was best supported (ΔAIC <2) and negatively correlated with two predictors (Table 3.5): total tree-species shrub-stage cover (-0.05) and deciduous tree-species shrub-stage cover (-0.05). Black locust tree cover was best supported and negatively correlated with three predictors: total tree-species shrub-stage cover (-0.04), deciduous tree shrub-stage cover (-0.04), and herb cover (-0.01). Black locust shrub cover was best supported and positively correlated with grass cover (0.02), with a ΔAIC > 10. Black locust shrub cover was negatively correlated with native tree canopy cover (-0.01), and deciduous tree shrub-stage cover (-0.03). Black locust recruit cover was best supported by three predictors (ΔAIC <2): total native canopy cover (-0.01), shrub-species cover (0.01), and grass cover (0.01) (Table 3.5). Black locust recruit correlation with specific native tree and shrub species cover is explored in later in Section 3.2.4 “Tree and Shrub Species Associations” and Section 3.2.5 “Black Locust Colonization Under Native Tree Species and Native Tree Species Colonization Under Black Locust”.

Black Locust Cover Correlation with Vegetation Structure

Black locust tree cover was a significant ($p < 0.5$) negative predictor for (1) total tree-stage cover (2) deciduous tree-stage cover (3) tree shrub-stage cover (4) deciduous tree shrub-stage cover, and (5) herb cover (Table 3.6). Black locust shrub cover was a significant negative predictor for (1) total tree-stage cover (2) coniferous tree-stage cover (3) tree shrub-stage cover (4) deciduous tree shrub-stage cover, and (5) herb cover, and a significant positive predictor for grass cover. Black locust recruit cover was a significant negative predictor for coniferous tree-stage cover, supporting the negative relationship between black locust recruit cover and coniferous tree cover found in spearman correlation coefficients.

3.2.4. Tree and Shrub Species Associations

Following Goal 2 and Objective 2.3, I characterized black locust tree, shrub, and recruit cover associations with native tree and shrub species cover using correlation analysis and multi-variable models.

Shrub Species

Correlation

Black locust total cover was significantly positively correlated (Table 3.7) with Oregon grape (*Berberis aquifolium*), common snowberry (*Symphoricarpos albus*), chokecherry (*Prunus virginiana*), rose species (*Rosa* spp.), and beaked hazelnut (*Corylus cornuta*) cover. Black locust tree cover was significantly positively correlated with Oregon grape cover. Black locust shrub cover was significantly positively correlated with common snowberry, Oregon grape, chokecherry, beaked hazelnut, rose species, mock orange (*Philadelphus lewisii*), and willow species (*Salix* spp.) cover. Black locust recruit cover was significantly positively correlated with common snowberry, chokecherry, beaked hazelnut, Oregon grape, and mock orange cover.

Modelling

In single variable models (Table 3.8) black locust total cover was best supported by and positively correlated with Oregon grape. Black locust tree cover was best supported by Oregon grape, but no ΔAIC scores were greater than 3. Black locust shrub cover was best supported by and positively correlated with Oregon grape. Black locust recruit cover was not best supported by or statistically significant with any shrub species. In multi-variable models with black locust shrub and recruit cover modelled against all native shrub species (Table 3.9), all black locust total and tree structural stages except the recruit stage were significantly positively correlated with Oregon grape. Black locust shrubs were positively correlated with Oregon grape, mock orange, and willow species. Black locust recruit cover was not correlated with Oregon grape; it was positively correlated with Douglas maple (*Acer glabrum* var. douglasii). In single-variable models of native shrub species' responses modelled against black locust cover across structural stages as a predictor variable, only Oregon grape had a significant ($P < 0.05$) and positive response to Black locust total, tree, and shrub cover (Table 3.10).

Tree Species

Paper birch was the most abundant tree species on plots in the study area: 120 of 137 (87.5 %) plots had paper birch present. Black locust was present on 75 percent of plots, western white pine was present on 64 percent of plots, trembling aspen was present on 52 percent of plots, Douglas-fir was present on 45 percent of plots, and black cottonwood was present on 39 percent of plots (Table 3.11).

Correlation

Black locust total cover was positively correlated (Table 3.12, Figure 3.5) with black cottonwood total cover. Black locust total cover was negatively correlated with paper birch, Douglas-fir, and western hemlock total cover. Black locust tree cover was positively correlated with black cottonwood cover. Black locust shrub cover was positively correlated black cottonwood shrub cover and negatively correlated with paper birch cover. Black locust recruit cover was positively correlated with black cottonwood recruit cover. Black locust cover was not significantly correlated with trembling aspen or western white pine at any structural stage. Black locust recruits and shrubs occur at moderate densities under trembling aspen and on disturbed sites alongside western white pine trees (but not dense stands), and both these species' recruit and shrub stages occur under mature black locust trees.

Modelling

Black locust total cover was best supported by and negatively correlated with paper birch total cover (Table 3.13). Black locust total cover was moderately well supported (ΔAIC

< 4) by and positively correlated with black cottonwood total cover and negatively and *not significantly* correlated (p = 0.053) with Douglas-fir total cover. Black locust tree cover was not best supported by any model, all ΔAIC were within 2, and no models were significant. Black locust shrub cover was best supported by and negatively and *not significantly* correlated (p = 0.06) with paper birch shrub cover. All ΔAIC for black locust shrub cover except the global model were within 4. Black locust recruit cover was equivalently supported (ΔAIC < 2) by a positive correlation with black cottonwood recruit cover, and a positive correlation with paper birch recruit cover.

Paper birch and black cottonwood predictors supported the most variability for black locust total, shrub, and recruit cover models. Black locust correlation coefficients were positive with black cottonwood for all structural stages, negative with paper birch for the total and shrub stages, and positive with paper birch at the recruit stage. Black locust tree models did not have a clear best model in terms of AIC scores or p-values but had significant and positive spearman correlations with black cottonwood and silver maple tree cover. Multi-variable models with black locust structural stages modelled against equivalent native tree-species structural stages indicated black locust recruit cover was positively and significantly correlated with black cottonwood recruit cover (Figure 3.6).

3.2.5. Black Locust Colonization Under Native Tree Species and Native Tree Species Colonization Under Black Locust

Following Goal 2 and Objective 2.3, I characterized black locust shrub- and recruit-stage cover under native tree species tree-stage cover and native tree species shrub- and recruit-stage cover under black locust tree cover using correlation analysis and multi-variable models.

Black Locust Colonization Under Native Tree Species

<u>Plot Cover Comparisons</u>

Mean black locust shrub cover was higher on plots with black cottonwood than without black cottonwood (Table 3.14). Mean black locust shrub cover was lower on plots with paper birch, trembling aspen and silver maple than plots without these trees. Mean black locust recruit cover was higher on plots with black cottonwood than without black cottonwood, and slightly higher on plots with paper birch than without paper birch. Mean black locust recruit cover was lower on plots with trembling aspen, western white pine, and silver maple than plots without these tree species.

Correlation and Modelling

Black locust shrub cover was positively correlated with black locust tree cover. Black locust shrub cover was positively correlated with black cottonwood tree cover, and negatively correlated with trembling aspen, western hemlock, and paper birch tree cover. Black locust recruit cover was positively correlated with black locust tree cover and black cottonwood tree cover and negatively correlated with western hemlock tree cover (Figure 3.7). In single variable models (

Table 3.15), black locust shrub cover was almost equally supported ($\Delta AIC = 2.085$) by positive correlations with black locust tree cover and black cottonwood tree cover. Black locust tree cover, black cottonwood tree cover, and paper birch tree cover single-variable models all were better supported than the global tree-species cover model as predictor variables for black locust shrub cover. Black locust recruit cover was not best supported or statistically significant with any predictors, but was positively correlated with black cottonwood tree cover and negatively correlated with spruce species tree cover. The only conifer species predictor with a positive correlation to black locust shrub or recruit cover was western larch – all other conifer species were not well-supported, significant, or positively associated with black locust shrub or recruit cover.

Native Tree Species Colonization Under Black Locust

Plot Cover Comparisons

Black locust trees were associated with the presence of some native tree-species recruits in their understories (Table 3.16). Plots invaded with greater than 15% black locust tree-stage cover did not have any higher native shrub cover than plots with less than 15% black locust tree cover. Plots with greater than 15% black locust tree-stage cover had higher black cottonwood recruit cover, western white pine recruit cover, silver maple recruit cover, and very slightly higher Douglas-fir recruit cover than plots with less than 15% black locust tree-stage cover.

Correlation and Modelling

Black locust tree cover was positively correlated with black locust shrub cover (correlation = 0.65) and negatively correlated with paper birch shrub cover (- 0.18). Black locust tree cover was positively correlated with black locust recruit cover (0.45) and silver maple recruit cover (0.22) (Figure 3.8). In single-variable models (Table 3.17) of native tree-species shrub and recruit cover modelled against black locust tree-stage cover compared against null models without black locust using likelihood ratio tests, black locust tree cover was a significant positive predictor for black locust shrub cover (cor = 0.02) and a significant negative predictor for silver maple shrub cover (-0.03) and paper birch shrub cover (-0.01). Black locust tree cover was a significant positive predictor for black cottonwood recruit cover (0.03).

3.3. Results – Tables and Figures

Tables

Table 3.1: Confusion matrix for manual identification of black locust (*Robinia pseudoacacia* L.) on aerial imagery taken in July 2022. Black locust presence was recorded on 400 m^2 (11.28 m radius) vegetation monitoring plots and black locust was manually identified in 6 cm^2 resolution colour AUV imagery: identification of black locust in imagery was compared to real black locust presence on plots to obtain confusion matrix scores.

	True	False
Positive	61	3
Negative	98	38

Table 3.2: Plot cover summary data for black locust (*Robinia pseudoacacia* L.) total cover, tree-stage cover, shrub-stage cover, and recruit-stage cover on the 137 400 m^2 (11.28 m radius) plots deployed from June to September 2022 used in analysis of black locust's associations with abiotic conditions and native vegetation communities. Cover was assessed visually following the BC Terrestrial Ecosystem Monitoring Protocol (British Columbia Ministry of Forests and Range & British Columbia Ministry of Environment 2010). Total cover represents all non-overlapping black locust present on plots. Tree cover represents black locust cover above 10 m height. Shrub cover represents black locust cover between 2 m and 10 m height. Recruit cover represents black locust cover below 2 m height.

	Black Locust Structural Stage	Min	Median	Max	Mean	SD	Plot Count (of 137)
1	BL Total Cover	0	8	80	15.882	19.896	102
2	BL Tree Cover	0	1	70	7.391	14.255	74
3	BL Shrub Cover	0	5	55	8.289	11.145	98
4	BL Recruit Cover	0	0.25	12	1.37	2.279	77

Table 3.3: Model ranking table of single-variable GLMMs representing black locust (*Robinia pseudoacacia* L.) total (Tot), tree (Tr), shrub (Sh), and recruit (Rc) cover modelled as a response to abiotic predictor variables derived at the centers of 400 m^2 (11.28 m radius) plots from GIS data of the study area. All plots were deployed from June to September 2022. Insolation Summer represents total May 1 to September 1 2022 insolation, and Insolation Winter represents total November 1 2021 to February 1 2022 insolation at plot centers calculated using a 1 m^2 DEM. Slope and aspect were both derived from the same 1 m^2 DEM used to calculate insolation. NDMI Mean represents mean July 2021 and July to September 2022 Normalized Difference Moisture Index (NDMI) values at plot centers calculated from eight 20 m^2 multi-band images. NDMI Difference represents the difference between highest and lowest NMDI values in July 2021 and July to September 2022 NDMI values calculated at plot centers calculated from 6 Sentinel-2 20 m^2 imagery. "Response" columns represent the predictor variable black locust total-, tree-, shrub-, and recruit-stage cover was modelled as a response to. "ΔAIC" columns represent the difference in AIC scores between models. "Coef" and "P" columns represent each single-variable model's correlation coefficient and P value for black locust response at the specified structural stage to the given predictor variable in the "Response" column.

Tot_Response	Tot.ΔAIC	Tot.Coef	Tot.P	Tr_Response	Tr.ΔAIC	Tr.Coef	Tr.P	Sh_Response	Sh.ΔAIC	Sh.Coef	Sh.P	Rc_Response	Rc.ΔAIC	Rc.Coef	Rc.P
Insolation Summer	0.00	0.19	0.052	NDMI Mean	0.00	2.74	0.153	Insolation Summer	0.00	0.24	0.013	Insolation Winter	0.00	0.24	0.031
Insolation Winter	-0.15	0.18	0.057	Insolation Summer	-1.46	0.08	0.442	Insolation Winter	-0.32	0.22	0.015	Insolation Summer	-2.37	0.18	0.132
NDMI Mean	-0.49	2.64	0.070	NDMI Difference	-1.46	-2.08	0.445	Aspect	-4.80	0.00	0.240	NDMI Mean	-3.13	1.70	0.220
Aspect	-2.89	0.00	0.350	Insolation Winter	-1.79	0.05	0.615	NDMI Mean	-5.91	-0.75	0.596	Aspect	-4.19	0.00	0.504
NDMI Difference	-2.97	-2.38	0.373	Slope	-1.89	0.00	0.692	NDMI Difference	-6.06	0.88	0.726	Slope	-4.22	0.01	0.516
Slope	-3.66	0.00	0.748	Aspect	-1.92	0.00	0.719	Slope	-6.09	0.00	0.755	NDMI Difference	-4.59	0.58	0.827

Table 3.4: Spearman correlation coefficients and p values calculated for black locust (*Robinia pseudoacacia* L.) total (Tot), tree (Tr), shrub (Sh), and recruit (Rc) cover and native vegetation structure characteristics visually estimated on 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. “Response” columns represent the variable black locust total-, tree-, shrub-, and recruit-stage cover was correlated with. “Cor” and “P” columns represent the spearman correlation coefficient and P value for black locust correlation at the specified structural stage with the given vegetation-structure variable in the “Response” column.

Tot_Response	Tot.Cor	Tot.P	Tr_Response	Tr.Cor	Tr.P	Sh_Response	Sh.Cor	Sh.P	Rc_Response	Rc.Cor	Rc.P
Grass Cover	0.36	0.00	Tree Shrub Cover	-0.26	0.00	Grass Cover	0.41	0.00	Grass Cover	0.39	0.00
Native Canopy Cover	-0.31	0.00	Herb Cover	-0.23	0.01	Native Canopy Cover	-0.27	0.00	Native Canopy Cover	-0.23	0.01
Tree Shrub Cover	-0.31	0.00	Decid Tree Shrub Cover	-0.22	0.01	Tree Shrub Cover	-0.25	0.00	Shrub Species Cover	0.22	0.01
Herb Cover	-0.28	0.00	Conif Tree Cover	-0.22	0.01	Herb Cover	-0.26	0.00	Conif Tree Cover	-0.16	0.07
Conif Tree Cover	-0.25	0.00	Conif Total Cover	-0.22	0.01	Shrub Species Cover	0.23	0.01	Conif Total Cover	-0.16	0.07
Conif Total Cover	-0.25	0.00	Shrub Species Cover	0.20	0.02	Conif Tree Cover	-0.19	0.02	Decid Tree Recruit Cover	0.15	0.09
Decid Tree Shrub Cover	-0.24	0.00	Native Canopy Cover	-0.11	0.22	Conif Total Cover	-0.19	0.02	Herb Cover	-0.13	0.13
Shrub Species Cover	0.24	0.00	Tree Recruit Cover	0.10	0.25	Decid Tree Shrub Cover	-0.19	0.03	Tree Shrub Cover	-0.12	0.15
Decid Tree Cover	-0.21	0.02	Grass Cover	0.10	0.26	Decid Tree Cover	-0.16	0.06	Conif Tree Shrub Cover	-0.11	0.20
Decid Total Cover	-0.21	0.02	Conif Tree Shrub Cover	-0.09	0.28	Decid Total Cover	-0.16	0.06	Tree Recruit Cover	0.09	0.31
Conif Tree Shrub Cover	-0.14	0.12	Decid Tree Recruit Cover	0.09	0.30	Conif Tree Recruit Cover	0.12	0.17	Total Shrub Layer Cover	0.08	0.32
Total Shrub Layer Cover	-0.07	0.42	Total Shrub Layer Cover	-0.08	0.34	Conif Tree Shrub Cover	-0.09	0.29	Decid Tree Cover	-0.08	0.32
Tree Recruit Cover	0.06	0.45	Decid Tree Cover	-0.06	0.46	Tree Recruit Cover	0.07	0.40	Decid Total Cover	-0.08	0.32
Conif Tree Recruit Cover	0.05	0.59	Decid Total Cover	-0.06	0.46	Decid Tree Recruit Cover	0.04	0.66	Decid Tree Shrub Cover	-0.05	0.53
Decid Tree Recruit Cover	0.04	0.64	Conif Tree Recruit Cover	-0.01	0.94	Total Shrub Layer Cover	-0.01	0.92	Conif Tree Recruit Cover	-0.03	0.73

Table 3.5: Model ranking table of single-variable GLMMs representing black locust (*Robinia pseudoacacia* L.) total (Tot), tree (Tr), shrub (Sh), and recruit (Rc) cover modelled as a response to native vegetation-structure percent-cover values visually estimated on 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. "Response" columns represent the predictor variable black locust total-, tree-, shrub-, and recruit-stage cover was modelled as a response to. "ΔAIC" columns represent the difference in AIC scores between models. "Coef" and "P" columns represent each single-variable model's correlation coefficient and P value for black locust response at the specified structural stage to the given vegetation-structure predictor variable in the "Response" column.

Tot_Response	Tot.ΔAIC	Tot.Coef	Tot.P	Tr_Response	Tr.ΔAIC	Tr.Coef	Tr.P	Sh_Response	Sh.ΔAIC	Sh.Coef	Sh.P	Rc_Response	Rc.ΔAIC	Rc.Coef	Rc.P
Decid Tree Shrub Cover	0.00	-0.05	0.000	Tree Shrub Cover	0.00	-0.04	0.016	Grass Cover	0.00	0.02	0.000	Grass Cover	0.00	0.01	0.058
Tree Shrub Cover	-0.96	-0.05	0.000	Decid Tree Shrub Cover	-0.50	-0.04	0.022	Native Canopy Cover	-10.13	-0.01	0.027	Total Shrub Layer Cover	-1.06	0.01	0.112
Grass Cover	-9.82	0.01	0.052	Herb Cover	-1.51	-0.01	0.039	Decid Tree Shrub Cover	-10.54	-0.03	0.034	Native Canopy Cover	-1.65	-0.01	0.165
Herb Cover	-11.05	-0.01	0.111	Native Canopy Cover	-2.52	-0.01	0.071	Tree Shrub Cover	-11.24	-0.02	0.052	Shrub Species Cover	-2.10	0.01	0.224
Tree Recruit Cover	-11.32	0.07	0.132	Tree Recruit Cover	-2.63	0.09	0.076	Decid Tree Cover	-13.39	-0.01	0.203	Tree Shrub Cover	-2.57	-0.01	0.313
Native Canopy Cover	-11.55	-0.01	0.153	Conif Tree Recruit Cover	-3.16	0.24	0.105	Decid Total Cover	-13.39	-0.01	0.203	Decid Tree Shrub Cover	-2.64	-0.01	0.331
Conif Tree Cover	-11.85	-0.02	0.187	Conif Tree Cover	-3.65	-0.04	0.145	Herb Cover	-13.86	-0.00	0.283	Conif Tree Recruit Cover	-2.76	-0.13	0.363
Conif Total Cover	-11.85	-0.02	0.187	Conif Total Cover	-3.65	-0.04	0.145	Conif Tree Recruit Cover	-14.37	0.09	0.420	Herb Cover	-2.78	0.00	0.370
Decid Tree Recruit Cover	-12.08	0.06	0.219	Decid Tree Cover	-4.25	-0.01	0.216	Tree Recruit Cover	-14.60	0.03	0.516	Decid Tree Recruit Cover	-3.37	0.02	0.642
Shrub Species Cover	-12.40	0.00	0.274	Decid Total Cover	-4.25	-0.01	0.216	Conif Tree Cover	-14.61	-0.01	0.523	Conif Tree Cover	-3.40	-0.01	0.671
Conif Tree Recruit Cover	-12.45	0.14	0.284	Decid Tree Recruit Cover	-4.26	0.07	0.218	Conif Total Cover	-14.61	-0.01	0.523	Conif Total Cover	-3.40	-0.01	0.671
Decid Tree Cover	-12.98	-0.00	0.434	Total Shrub Layer Cover	-4.44	-0.01	0.248	Decid Tree Recruit Cover	-14.87	0.02	0.700	Conif Tree Shrub Cover	-3.41	-0.01	0.676
Decid Total Cover	-12.98	-0.00	0.434	Shrub Species Cover	-5.14	0.00	0.422	Total Shrub Layer Cover	-14.89	0.00	0.718	Tree Recruit Cover	-3.56	0.01	0.881
Conif Tree Shrub Cover	-13.20	-0.02	0.531	Conif Tree Shrub Cover	-5.44	-0.02	0.559	Conif Tree Shrub Cover	-14.95	-0.01	0.800	Decid Tree Cover	-3.57	0.00	0.906
Total Shrub Layer Cover	-13.55	-0.00	0.834	Grass Cover	-5.58	-0.00	0.657	Shrub Species Cover	-14.98	0.00	0.854	Decid Total Cover	-3.57	0.00	0.906

Table 3.6: Model ranking table of single-variable GLMMs representing native vegetation-structure cover modelled as a response to black locust (*Robinia pseudoacacia* L.) tree and shrub cover. Vegetation-structure cover and black locust cover were visually estimated on 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. "Response" columns represent the vegetation-structure variable black locust total-, tree-, shrub-, and recruit-stage cover was modelled as a predictor variable for. "Coef" and "P" columns represent the correlation coefficient and P value for the native vegetation-structure variable specified in the "Response" column black locust at the specified structural stage was modelled as a predictor variable for.

Tr_Response	Tr.Coef	Tr.P	Sh_Response	Sh.Coef	Sh.P	Rc_Response	Rc.Coef	Rc.P
Tree Shrub Cover	-0.02	0.000	Tree Shrub Cover	-0.02	0.000	Conif Tree Cover	-0.11	0.003
Tree Layer Cover	-0.02	0.001	Grass Cover	0.03	0.001	Conif Tree Recruit Cover	-0.08	0.070
Decid Tree Shrub Cover	-0.02	0.002	Tree Layer Cover	-0.02	0.002	Native Canopy Cover	-0.06	0.081
Herb Cover	-0.02	0.003	Herb Cover	-0.02	0.004	Tree Layer Cover	-0.06	0.086
Native Canopy Cover	-0.01	0.008	Conif Tree Cover	-0.02	0.007	Herb Cover	-0.06	0.102
Decid Tree Cover	-0.01	0.033	Native Canopy Cover	-0.02	0.009	Grass Cover	0.06	0.146
Conif Tree Cover	-0.02	0.143	Decid Tree Shrub Cover	-0.02	0.014	Decid Tree Recruit Cover	-0.05	0.151
Shrub Species Cover	0.01	0.149	Conif Tree Shrub Cover	-0.01	0.071	Tree Recruit Cover	-0.04	0.223
Total Shrub Layer Cover	-0.01	0.181	Decid Tree Cover	-0.01	0.076	Total Shrub Layer Cover	0.04	0.254
Decid Tree Recruit Cover	0.01	0.214	Conif Tree Recruit Cover	0.01	0.372	Tree Shrub Cover	-0.03	0.285
Conif Tree Recruit Cover	0.01	0.320	Decid Tree Recruit Cover	-0.01	0.425	Shrub Species Cover	0.05	0.291
Tree Recruit Cover	0.00	0.346	Tree Recruit Cover	-0.00	0.644	Conif Tree Shrub Cover	-0.04	0.333
Conif Tree Shrub Cover	-0.01	0.424	Shrub Species Cover	0.00	0.664	Decid Tree Cover	-0.02	0.581
Grass Cover	-0.00	0.918	Total Shrub Layer Cover	0.00	0.899	Decid Tree Shrub Cover	-0.00	0.988

Table 3.7: Spearman correlation coefficients and p values calculated for black locust (*Robinia pseudoacacia* L.) total (Tot), tree (Tr), shrub (Sh), and recruit (Rc) cover and native shrub cover visually estimated on 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. "BL Stage" represents the black locust total-, tree-, shrub-, and recruit-stage cover variable that native shrub cover was correlated with. "Species" represents the native shrub species correlated with black locust cover at the given structural stage in "BL_Stage". "Cor" and "P" columns represent the spearman correlation coefficient and P value for black locust correlation at the specified structural stage with the given shrub species in the "Species" column.

BL Stage	Species	Correlation	P-Value
BL.Tot	Berbaqu	0.32	0.00
BL.Tot	Sympalb	0.30	0.00
BL.Tot	Prunvir	0.24	0.00
BL.Tot	Rosa.spp	0.20	0.02
BL.Tot	Corycor	0.17	0.04
BL.Tr	Berbaqu	0.20	0.02
BL.Sh	Sympalb	0.33	0.00
BL.Sh	Berbaqu	0.32	0.00
BL.Sh	Prunvir	0.30	0.00
BL.Sh	Corycor	0.22	0.01
BL.Sh	Rosa.spp	0.20	0.02
BL.Sh	Phillew	0.18	0.04
BL.Sh	Salix	0.18	0.04
BL.Rc	Sympalb	0.30	0.00
BL.Rc	Prunvir	0.23	0.01
BL.Rc	Corycor	0.22	0.01
BL.Rc	Berbaqu	0.21	0.02
BL.Rc	Phillew	0.19	0.02

Table 3.8: Model ranking table of single-variable GLMMs representing black locust (*Robinia pseudoacacia* L.) total (Tot), tree (Tr), shrub (Sh), and recruit (Rc) cover modelled as a response to native shrub species cover visually estimated on 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. "Response" columns represent the predictor variable black locust total-, tree-, shrub-, and recruit-stage cover was modelled as a response to. "ΔAIC" columns represent the difference in AIC scores between models. "Coef" and "P" columns represent each single-variable model's correlation coefficient and P value for black locust response at the specified structural stage to the given shrub species predictor variable in the "Response" column.

Tot_Response	Tot.ΔAIC	Tot.Coef	Tot.P	Tr_Response	Tr.ΔAIC	Tr.Coef	Tr.P	Sh_Response	Sh.ΔAIC	Sh.Coef	Sh.P	Rc_Response	Rc.ΔAIC	Rc.Coef	Rc.P
Berbaqu	0.00	0.01	0.003	Berbaqu	0.00	0.01	0.082	Berbaqu	0.00	0.01	0.012	Acerglab	0.00	0.02	0.149
Rosa.spp	-7.37	0.03	0.242	Rosa.spp	-2.31	0.02	0.396	Salix	-2.18	0.06	0.042	Spirea	-1.08	0.29	0.317
Salix	-7.65	0.04	0.297	Prunvir	-2.47	-0.03	0.455	Phillew	-3.19	0.14	0.076	Salix	-1.10	0.03	0.321
Acerglab	-8.32	0.01	0.518	Rubuparv	-2.49	0.00	0.462	Corycor	-4.98	0.03	0.245	Corycor	-1.44	0.03	0.421
Phillew	-8.33	0.06	0.526	Sympalb	-2.59	0.01	0.507	Prunvir	-5.55	0.03	0.377	Phillew	-1.50	0.07	0.443
Rubuparv	-8.40	0.00	0.563	Corycor	-2.66	-0.02	0.543	Rosa.spp	-5.59	0.02	0.389	Cornser	-1.97	0.00	0.730
Elder	-8.45	0.15	0.593	Salix	-2.75	-0.02	0.598	Cornser	-5.62	-0.01	0.399	Rosa.spp	-1.98	0.01	0.752
Prunvir	-8.54	0.02	0.662	Spirea	-2.79	0.15	0.629	Spirea	-6.01	-0.19	0.569	Berbaqu	-2.01	0.00	0.782
Cornser	-8.62	-0.00	0.734	Phillew	-2.84	-0.04	0.668	Sympalb	-6.23	0.00	0.749	Elder	-2.02	0.16	0.797
Spirea	-8.65	-0.09	0.772	Elder	-2.85	0.12	0.676	Acerglab	-6.24	0.00	0.767	Rubuparv	-2.08	-0.00	0.944
Corycor	-8.72	0.00	0.890	Acerglab	-2.91	0.00	0.734	Rubuparv	-6.29	-0.00	0.844	Sympalb	-2.08	-0.00	0.961
Sympalb	-8.72	-0.00	0.914	Cornser	-2.99	-0.00	0.848	Elder	-6.31	0.04	0.882	Prunvir	-2.08	-0.00	0.972

Table 3.9: Model ranking table of multi-variable GLMMS representing black locust (*Robinia pseudoacacia* L.) total (Tot), tree (Tr), shrub (Sh), and recruit (Rc) cover modelled as a response to native shrub species cover visually estimated on 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. Multi-variable GLMMMS were built for black locust at each structural stage: only shrub species with statistically significant ($p < 0.05$) correlations with black locust are given in this table. "BL Stage" represents the black locust total-, tree-, shrub-, and recruit-stage cover variable that native shrub species cover was modelled as a predictor for. "Shrub Predictor" represents the native shrub species that was a significant predictor for black locust cover of the given structural stage in multi-variable models. "Estimate" and "St. Error" represent the shrub predictor variable's correlation coefficient and standard error with black locust, and "P Value" represents its p value.

BL Stage	Shrub Predictor	Estimate	St. Error	P Value
Total	Berbaqu	0.02	0.00	0.00
Tree	Berbaqu	0.02	0.00	0.01
Shrub	Berbaqu	0.01	0.00	0.00
Shrub	Phillew	0.16	0.08	0.04
Shrub	Salix	0.10	0.03	0.00
Recruit	Acerglab	0.03	0.01	0.02
Recruit	Salix	0.07	0.04	0.05

Table 3.10: Model ranking table of single-variable GLMMs representing native shrub-species cover modelled as a response to black locust (*Robinia pseudoacacia* L.) total-, tree-, shrub-, and recruit-stage cover visually estimated on 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. "Species" columns represent the shrub species for which black locust total (Tot), tree (Tr), shrub (Sh), and recruit (Rc) cover was modelled as a predictor variable. "Coef" and "P" columns represent the correlation coefficient and P value for the shrub species specified in the "Species" column black locust at the specified structural stage was modelled as a predictor variable for.

Species.Tot	Tot.Coef	Tot.P	Species.Tr	Tr.Coef	Tr.P	Species.Sh	Sh.Coef	Sh.P	Species.Rc	Rc.Coef	Rc.P
Berbaqu	0.01	0.010	Berbaqu	0.01	0.050	Berbaqu	0.02	0.050	Salix	0.13	0.020
Rosa.spp	-0.45	0.060	Rosa.spp	0.09	0.120	Salix	0.02	0.070	Prunvir	-0.11	0.220
Salix	0.01	0.080	Corycor	-0.01	0.320	Rosa.spp	-0.09	0.130	Corycor	-0.04	0.260
Corycor	0.00	0.280	Elder	0.02	0.400	Spirea	0.05	0.480	Rubuparv	0.17	0.380
Phillew	0.00	0.390	Rubuparv	0.02	0.420	Cornser	-0.01	0.480	Elder	-0.20	0.450
Rubuparv	0.01	0.430	Salix	0.01	0.500	Rubuparv	0.02	0.610	Spirea	0.11	0.470
Cornser	-0.01	0.600	Prunvir	-0.01	0.550	Phillew	0.00	0.620	Phillew	0.02	0.610
Prunvir	0.00	0.610	Phillew	-0.01	0.550	Elder	-0.01	0.640	Acerglab	0.01	0.810
Spirea	-0.01	0.680	Spirea	0.03	0.550	Sympalb	0.01	0.650	Sympalb	-0.01	0.840
Acerglab	0.00	0.760	Sympalb	0.00	0.780	Prunvir	-0.01	0.740	Rosa.spp	0.07	0.850
Elder	0.00	0.850	Cornser	0.00	0.940	Acerglab	0.00	0.740	Berbaqu	0.01	0.860
Sympalb	0.00	0.950	Acerglab	0.00	0.950	Corycor	0.00	0.840	Cornser	0.02	0.880

Table 3.11: Plot count summary for all tree species' structural stages and mean, max, and standard deviation for tree species' total cover on plots in the study area. All species covers were visually estimated on 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022.

Species Code	Common Name	Scientific Name	Total Count	Tree Count	Shrub Count	Recruit Count	Max	Mean	SD
EP	Paper birch	Betula papyrifera	120.00	95.00	112.00	63.00	65.00	15.90	15.53
BL	Black locust	Robinia pseudoacacia	102.00	74.00	98.00	77.00	80.00	15.42	19.78
PW	Western white pine	Pinus monticola	87.00	57.00	71.00	48.00	30.00	4.68	6.85
AT	Trembling aspen	Populus tremuloides	71.00	48.00	42.00	49.00	70.00	5.66	12.85
FD	Interior Douglas fir	Pseudotsuga menziesii	61.00	25.00	33.00	22.00	12.00	1.15	2.30
ACT	Black cottonwood	Populus trichocarpa	53.00	44.00	30.00	20.00	45.00	4.36	8.51
Picea	Spruce spp.	Picea spp.	22.00	6.00	19.00	6.00	10.00	0.48	1.58
HW	Western hemlock	Tsuga heterophylla	21.00	15.00	7.00	3.00	25.00	1.27	3.82
LT	Larch spp.	Larix spp.	18.00	12.00	8.00	2.00	12.00	0.41	1.56
MS	Silver maple	Acer saccharinum	9.00	5.00	5.00	7.00	75.00	1.35	8.08
YP	Pacific yew	Taxus brevifolia	9.00	1.00	2.00	7.00	7.00	0.08	0.63
CW	Western redcedar	Thuja plicata	8.00	3.00	6.00	4.00	10.50	0.21	1.15
FG	Grand fir	Abies grandis	5.00	1.00	1.00	3.00	4.00	0.04	0.35
FS	Subalpine fir	Abies lasiocarpa	5.00	1.00	3.00	2.00	10.00	0.10	0.87
FB	Balsam fir	Abies balsamea	4.00	0.00	4.00	0.00	2.00	0.04	0.26
PL	Lodgepole pine	Pinus contorta	4.00	3.00	1.00	0.00	2.00	0.05	0.28
PP	Ponderosa pine	Pinus ponderosa	3.00	0.00	2.00	1.00	1.00	0.01	0.10

Table 3.12: Spearman correlation coefficients and p values calculated for black locust (*Robinia pseudoacacia* L.) total (Tot), tree (Tr), shrub (Sh), and recruit (Rc) cover and native shrub cover visually estimated on 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. “BL Stage” represents the black locust total-, tree-, shrub-, and recruit-stage cover variable that native tree cover was correlated with. “Species” represents the native tree species correlated with black locust cover at the given structural stage in “BL Stage”. “Cor” and “P” columns represent the spearman correlation coefficient and P value for black locust correlation at the specified structural stage with the given native tree species in the “Species” column.

BL Stage	Species	Correlation	P-Value
BL.Tot	EP.Tot	-0.35	0.000
BL.Tot	ACT.Tot	0.26	0.002
BL.Tot	MS.Tot	0.22	0.011
BL.Tot	FD.Tot	-0.21	0.012
BL.Tot	HW.Tot	-0.21	0.015
BL.Tot	PW.Tot	-0.15	0.088
BL.Tr	MS.Tr	0.18	0.033
BL.Tr	ACT.Tr	0.18	0.039
BL.Tr	LT.Tr	-0.16	0.065
BL.Tr	CW.Tr	-0.15	0.086
BL.Sh	ACT.Sh	0.21	0.015
BL.Sh	EP.Sh	-0.17	0.050
BL.Sh	FD.Sh	-0.16	0.060
BL.Rc	ACT.Rc	0.25	0.003

Table 3.13: Model ranking table of single-variable GLMMs representing black locust (*Robinia pseudoacacia* L.) total (Tot), tree (Tr), shrub (Sh), and recruit (Rc) cover modelled as a response to native tree total-, tree-, shrub-, and recruit-stage cover visually estimated on 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. "Response" columns represent the native tree-species total-, tree-, shrub-, and recruit-stage cover predictor variable black locust total-, tree-, shrub-, and recruit-stage cover was modelled as a response to. Each black locust structural stage was modelled with the same native tree-species structural stage, for example, black locust total cover as a response to other tree species' total cover. "ΔAIC" columns represent the difference in AIC scores between models. "Coef" and "P" columns represent each single-variable model's correlation coefficient and P value for black locust response at the specified structural stage to the given tree-species predictor variable of cover at the same structural stage as black locust in the "Response" column.

Tot_Response	Tot.ΔAIC	Tot.Coef	Tot.P	Tr_Response	Tr.ΔAIC	Tr.Coef	Tr.P	Sh_Response	Sh.ΔAIC	Sh.Coef	Sh.P	Rc_Response	Rc.ΔAIC	Rc.Coef	Rc.P
EP	0.00	-0.019	0.01	EP	0.000	-0.01	0.26	EP	0.00	-0.03	0.06	ACT	0.00	0.18	0.03
ACT	-3.06	0.020	0.05	PW	-0.165	-0.04	0.30	ACT	-2.47	0.04	0.31	EP	-0.58	0.27	0.05
FD	-3.25	-0.087	0.05	HW	-0.701	-0.03	0.46	MS	-2.60	-0.02	0.35	MS	-0.68	-0.45	0.05
Picea	-6.23	-0.061	0.38	YP	-0.760	-0.09	0.48	AT	-2.79	-0.04	0.40	HW	-3.68	1.53	0.37
HW	-6.60	-0.024	0.53	AT	-0.798	-0.01	0.50	FD	-2.96	-0.07	0.47	Global	-3.73	-0.00	0.12
MS	-6.72	-0.005	0.60	ACT	-1.085	0.00	0.69	HW	-2.98	-0.06	0.47	PW	-3.81	-0.16	0.42
AT	-6.86	-0.004	0.71	MS	-1.124	-0.01	0.72	FG	-2.99	0.63	0.48	AT	-4.01	-0.04	0.50
FG	-6.89	0.077	0.74	Picea	-1.185	-0.08	0.80	Picea	-3.22	-0.06	0.60	FD	-4.08	-0.21	0.53
PW	-6.97	-0.003	0.88	FG	-1.192	-0.06	0.81	YP	-3.23	0.32	0.61	Picea	-4.39	-0.58	0.77
YP	-6.99	-0.010	0.94	FD	-1.229	-0.02	0.89	PW	-3.40	0.01	0.76	YP	-4.46	-0.10	0.89
Global	-9.89	-0.005	0.20	Global	-8.717	-0.01	0.72	Global	-6.50	-0.06	0.32	FG	-4.47	-0.36	0.97

Table 3.14: Plot cover summary table representing average black locust (*Robinia pseudoacacia* L.) shrub and recruit cover under native tree-species tree-stage cover visually estimated on 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. Plots were filtered to those with greater than 10% cover of each native tree species (column "Plots w/ Nat.Tree Cov. > 10%") and black locust shrub and recruit cover was summarized on these plots. Column "Plots w/ Nat.Tree Cov. > 10%" represents the total plots with both > 10% cover for a given tree species and black locust shrub or recruits present. Column "Avg. BL.Sh Cov w/ Nat.Tr" represents average black locust shrub cover on plots with greater than 10% cover of the native tree species in the "Tree" column. Column "Avg. BL.Sh Cov w/o Nat.Tr" represents average black locust shrub cover on plots with less than 10% cover of the native tree species in the "Tree" column. The subsequent two columns list average black locust recruit over on plots with and without greater than 10% of the given native tree species cover.

Tree	Plots w/ Nat.Tree Cov. > 10%	Plots w/ Nat.Tree Cov. > 10% & BL.Sh or BL.Rc present	Avg. BL.Sh Cov w/ Nat.Tr	Avg. BL.Sh Cov w/o Nat.Tr	Avg. BL.Rc Cov w/ Nat.Tr	Avg. BL.Rc Cov w/o Nat.Tr
ACT	19	19	17.20	11.00	2.78	1.85
BL	32	31	16.30	10.20	2.52	1.80
EP	53	26	10.00	13.30	2.19	1.99
HW	7	2	5.80	12.40	2.00	2.05
AT	15	9	4.30	13.20	1.40	2.12
PW	17	7	14.90	12.10	1.32	2.11
CW	1	1	5.00	12.40	1.00	2.06
MS	3	3	3.70	12.60	0.07	2.12
FD	1	0.00	NaN	12.30	NaN	2.05
LT	0.00	0.00	NaN	12.30	NaN	2.05
Picea	0.00	0.00	NaN	12.50	NaN	2.09
YP	0.00	0.00	NaN	12.30	NaN	2.05

Table 3.15: Model ranking table of single-variable GLMMs representing black locust (*Robinia pseudoacacia* L.) shrub (Sh) and recruit (Rc) cover modelled as a response to native tree tree-stage cover visually estimated on 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. "Response" columns represent the native tree-species tree-cover predictor variable black locust shrub and recruit cover was modelled as a response to. "ΔAIC" columns represent the difference in AIC scores between models. "Coef" and "P" columns represent each single-variable model's correlation coefficient and P value for black locust response at the specified structural stage to the given tree-species tree-cover predictor variable in the "Response" column.

Sh_Response	Sh.ΔAIC	Sh.Coef	Sh.P	Rc_Response	Rc.ΔAIC	Rc.Coef	Rc.P
BL	0.00	0.02	0.002	MS	0.00	-0.04	0.058
ACT	-2.08	0.03	0.005	ACT	-1.11	0.02	0.116
EP	-6.22	-0.01	0.053	Picea	-1.50	-0.14	0.149
Global	-7.17	-0.01	0.032	FG	-3.01	0.16	0.450
LT	-7.30	0.29	0.102	AT	-3.20	-0.01	0.537
AT	-8.22	-0.02	0.185	LT	-3.22	0.07	0.546
HW	-8.33	-0.05	0.199	EP	-3.42	0.00	0.687
FD	-8.65	-0.08	0.250	PW	-3.43	-0.01	0.697
MS	-8.67	-0.02	0.253	FD	-3.54	-0.01	0.847
Picea	-9.25	-0.08	0.393	BL	-3.57	-0.00	0.901
FG	-9.87	0.08	0.736	CW	-3.57	0.01	0.918
PW	-9.92	0.01	0.803	HW	-3.58	-0.00	0.943
CW	-9.95	-0.02	0.855	Global	-11.50	-0.00	0.771

Table 3.16: Plot cover summary table representing average tree-species shrub- and recruit-stage cover on plots with greater than 15% black locust (*Robinia pseudoacacia* L.) tree-stage cover, visually estimated on 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. Plots were filtered to those with greater than 15% black locust tree-stage cover (column "Plots w/ BL.Tr cover > 15%") and tree-species shrub and recruit cover was summarized on these plots. Column "Plots w/ BL.Tr cover > 15%" represents the total plots with both > 15% black locust tree-stage cover and a given tree species' shrubs or recruits present (species given in column "Tree Species Shrub or Recruit "). Column "Avg. Nat.Sh Cov. w/ BL" represents average native shrub cover on plots with greater than 15% black locust tree-stage cover. Column "Avg. Nat.Sh Cov. w/o BL" represents average native shrub cover on plots with less than 15% black locust tree-stage cover. The subsequent two columns list average native species recruit over on plots with and without greater than 15% black locust tree-stage cover. Black locust was included as a "native tree" to indicate its own shrub and recruit cover on plots with greater than 15% and less than 15% tree-stage cover: this indicates its ability to recruit in its own understory.

Tree Species Shrub or Recruit	Plots w/ BL.Tr cover ≥ 15%	Plots w/ BL.Tr cover < 15%	Avg. BL.Tr Cover	Avg. Nat.Sh Cov. w/ BL	Avg. Nat.Sh Cov. w/o BL	Avg. Nat.Rc Cov. w/ BL	Avg. Nat.Rc Cov. w/o BL
ACT	5	20	34.00	0.20	3.80	3.40	0.65
BL	24	65	30.90	18.60	9.90	2.97	1.71
AT	8	43	36.80	1.70	3.10	2.19	2.67
PW	9	48	25.60	3.10	3.40	1.42	0.87
MS	3	5	55.00	0.00	19.40	1.12	0.44
FD	3	22	17.70	0.80	1.20	0.67	0.27
EP	18	84	28.30	4.20	8.00	0.56	0.78
CW	1	3	30.00	0.00	3.00	0.50	0.37
Picea	1	9	15.00	3.00	2.30	0.00	0.10
HW	0	5	NaN	NaN	4.00	NaN	0.15
LT	0	2	NaN	NaN	2.50	NaN	1.02
YP	0	7	NaN	NaN	0.10	NaN	0.30

Table 3.17: Model ranking table of single-variable GLMMs representing tree-species shrub (Sh) and recruit (Rc) cover modelled as a response to black locust (*Robinia pseudoacacia* L.) tree cover visually estimated on 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. "Sh_Response" and "Rc_Response" columns represent the native tree shrub or recruit cover variable black locust tree cover was modelled as a predictor variable for. "Coef" and "P" columns represent the correlation coefficient and P value for the native tree-species shrub or recruit cover specified in the "Response" column black locust tree cover was modelled as a predictor variable for.

Sh_Response	Sh.Coef	Sh.P	Rc_Response	Rc.Coef	Rc.P
BL	0.02	0.000	ACT	0.03	0.020
MS	-0.03	0.010	FG	0.24	0.020
EP	-0.01	0.040	YP	-0.12	0.240
ACT	-0.02	0.240	EP	-0.01	0.290
CW	-0.03	0.260	CW	0.02	0.350
AT	-0.02	0.330	PW	0.01	0.370
FD	-0.01	0.350	Picea	0.04	0.610
LT	-0.14	0.460	FD	0.01	0.690
HW	-0.02	0.630	MS	0.00	0.900
Picea	-0.01	0.640	BL	0.00	0.900
PW	0.00	0.640	AT	0.00	0.950
Fir.spp	-0.05	0.770	HW	0.00	NA
Pine.spp	0.01	0.800	LT	-0.74	NA
FG	-0.25	NA	Fir.spp	0.00	NA
YP	0.00	NA	Pine.spp	-1.29	NA

Figures

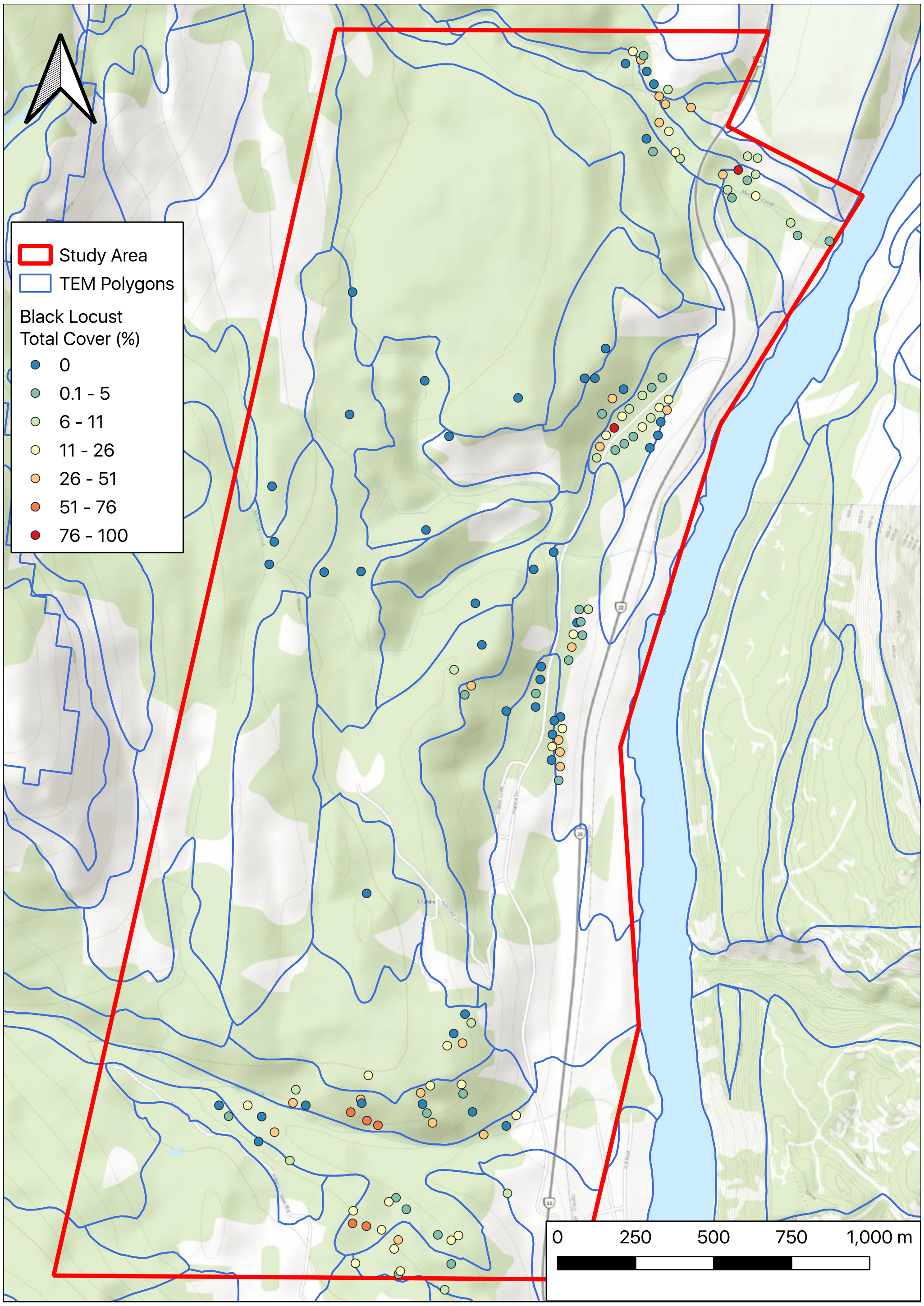


Figure 3.1: Black locust (*Robinia pseudoacacia* L.) total cover (%) visually estimated on 151 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022.

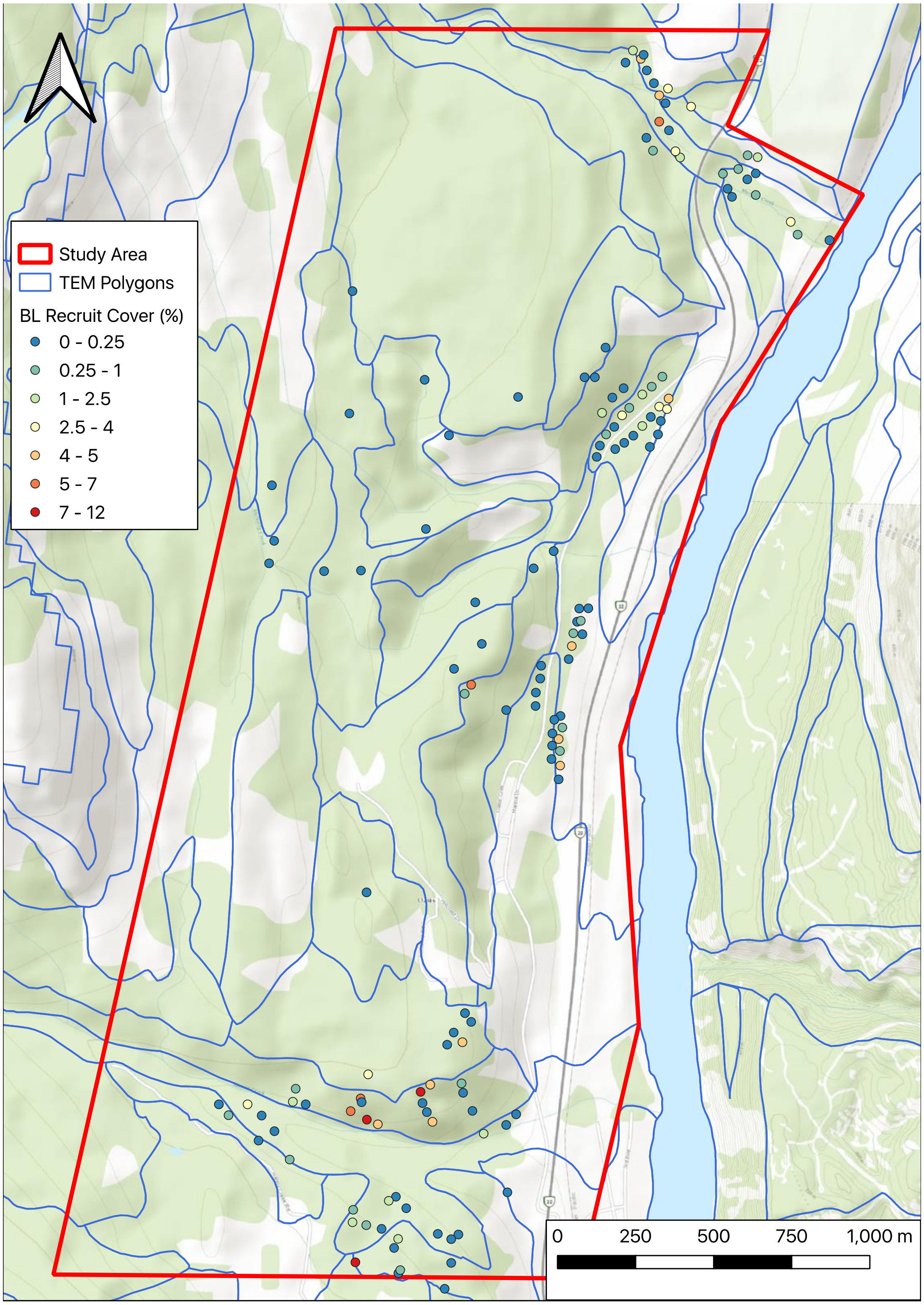


Figure 3.2: Black locust (Robinia pseudoacacia L.) recruit cover (%) visually estimated on 151 400 m2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022.

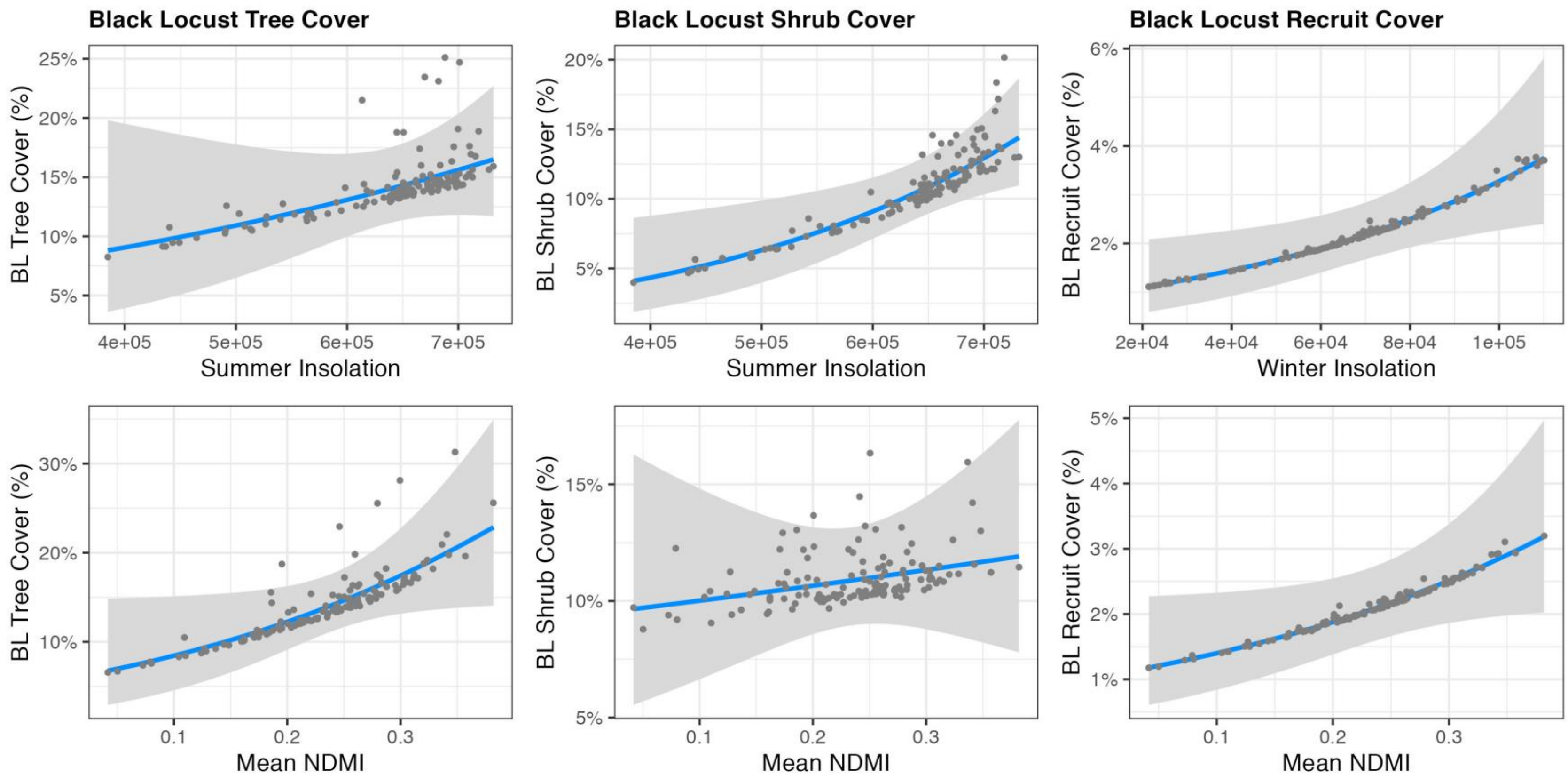


Figure 3.3: Black locust (*Robinia pseudoacacia* L.) tree, shrub, and recruit cover responses to total summer insolation (tree and shrub cover) and total winter insolation (recruit cover) and mean NDMI. Dots show model residuals, not data points. Black locust cover was visually estimated on 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. Summer Insolation represents total May 1 to September 1 2022 insolation, and Winter Insolation represents total November 1 2021 to February 1 2022 insolation, calculated at plot centers using a 1 m^2 DEM. NDMI Mean represents mean July 2021 and July to September 2022 Normalized Difference Moisture Index (NDMI) values at plot centers calculated from eight 20 m^2 multi-band images.

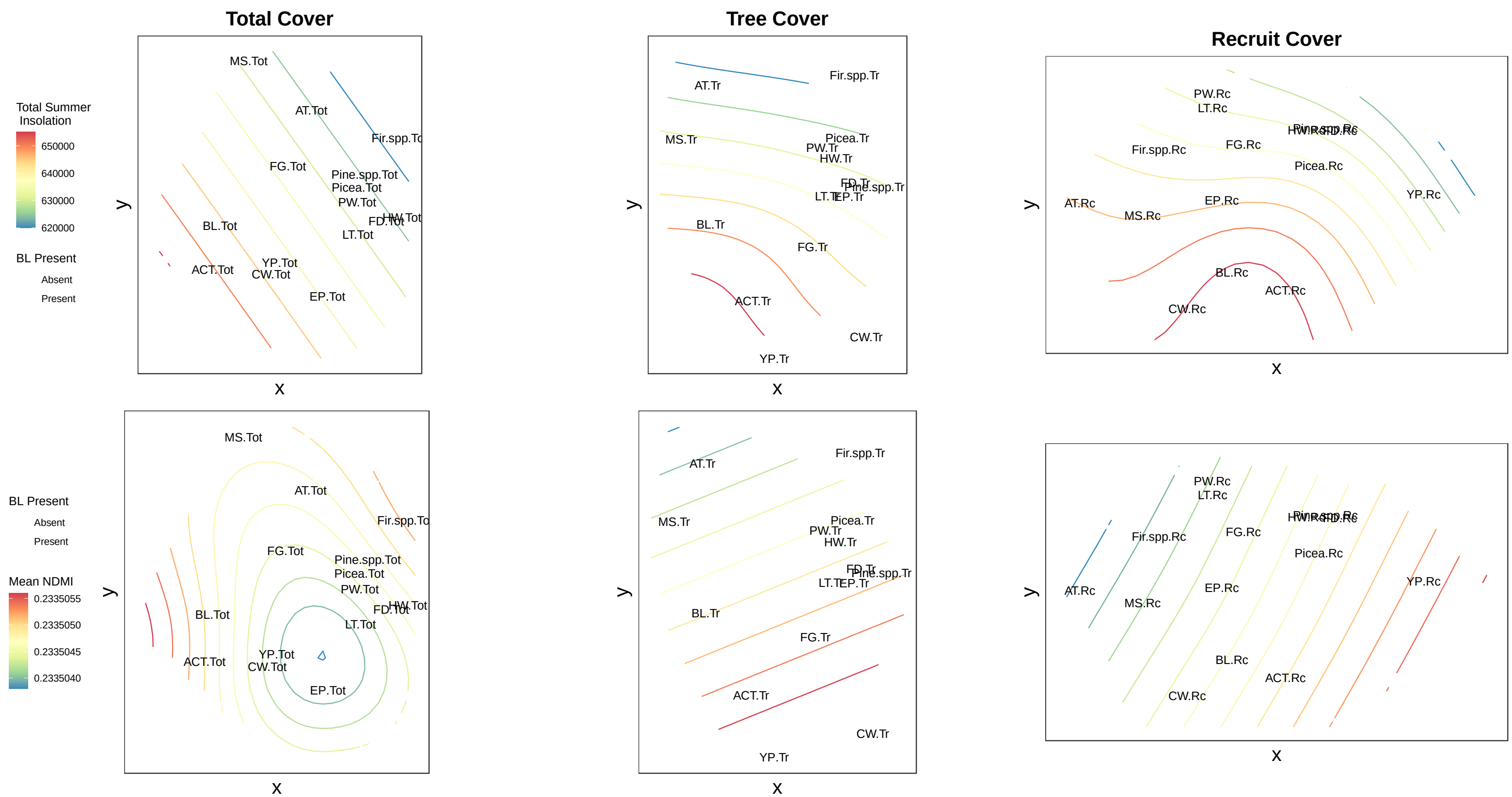


Figure 3.4: NDMS on black locust (*Robinia pseudoacacia* L.) and native tree-species total-, tree-, and recruit-stage cover, plotted over contours representing observed total summer insolation (upper row) and mean Normalized Difference in Moisture Index (NDMI) (bottom row) on plots. Red polygons represent individual plots (locations calculated on plots but not shown on graph) where black locust was present, and blue polygons represent plots where black locust was absent. Tree species cover was visually estimated on 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. Summer Insolation represents total May 1 to September 1 2022 insolation, and Winter Insolation represents total November 1 2021 to February 1 2022 insolation, calculated at plot centers using a 1 m^2 DEM. NDMI Mean represents mean July 2021 and July to September 2022 Normalized Difference Moisture Index (NDMI) values at plot centers calculated from eight 20 m^2 multi-band images.

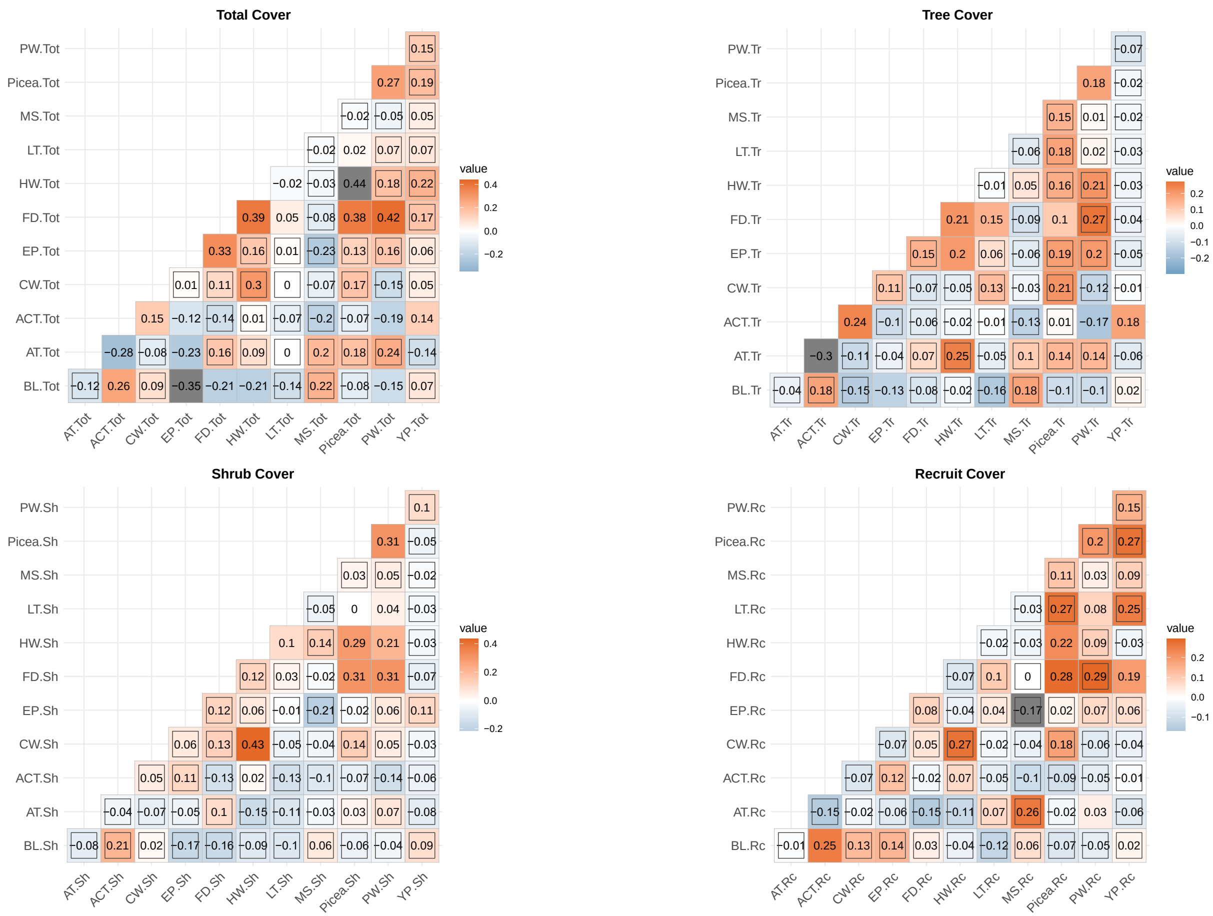


Figure 3.5: Spearman correlation coefficients and significance boxes calculated for black locust (*Robinia pseudoacacia* L.) and native tree-species total-, tree-, shrub-, and recruit-stage stage cover visually estimated on 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022.. Box colour and value represents strength and sign of correlation coefficient. Plots *without* boxes have significant correlations with $p < 0.05$.

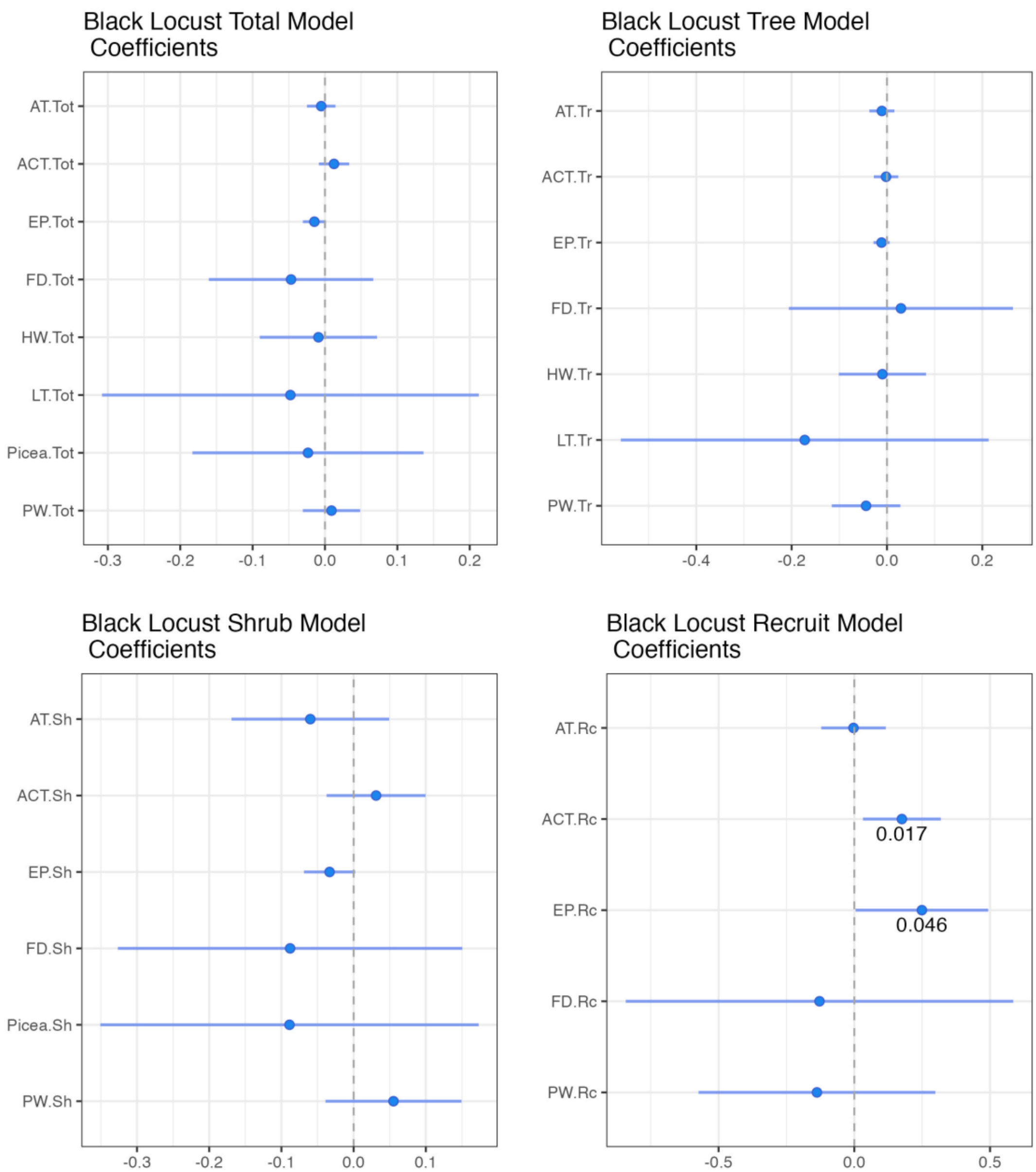
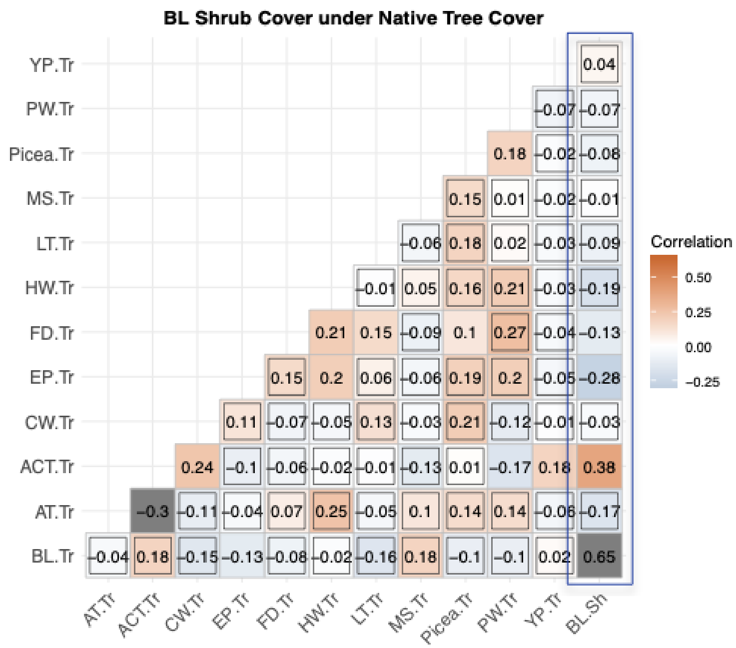


Figure 3.6: Coefficients, standard error, and significance values (labelled) for multi-variable GLMMS modelling black locust (*Robinia pseudoacacia* L.) total-, tree-, shrub-, and recruit-stage cover as a response to native tree-species total-, tree-, shrub-, and recruit-stage cover visually estimated on 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. Dots represent correlation coefficients for black locust cover (response variable) and tree-species predictor variables in the multi-variable models. Bars represent standard error. Significant correlations are labelled.



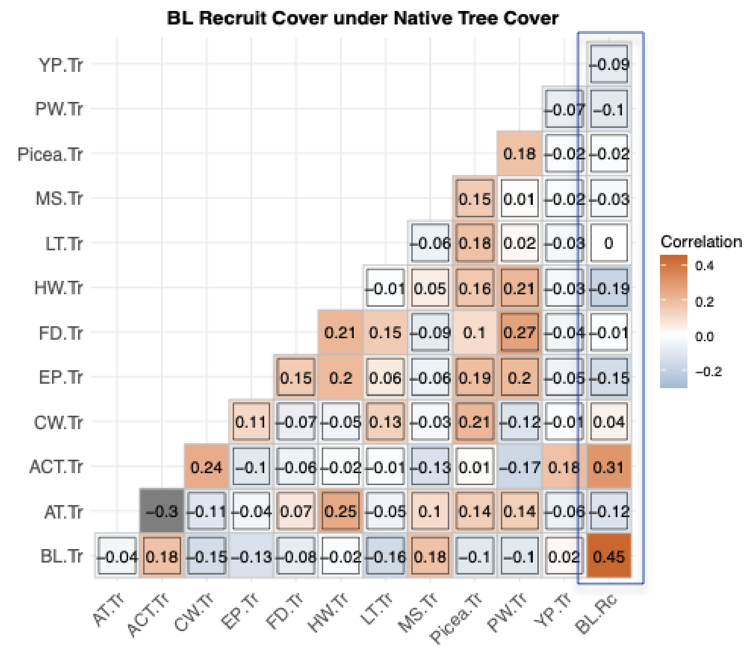


Figure 3.7: Spearman correlation coefficients and significance boxes calculated for black locust (*Robinia pseudoacacia* L.) shrub and recruit cover and native tree-species tree cover visually estimated on 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. Box colour and value represents strength and sign of correlation coefficient. Plots *without* boxes have significant correlations with $p < 0.05$.

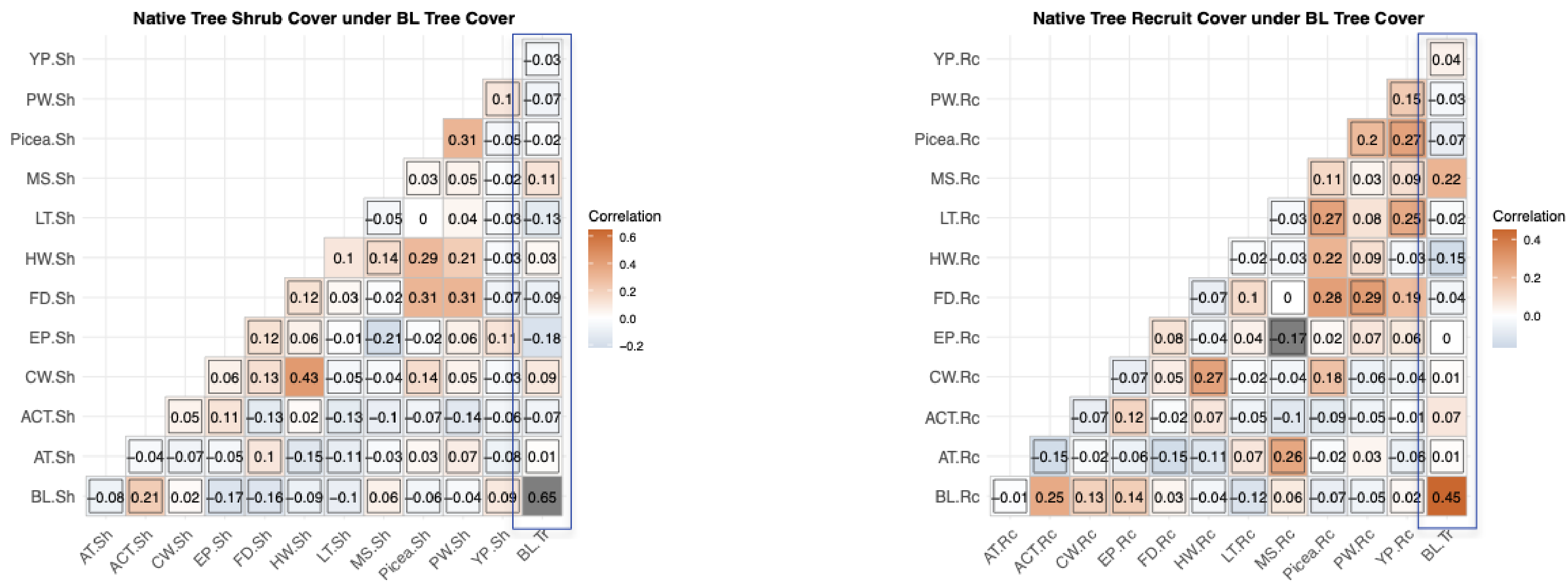


Figure 3.8: Spearman correlation coefficients and significance boxes calculated for native tree-species shrub and recruit cover and black locust (*Robinia pseudoacacia* L.) tree cover visually estimated on 400 m^2 (11.28 m radius) plots deployed in a 600 ha study area north of Trail BC from July to September 2022. Box colour and value represents strength and sign of correlation coefficient. Plots *without* boxes have significant correlations with $p < 0.05$.

Figure 3.7

4. Discussion

4.1. Aerial Image Validation

Following Goal 1 and Objective 1.1, I compared the presence of black locust identified on aerial imagery to the true presence and absence of black locust in ground plots to assess the effectiveness of aerial imagery as a tool for visually identifying black locust stands. Aerial imagery was helpful at identifying locations where black locust trees were present on plots (61% true positive rate) and locations where black locust trees were absent on plots (98% true negative rate), but often supported mistaken identification of locations where black locust appeared to be absent in imagery but were present on plots (38% false negative rate). The false positive rate for black locust identification was low (3%) – this may have reflected my own bias towards only positively identifying black locust in aerial imagery on plots where I was very confident it appeared present. These values represent success and failure rates in manual visual identification of black locust on aerial imagery after I had familiarized myself with black locust's appearance in the imagery while conducting field-work. As is generally true of air photo interpretation, reliability is influenced by surveyor knowledge and experience.

Detection of black locust in aerial imagery differed based on its structural stage and the sites it occurred on. Aerial imagery successfully helped identify flowering black locust trees but did not help identify non-flowering trees and black locust shrubs and recruits. Black locust trees were most easily detectable on low to moderate slopes in mesic to moist forested sites. Black locust in moist forests often grew alongside black cottonwood: this tree species was often mistaken for black locust even when no black locust was present on sites. This resulted in a greater opportunity for false positive detection errors on moist sites. Black locust on open slopes should have been easy to detect due to the absence of overstory tree canopy cover. Unfortunately, the temperature extremes and low moisture conditions experienced by many exposed slopes often arrested black locust development in shrub and stunted tree forms, preventing the formation of dense crowns and the white flowers used to identify black locust. Black locust shrubs on open sites were not possible to detect on imagery even when densely present on plots. Black locust shrubs and recruits growing under forest canopy cover were also not possible to detect through overstory tree canopies.

Because black locust shrubs and recruits were not visible on aerial imagery, no indication of propagule pressure and the density of new invasions is indicated around flowering black locust trees visible on aerial imagery. As discussed later, aerial imagery can be combined with other field and desktop surveys to assess possible invasion densities around visible black locust trees.

Errors in identifying black locust on aerial imagery were introduced by the presence of other deciduous tree species, especially black cottonwood and trembling aspen, and by other flowering shrubs including red elderberry (*Sambucus rascemosa*), that looked like flowering black locust. Wind during aerial image collection exposed the undersides of black cottonwood and trembling aspen leaves, causing bright white reflections on imagery that looked like black locust flowers. Tall black cottonwood trees over 20 metres have unique crown shapes very different from black locust, but short cottonwood have not established their wide, branching crowns and were hardest to tell apart from black locust. Shadows cast in the morning when the aerial imagery was taken also obscured large areas of steep west facing slopes.

Following Objective 1.2 I identified strategies to improve the collection of aerial imagery to improve the visual identification of black locust stands. Suggested modifications to the aerial imagery sampling protocol are listed as follows. First, I recommend conducting drone flights on very calm days when black cottonwood leaves will not be disturbed and reflect white and silver in the imagery, mimicking black locust flowers. Second, I recommend considering adding LIDAR or overlapping visual coverage of transects to create stereoscopic 3D images capable of differentiating tall tree canopy crowns from lower vegetation canopies. Third, I recommend stratifying black locust study areas and sampling based on probable flowering periods: for example, sampling lower elevations and south facing slopes separate from higher elevations and north facing slopes. Fourth, I recommend flying as close to solar noon as possible, when shadows cast by overstory trees have the smallest surface area and are least obstructive to viewing and identifying lower-canopy vegetation in UAV images. Of all these suggestions flying on a calm day will be the most important to improving image identification in the future to avoid mistaking black cottonwood and trembling aspen leaf undersides for black locust flowers.

Following Objective 1.3, I identified black locust structural stages not visible on aerial imagery and suggest strategies below for identifying areas at high and low risk of new invasions using aerial imagery, GIS data and field data. Non-flowering black locust trees and black locust shrubs and recruits were not visible on aerial imagery. Black locust associations with abiotic conditions and native vegetation species can be used to identify sites with a high likelihood of black locust presence. Black locust shrubs and recruits were associated with increasing insolation and increasing moisture availability (represented by NDMI) in areas without prolonged soil saturation and often occurred under black cottonwood, paper birch, and trembling aspen overstories and moderate deciduous shrub cover on warm slopes with moderate to high insolation. Black locust shrubs and recruits were also associated with canopy gaps and soil disturbance on active and legacy anthropogenic features including trails, roads, logged areas, and rural developments. Natural and anthropogenic features capable of supporting high densities of black locust recruits and shrubs can be identified using aerial imagery, GIS datasets, and field data. The presence of anthropogenic and natural features associated with recruit and shrub colonization near black locust trees visible on aerial imagery may indicate locations subject to high densities of invading recruits and shrubs, while the absence of these features may indicate areas where black locust invasions are more contained to visible trees.

4.2. Abiotic Conditions and Vegetation Species Associations

4.2.1. Black Locust Mapping

Following Objective 2.1, I mapped black locust cover within the study area using ground sampling plots to identify natural and anthropogenic features associated with black locust colonization. Black locust was distributed throughout the study area in a north-south pattern along Highway 22 and a parallel rural road (Hanna Road) and had colonized surrounding native forests along active and legacy anthropogenic disturbances and natural features. Black locust was present on active and legacy anthropogenic disturbances including trails, roads, utility corridors, and rural and residential areas along the eastern and south-western sides of the study area and on logging camps and rural areas in the south-central part of the study area. Mature black locust stands were present 500 to 1000 m upstream of road crossings on two of the three creeks in the study area – Murphy Creek to the north, and Hanna Creek to the south. The central creek, McNally Creek did not have black locust present on it upstream of its junction with Hanna Road. McNally Creek is about half the width of Murphy Creek and Hanna Creek, and its smaller and narrower profile limits floodplain width and the region of increased airborne and soil moisture availability along its banks. A steep south hillside parallel to McNally Creek also shades the stream's banks, decreasing suitability for black locust in the moist region beside the creek. Black locust was present on narrow warm-aspect gullies and mass-wasting channels leading up glaciofluvial slopes from rivers to plateau tops and from low terraces to high terraces. Mature and young black locust stands were also present on open mid-slopes around plateau edges – these dry to submesic stands were usually less dense than stands on valley bottoms and black locust occurred most densely in microsites with increased moisture availability. Black locust recruits and shrubs rarely colonized mature paper birch and trembling aspen forests in plateau interiors even when established stands were present on nearby plateau edges. Black locust were present on open warm aspects at the edges of these stands. Black locust recruits and shrubs were present in the understories of moderate-density deciduous and mixedwood forests on warm aspects with mesic to moist soils, especially on sites that received surface and ground water runoff. On these sites, black locust recruits and shrubs appeared to have colonized most densely and matured into trees most successfully in areas with soil and vegetation disturbances and in areas where natural canopy gaps caused by maturing and decaying overstory trees provided increased understory light availability.

4.2.2. Abiotic Conditions

Following Objective 2.2, I characterized black locust tree, shrub, and recruit cover associations with abiotic conditions in the study area using correlation analysis, multi-variable models, and field observations. Models and correlation coefficients indicated black locust tree, shrub, and recruit cover increased with increasing insolation and NDMI. Summer insolation was the best supported predictor for black locust tree and shrub cover, and winter insolation was the best supported predictor for black locust recruit cover, possibly indicating black locust vulnerability to cold temperatures at the youngest stages of growth. Black locust tree cover appeared to increase more with increasing NDMI than did black locust shrub and recruit cover.

I was not able to consider all factors that affect black locust colonization due to data limitations. I used the remote-sensed variables insolation and NDMI to represent abiotic variables of interest in my study area, including light availability, temperature, and moisture availability. I used insolation (total incoming solar radiation per unit area over a given time period) to represent light availability and temperature on plots. Insolation accounts for the effect of topographic exposure and shadows as well as sun movement and height throughout the season. It does not account for tree canopy or shrub canopy cover. I visually estimated tree and shrub canopy cover on plots to account for vegetation shading, but vegetation outside plot boundaries often shaded vegetation on plots. Insolation also provides an indication of temperature, but this can be confused due to slope position. South- and west-facing slopes are warmer than north- and east-facing slopes, but sheltered (low insolation) slope positions may be warmer in cooler months than exposed high-insolation slope positions that experience both higher high temperatures in summers and lower low temperatures in winters. I used NDMI to represent soil and vegetation moisture content. Input Sentinel-2 dataset resolution was raster cells of 20 m per side 400 m^2 area, equal to the area of my vegetation plots. NDMI represents overall moisture availability in vegetation, exposed soil, or exposed bedrock aggregated across every cell, but it does not represent an actual measure of moisture above, at, or below the plot surface (EOS Data Analytics 2022; USGS n.d.; Ecosystems Working Group et al. 1998). Black locust colonizes high moisture sites but does not colonize sites with permanently saturated soils due to lack of air availability (Nicolescu et al. 2020). Black locust cover increased with increasing NDMI but would not have continued increasing at the highest NDMI values on permanently saturated sites. Insolation and NDMI are representative of plot conditions relative to each other but not of absolute light, temperature, or moisture values on plots.

Field observations in the study area showed black locust has colonized (1) deciduous and mixedwood forest understories on warm aspects with submesic to moist soils, (2) canopy gaps and soil disturbances on forested sites with cool aspects, and (3) moisture-receiving sites including slope breaks and gullies in open areas and the understories of moderate-density forests with warm aspects and dry to mesic soils. The most important abiotic conditions limiting and encouraging black locust colonization varied based on dominant abiotic conditions on sites. On open sites with gentle slopes, warm aspects, moderate insolation, and dry to mesic soils, black locust cover increased with increasing moisture availability – especially along creek edges, slope breaks, gullies, and surface and sub-surface seeps. On open sites with steep slopes, warm aspects, high insolation, and dry soils, black locust cover increased in areas where topographic influences increased moisture availability relative to surrounding dry forests – especially in gullies and areas with surface and subsurface water flow. On forested sites with cool aspects, low insolation, and mesic to moist soils, black locust cover increased (1) under canopy gaps created by natural and anthropogenic disturbances and decaying overstory tree cover, (2) on loose soils created by natural mass wasting events, and (3) on legacy and active anthropogenic disturbances including trails, roads, logging, and rural development. On forested sites with warm aspects, high insolation, and mesic to moist soils, black locust occurred in the understories of mature deciduous tree species including paper birch, trembling aspen, and black cottonwood. I did not observe black locust colonizing intact (rather than disturbed) densely forested sites with cool aspects and low light availability, regardless of soil moisture availability. I also did not observe black locust colonizing open or moderately forested sites with high insolation and very dry soils, regardless light availability.

Field observations showed black locust trees grew taller and healthier on moist sites than on dry sites, and shrubs and trees colonizing dry sites grew in stunted and unhealthy forms with limb dieback and root-crown resprouting. Black locust trees grew tallest (greater than 20 meters) on lowland moist sites with warm aspects and grew more stunted on higher slope positions with greater exposure. On steep slopes with south and west aspects, high insolation, low canopy cover, and thin soils, black locust appeared able to persist long-term as shrubs and short trees (less than 15 meters in height) with multiple living and dead limbs emerging from single root crowns and thin canopy cover. These stunted black locust stands most often occurred on sites with poor slope stability, natural mass wasting disturbances, and thin soils and leaf litter with scattered grasses and herbs. These observations indicate black locust often established at its upper tolerance to heat and cold exposure and its lower tolerance to moisture availability in the study area. Exposure-stressed black locust shrubs and short trees likely experience high heat stress and low moisture stress during summers and wind-driven cold stress, low moisture stress, and sun-scald during winters. Native tree-species shrubs and recruits were rarely observed alongside exposure-stressed open stands of black locust shrubs and short trees, even when grass and herb species cover was low and canopy cover was open. Low tree species recruit and shrub cover may be caused by black locust modifying site conditions to discourage native species recruitment (discussed later), or may be a result of black locust possessing similar or greater tolerances to exposure stress than native tree species. This capacity to grow as shrubs and short trees on exposure stressed sites with thin and unstable soils re-enforces black locust's original use for revegetating exposed slopes where soil depth and soil organic matter had been lost to logging, fires, wind and water erosion, and smelter emissions.

Black locust was associated with disturbances to soils and vegetation cover in the study area. Black locust vigorously resprouts from its stem and roots following fire, herbicide application, and mechanical thinning and clearing (Stone 2009). I considered modelling black locust cover as a response to different types and intensities of natural and anthropogenic disturbances; however, ranking the different disturbance types in the study area along one common quantitative axis was too ambiguous without physically investigating the abiotic and vegetation impacts associated with each disturbed site. Instead of recording disturbances for modelling, I constrained plot locations to only outside the footprints of active disturbances (including power line and natural gas corridors, road edges, and trails) to minimize the confounding influence of active disturbances on black locust cover. While I sampled plots only adjacent to active disturbances I did sample plots on the footprints of legacy disturbances, including rural areas and roads.

Soil structure and soil nutrients also influence black locust colonization success on sites (Nicolescu et al. 2020). Black locust preferentially colonizes loose and aerated soils over compact soils (Nicolescu et al. 2020) and appears to have greater competitive ability and colonization success in low-nutrient soils than high-nutrient soils (Stone 2009). As soil structure and soil nutrients are both known to influence black locust colonization success, they should be considered in future studies of black locust in the Lower Columbia Valley.

Although not shown in modeling, I recorded percent covers of eroded surfaces and bare soil on plots. Two confounding factors meant I was not able to use soil surface data in modelling. First, regarding erosion, black locust stabilizes sites as it matures and reduces erosion by connecting sites with its root-mass, intercepting eroded material with its stem and leaf mass, and reducing erodible material by depositing leaf litter on the soil surface. Sites with higher black locust tree, shrub, and recruit cover had less eroded surface area than sites with lower black locust cover, even if black locust had established on loose and eroded surfaces. Likewise, regarding bare soil patches not due to erosion, black locust deposits leaf litter as trees mature. Sites with high black locust cover had less bare soil than sites with low black locust cover even if black locust had established on bare soil. Black locust influence on sites made it difficult to infer soil conditions at the time of its establishment from conditions observed during field studies. Field observations showed black locust short trees, shrubs, and recruits colonizing open slopes with recent mass wasting events, revegetated gullies with evidence of historic mass wasting events, and loose soils at the edges of trails and roads. These observations are supported by literature indicating black locust seeds germinate best on bare soil (Stone 2009; Vitková et al. 2015), soil disturbances break seed dormancy and increase germination (Morimoto et al. 2010), and loose and eroded soils allow establishment from clonal rhizomes (Stone 2009; Vitková et al. 2015).

Natural and anthropogenic disturbances assisted black locust colonizing otherwise less-suitable light, temperature, and moisture conditions in the study area. I observed black locust colonizing coniferous and mixedwood forests on cool aspects with low insolation where trails and historic rural activities had disturbed soils and opened canopy gaps. Natural and anthropogenic disturbances and canopy gaps appeared more important for black locust colonization on cool aspects than on warm aspects. Black locust colonization in forests with cool aspects was often constrained to the footprints and edges of legacy disturbances and was not present in surrounding intact shaded forests. This was true even when mature black locust trees growing on disturbance features indicated there have been many years of propagule pressure exerted into surrounding uninvaded areas. Black locust colonization in forests on warm aspects with mesic to moist soils was not constrained to disturbance footprints: on sites with adequate moisture availability, black locust on disturbance footprints was often surrounded by recruit and shrub invasions into intact native forests especially when these forests were naturally open or thinning due to stand age. Very dry and warm sites including ponderosa pine forests, and very cool and shaded sites including coniferous forests on north and east facing slopes, were infrequently colonized even when disturbed.

4.2.3. Vegetation Structure

Following Objective 2.3, I characterized the structural characteristics of native vegetation communities associated with black locust stands of different structural stages using correlation analysis, multi-variable models, and field observations. In correlation and modelling analysis, black locust shrub and recruit cover were positively correlated with grass cover and negatively correlated with native tree canopy cover, especially coniferous tree cover. Black locust shrub cover was positively correlated with shrub-species cover but negatively correlated with tree-species shrub-stage cover. This may indicate black locust are able to grow in disturbed or exposed sites where few other native tree-species are able to survive, likely due to their ability to access deep water tables with vertical roots (Stone 2009). Soil acidification, nitrogen supplementation, and allelopathy from leaf litter deposition and root exudates may allow black locust to outcompete and displace native tree species at early seral stages; however, competitive displacement is more likely caused by black locust's ability to form dense clonal shrub stands capable of shading-out and physically occupying above- and below-ground space other early-seral tree species would occupy during their recruit and shrub stages (Nicolescu et al. 2020). In contrast, black locust recruit cover was positively correlated with both native tree species shrub-layer cover and native shrub species cover. Field observations showed black locust recruits colonizing native deciduous tree and shrub stands on gentle to moderate slopes with warm aspects and submesic to moist soils. On these sites, understory light availability was high due to warm aspects, yet shelter provided by tree- and shrub-layer overstories reduced temperature extremes and increased soil moisture retention. Well-lit, low to moderate-density deciduous tree and shrub stands with decreased temperature and drought stress due to shelter from overstory tree and shrub cover appeared ideally suitable for black locust colonization and maturation.

Black locust colonization under native tree and shrub canopies was lower on north or east facing slopes and enclosed topography than on south and west facing slopes and exposed topography where soil moisture was also available. Deciduous tree and shrub stands were invaded by black locust recruits more commonly on submesic to moist sites than on either very dry and exposed sites (south and west facing slopes with very little ground cover) or on depressions with permanently saturated soils. Black locust recruit cover reached its maximum value between 15 to 35 percent native tree canopy cover. Because black locust recruits occurred under coniferous tree species less frequently than under deciduous tree species dominant coniferous stands were encountered less often and sampled less frequently than dominant deciduous stands when searching for black locust. This means there is not enough plot data to accurately compare black locust colonization under deciduous tree species to black locust colonization under coniferous tree species. During field surveys I frequently observed mature coniferous stands uninvaded by black locust near deciduous and mixedwood or disturbed plots with mature black locust trees present. I also sampled a small number of plots on coniferous stands that remained uninvaded despite being located near mature black locust stands. The proximity of mature black locust stands with high propagule dispersal ability to uninvaded mature coniferous forests indicates low recruitment in coniferous forests. This may be due to coniferous shade cover decreasing black locust recruitment from seeds and roots, or due to underlying abiotic conditions including light, temperature, moisture, and nutrient availability. In contrast to deciduous and mixedwood forests on warm submesic to moist sites which were commonly associated with black locust stands, mature coniferous forests often occurred on sites that appeared either too cool or too dry for successful black locust colonization. Cool and moist forests with north and east aspects were represented by larch, spruce species, true fir species, and western hemlock, while warm and dry sites with gentle south and west or flat aspects were represented by Douglas-fir, Ponderosa pine, and Lodgepole pine.

The positive relationship of black locust shrub and short tree cover with grass cover matches observations of arrested succession in black locust's native and introduced ranges. Arrested succession occurs when black locust prevents the succession of otherwise suitable early seral sites to forested conditions when it fails to mature into tree height individuals due to disease or stress and persists in shortened shrub and short-tree structural stages (Groninger et al. 2007). Black locust enriches soils with nitrogen from root exudates and leaf litter (Von Holle et al. 2006). When black locust – especially on exposed or disturbed and reclaimed sites – fails to mature into trees, it continues enriching soils with nitrogen without creating suitable shade and moisture conditions for the establishment and maturation of mid-and later-seral tree and shrub species. Nitrogen enrichment on sites with exposed conditions can support the dense colonization and long-term persistence of grass and herb species capable of outcompeting tree species recruitment and preventing the formation of forests (Groninger et al. 2007).

Exposed sites with stunted black locust and increased grass and herb species cover can arrest vegetation community succession at early or disclimax seral stages and prevent the formation of later-seral tree canopies which are capable of outcompeting new black locust recruits and leading to the establishment of mid- or late-seral forests (Groninger et al. 2007). When black locust matures into tree forms it can displace grass and herb species with shade cover and leaf-litter, stabilize and build soils, and create favourable microclimate conditions with low insolation and moderate moisture retention to facilitate native tree species establishment (Groninger et al. 2007). Arrested succession is observed in black locust's native range in the Southeastern United States (Groninger et al. 2007), indicating it can occur even when tree species adapted to establishing and maturing amidst black locust are present.

On open-canopy, high slope, and warm aspect sites with soils loosened by natural mass wasting and anthropogenic disturbances including trails I observed arrested shrub and short tree black locust forms growing intermixed with thin grass and herb cover and low-density native trees and shrubs. Natural tree recruitment on these exposed slopes in the Lower Columbia Valley has historically been low, and even plantings of dry-adapted species including Ponderosa Pine and Douglas-fir have been difficult to establish (Hodson 1971).

On flat to gently sloping sites with moderate aspects and submesic to mesic soils I observed mature black locust trees with large multiple-stemmed crowns establishing shade cover and depositing leaf litter that appeared to displace grass and herb cover. I observed western white pine, trembling aspen, black cottonwood, and introduced silver maple establishing and maturing in the areas under black locust canopies where grass and herb species were displaced. Where black locust canopies had very dense crown closure (greater than 70 percent cover) I observed low grass and herb species cover but I also observed fewer tree- and shrub-species recruits than on more open stands, except at stand edges. Native conifer recruitment in these stands could be diminished by their location in unsuitable areas for shade-tolerant species including western hemlock, modification of abiotic limiting factors by mature black locust especially decreased light and decreased moisture availability from black locust's deep root systems (Vitková et al. 2015), or increased soil nitrogen content and acidity from black locust root exudates and leaf litter decomposition (Vitková et al. 2017).

On warm aspects with mesic to moist soils in valley bottoms and at slope bases, black cottonwood established underneath black locust where surface water runoff and other disturbances removed vegetation cover and exposed mineral soil. Conifers and trembling aspen sometimes established in these areas on higher topography.

4.2.4. Tree and Shrub Species Associations

Following Objective 2.3, I characterized black locust tree, shrub, and recruit cover associations with native tree and shrub species cover using correlation analysis, multi-variable models, and field observations. Black locust tree and shrub cover were associated with Oregon grape cover, a perennial evergreen shrub with low height and the ability to form dense mono-species stands in tree understories and snowberry, a clonal deciduous species with deep roots also capable of forming dense mono-species stands in moderately shaded tree understories. Bitter cherry, beaked hazelnut cover and mock orange cover were often occurred alongside black locust on sites with low or patchy tree cover, warm to neutral aspects, and moderate amounts of surface moisture, including receiving areas at slope bases and mid-slope breaks. Black locust shrub and recruit cover was associated with Douglas maple cover on cool sites and mesic deciduous shrubs including beaked hazelnut, mock orange, and Scouler's willow (*Salix scouleriana*) on warm sites. Dense colony-forming shrubs including snowberry and Oregon grape, and shrubs capable of tolerating extended periods of saturated soils including red-osier dogwood and thimbleberry, are not associated with high levels of black locust recruitment. Black locust appeared capable of establishing in gaps in clonal shrub stands and on slightly raised topography in damp sites with these species.

Black locust cover was correlated with specific tree species' cover. Black locust cover across all structural stages was consistently correlated with black cottonwood cover across all stages. In the field I observed black locust associated with black cottonwood on warm and well-lit sites with submesic to moist soils due to surface water runoff and temporary water accumulation. These included riverbank flood-benches, mid-slope breaks including roads and natural terraces, warm creeks and gullies, mass-wasting channels, and warm upper slopes with good drainage that received runoff from plateau edges. Black locust total cover was negatively correlated with paper birch total cover. In the field, I observed black locust shrubs and recruits on the edges of paper birch stands, but did not observe black locust trees or abundant shrubs and recruits mixed with mature paper birch trees, even when black locust and paper birch grew nearby each other. Black locust total cover was significantly and negatively correlated with Douglas-fir and western hemlock cover. Douglas-fir and black locust distributions likely have minimal overlap because Douglas-fir is capable of maturing into tree-height individuals on dry and warm conditions not normally associated with black locust colonization unless microsites with soil disturbance or increased moisture availability are also present (Banner & Ehman 2016; BC Ministry of Forests n.d.). While Douglas-fir appears capable of maturing on warmer and drier conditions than black locust, black locust appears more capable than Douglas-fir of colonizing exposed slopes with unstable soils, especially due to its ability to persist in arrested shrub and tree forms. Western hemlock appears to grow on sites with similar surface moisture to black locust but on shaded and cool rather than well-lit and warm aspects. I often observed western hemlock and black locust stands growing on opposite sides of gullies and ridgelines at similar elevation contours, with black locust growing on the well-lit and warmer gully or ridge-line side opposite mixed stands of western hemlock, Douglas-fir, true fir species, and spruce species on the cooler side. Black locust shrub cover was negatively correlated with paper birch shrub cover. This was likely because paper birch cover in the shrub layer was more often represented by paper birch stems ending in the shrub layer (2 to 10 m tall) coming from paper birch trees than by independent paper birch shrub-height individuals. Black locust cover was not correlated with either western white pine cover or trembling aspen cover. In the field I observed black locust associated with western white pine and trembling aspen on moderately dry to moderately moist sites with moderate to warm aspects. Black locust recruits and shrubs occasionally grew underneath sparse western white pine stands on sites with subxeric to submesic soils, and commonly grew underneath moderate-density trembling aspen stands on sites with submesic to mesic soils, especially near canopy gaps. Black locust cover health, stem density, and cover tended to be greater under trembling aspen than western white pine. I did not observe black locust associated with either western white pine or trembling aspen on cool aspects and shaded sites.

4.2.5. Black Locust Colonization Under Native Tree Species and Native Tree Species Colonization Under Black Locust

Black Locust Colonization Under Native Tree Species

Following Objective 2.3, I characterized black locust shrub- and recruit-stage cover under native tree-species cover to investigate the ability of black locust to colonize the understories of native tree species stands. I observed black locust frequently colonizing deciduous and mixedwood forests on moderate to warm sites with submesic to moist soils, and colonizing coniferous forests more rarely on cool sites with legacy or active anthropogenic disturbances. I did not observe black locust colonizing undisturbed coniferous stands on either cool and moist or warm and dry conditions. Black locust shrub and recruit cover were positively correlated with black cottonwood tree cover and negatively correlated with paper birch and western hemlock tree cover. I often observed black locust recruits, shrubs, and short trees growing on sites with moist but not saturated soils underneath tall (greater than 20 m) black cottonwood stands showing signs of over-maturation and die-back based on the presence of recent black cottonwood snags. Black locust occurred intermixed with paper birch and trembling aspen trees, shrubs, and recruits more often on warm sites with south and west exposures and submesic to moist soils than on cool sites with north and east exposures and either dry or moist soils. Trembling aspen and paper birch stands colonized by black locust tended to occur on warm sites and consisted most often of young- to moderate-aged trees with low to moderate stem densities and moderate crown cover. In contrast, black locust colonized mature black cottonwood stands in almost all sites without permanently saturated soil – it often colonized overmature black cottonwood stands that had begun dying back. It is unclear why paper birch cover was negatively associated with black locust cover across structural stages – both species are associated with open, early seral, and well-lit sites with moderate soil moisture. Paper birch is frost-tolerant, whereas black locust, coming from a native range further south, has lower frost tolerance (BC Ministry of Forests n.d.). Western white pine was not significantly associated with black locust in correlation analysis or GLMMs.

I observed black locust colonising western white pine stands in open areas nearby anthropogenic disturbances. Invaded western white pine stands were often open with low crown cover (rarely greater than 20%) consisting of large trees. Mature western white pine stands with moderate to dense canopy cover occurring near black locust stands were often uninvaded even when temperature and soil moisture conditions appeared similar. Western white pine is associated with fresh to moist soil conditions and tolerates wet sites and inundation well, similar to soil moisture conditions preferred by black locust (BC Ministry of Forests n.d.). Western white pine is less tolerant than interior Douglas fir to cold and dry conditions also avoided by black locust (BC Ministry of Forests n.d.). Despite their requirements for similar abiotic conditions, black locust cover was lower under open western white pine stands than open deciduous stands. This could be caused by greater tolerance of western white pine than black locust for cool temperatures and shaded slopes

(BC Ministry of Forests n.d.), increased shade cover from pine canopies compared to deciduous canopies, or unique physical and chemical soil conditions created by pine needle cover and decomposition. Of all native conifers, western white pine appears to overlap the closest with black locust in terms of temperature and moisture requirements on undisturbed sites (BC Ministry of Forests n.d.). These similar growing conditions and lack of black locust cover under western white pine in field plots suggest it may be a suitable conifer species to cultivate around and contain black locust invasions through shade cover establishment and leaf liter deposition.

Native Tree Species Colonization Under Black Locust

Following Objective 2.3, I characterized native tree-species recruit and shrub cover under black locust tree cover to investigate the ability of native tree species to establish and mature in the understories of established black locust stands. Native tree-species recruit-stage cover under black locust stands was higher than native tree-species shrub-stage cover. As black locust stands matured past the young-seral stage (where competitive exclusion from the initial cohort's canopy cover prevents tree recruitment in the understory) (British Columbia Ministry of Forests and Range & British Columbia Ministry of Environment 2010) they appeared to begin a natural process of canopy thinning and stem dieback allowing some native tree establishment in their understories. This indicates native tree species may have potential to mature underneath and slowly replace black locust stands if disturbances are minimized. Low native tree shrub-stage cover under black locust stands indicated these stands may still have been in the young-seral stage five to ten years ago, when their short height, dense stem densities, and dense crown cover prevented tree recruitment that would have developed into shrub-height trees at the time of this study. I observed black cottonwood, trembling aspen, western white pine establishing and maturing in moderate numbers around and under black locust stands, and paper birch, Douglas-fir, true fir species, and spruce species establishing and maturing in lower numbers. If disturbances that would encourage renewed black locust establishment are minimized black locust stands may continue opening up as stems mature and decay, allowing native tree species suited to underlying abiotic conditions on sites to establish in their understories and replace stands over time.

Deciduous establishment under black locust stands was represented on moist sites by black cottonwood recruitment and on slightly cooler or drier sites by trembling aspen recruitment. Black cottonwood established abundantly underneath black locust trees in canopy gaps where mass wasting or water had exposed mineral soil. Trembling aspen established abundantly under black locust trees when mature aspen trees were present nearby. On most plots with both black locust trees and trembling aspen recruits, I observed greater cover for trembling aspen recruits than black locust recruits in the immediate understories of black locust trees. The recruitment strategies for these two clonal trees are different: black locust recruits tended to colonize trembling aspen stands in discrete clumps, often under canopy gaps, with few numbers of recruits and short shrubs with large cover per individual plant. In contrast, trembling aspen tended to colonize black locust in "nets" of very narrow recruits dispersed evenly throughout black locust stands, presumably following underground trembling aspen clonal rhizomes. On some 400 m^2 plots with black locust overstories exceeding 30% cover, 50 to 150 trembling aspen were observed – dwarfing the number of black locust recruits, even though black locust recruits had greater cover area per plant than trembling aspen.

The pattern observed across the Lower Columbia Valley vegetation plots of alternating stands of mature trembling aspen colonized by juvenile black locust and stands of mature black locust colonized by juvenile trembling aspen resembles the "shifting mosaic" pattern of tree and shrub species succession observed in some forests. The shifting mosaic pattern occurs where different early- and mid-seral tree and shrub species alternate presence on sites with similar underlying abiotic conditions due to the influence of heterogeneous natural disturbances and community succession (Spies & Turner 1999). As a tree or shrub species colonizes disturbed sites and matures, it can create conditions for mid- and later-seral tree or shrub species to thrive in its understory, which may replace it as sites mature. Over time – or on adjacent sites at different seral stages – these mid to later-seral species may be displaced by "earlier" seral species following aging and disturbances, leading to a mosaic of sites shifting locations over time where the same sets of species may be playing both apparent early and later-seral roles (Spies & Turner 1999; Clark 1996). Stochastic disturbances moving across the landscape at different scales (fires, windthrow, insects) further accentuate this patchy distribution changing over time (Spies & Turner 1999; Clark 1996). Trembling aspen, black cottonwood, and western white pine appear to be beginning a shifting mosaic successional pattern with black locust on sites with suitable temperature, light, moisture, and soils for these species.

Coniferous establishment under black locust stands on submesic to moist conditions was best represented by western white pine and to a lesser extent Douglas fir. I observed abundant western white pine recruit and shrub cover occurring under moderately dense (40 to 70 percent) black locust canopy cover on submesic to mesic sites where gaps between black locust tree crowns and clearings at stand edges provided increased understory light availability relative to closed-canopy stands. Black locust stands with abundant western white pine recruitment were predominantly even aged and relatively short for the tree height class (less than 15 meters). Most of these black locust stands appeared to have established in single cohorts following fire and logging on sites with high exposure stress caused by warm aspects and thin, dry soils. These harsh conditions may have prevented black locust stands from achieving greater heights, stem densities, and canopy cover at maturation. On these sites, I observed coniferous (western white pine) and deciduous (trembling aspen, black cottonwood, and silver maple) tree-species recruits and shrubs maturing directly under black locust canopy cover (surrounded by black locust leaf litter) where dominant grass cover farther away from black locust stems had been displaced – apparently by shade cover and leaf litter deposition. I observed Douglas-fir recruiting under black locust, but this species appeared to be rare throughout the study area. Low Douglas-fir recruit and shrub cover under black locust stands may reflect low propagule availability and dispersal as much as the presence or absence of suitable conditions for its recruitment under black locust trees.

Coniferous tree-species shrubs and recruits did not grow as abundantly under mature black locust on moist sites and sites shaded by fully closed canopy cover under even-aged black locust stands. Western white pine under closed black locust canopies often failed to mature past the recruit or shrub stage and appeared to establish best on raised micro-sites in moist areas near gaps in closed-canopy black locust stands created by decaying overstory trees. Based on the low health of black locust trees on dry sites compared to moist sites, the abiotic conditions where black locust overlaps with and supports western white pine establishment and maturation appear near edge of its ideal range and more in the normal boundaries of western white pine's ideal range. Western hemlock did not often occur under black locust stands on warm and moist sites, possibly because it is more suited to cooler moist conditions. Western redcedar is associated with similar temperature and moisture conditions to black cottonwood, the deciduous species that occurred most abundantly alongside black locust on warm and moist sites, (BC Ministry of Forests n.d., n.d.a). Western redcedar was rare throughout the study area, occurring most often as young trees and shrub-height individuals near creeks and river banks. This indicates western redcedar may not yet be recovering from historic logging, fires, and airborne contamination, or it may continue to be affected by hot and dry summers outside of sites with high moisture availability. Low western redcedar recruitment under black locust may reflect poor propagule availability and dispersal as much as the presence or absence of suitable conditions for its establishment.

Black locust was planted in the Lower Columbia Valley to revegetate disturbed sites, stabilize eroded slopes, and enrich soils with nitrogen and organic matter (Hodson 1971). On these sites it may not be capable of maturing into dense enough stands to shelter native tree-species recruits and facilitate further species diversity and structural maturation. I observed low densities of native tree-species recruits and shrubs growing alongside exposure-stressed open stands of black locust shrubs and trees, even when grass and herb species cover was low and canopy cover was open. Low native tree-species recruit and shrub cover was likely caused by exposure stress given the historic difficulty of establishing native species on exposed slopes with low organic matter in the Lower Columbia Valley (Hodson 1971). While allelopathic influences have not been demonstrated by black locust on native vegetation species in its invasive range (Nicolescu et al. 2020) it is possible low native tree species recruitment may be caused by soil nitrogen inputs and soil acidification from black locust root exudates and leaf litter (Nicolescu et al. 2020). Soil nitrogen is an essential plant nutrient and leaf litter decreases thermal stress from soils and increases soil nutrient- and water-holding capacity (Hodson 1971). These changes to soil structure and chemistry normally facilitate the establishment of native tree species underneath maturing black locust stands in both black locust's native and invasive ranges (Nicolescu et al. 2020; Motta et al. 2009; Stone 2009) but they can also increase the cover of grass and herb species capable of outcompeting tree-species recruits and slow or arrest succession on open sites (Groninger et al. 2007). Strategies for establishing native tree and shrub species under aging black locust stands should be explored to maintain slope stability and retain soil organic matter that has built up over the last 80 years.

The long-term succession trajectories of sites colonized by black locust reflect the ability of both black locust and mid-to-late seral tree species to establish and mature in the understory of mature black locust stands. Black locust trees were positively correlated with black locust recruit and shrub cover, occurring near but not under mature trees. In open sites, black locust forms impenetrable thickets of saplings near mature trees that exclude other tree and shrub species and advance black locust invasions (Young & Peffer 2010). In contrast, black locust recruits did not appear to establish as abundantly under black locust tree canopy cover in the absence of soil disturbances and large canopy gaps. This indicates that mature black locust stands, although continuing to exert propagule pressure on adjacent areas, may support declining black locust cover and increasing native tree and shrub species cover as they mature. Native mid and late seral tree and shrub species may continue establishing and maturing around and underneath mature black locust stands if (1) native species propagules exist in nearby forest stands and the soil seedbanks under black locust, (2) biophysical conditions for native species establishment and maturation remain suitable under naturally thinning black locust stands, and (3) disturbances that would stimulate black locust recruitment are minimized both under maturing black locust stands and near less dense black locust trees.

5. Management Recommendations

5.1. Black Locust Abiotic Associations, Invasion Locations, and Vegetation Species Associations

Abiotic Associations and Invasion Locations

Following Objective 3.1, I identified abiotic conditions and landscape features associated with high and low risk of black locust invasions. Black locust has colonized and is continuing to colonize natural and anthropogenic disturbance features in the study area. Increased water availability without prolonged soil saturation, increased light availability, and increased soil disturbance appear critical factors in facilitating black locust invasion. Anthropogenic features and natural features can provide these conditions. Excluding depressions, water availability is highest in the study area adjacent to creeks, in transverse gullies, and on slope breaks paralleling slope contours. Black locust abundance on areas with high moisture was highest where light availability was also high – for example, on open topography creeks, the warm aspect slopes of narrower creeks, and on transverse gullies and parallel slope breaks with warm or open aspects. Black locust was not observed growing abundantly on cool, shaded, and moist areas (for example, narrow gullies on cool slope aspects) and on warm or cool areas with permanently saturated soils. Light availability in the study area is highest on the upper slopes encircling the edges of plateaus and on open disturbed plateau tops – black locust abundance was often higher on comparatively well-lit plateau edges than on either undisturbed plateau centers or on shaded (east and north facing) slopes leading up to plateau edges. Soil disturbance is highest in the study area on active and legacy roads, utility corridors, rural and resource development areas, and on natural mass wasting channels and steep slope sides. Soil disturbance was often associated with canopy disturbance and high light availability, leading to black locust colonization along disturbance footprints in otherwise cool and shaded areas such as north facing slopes.

Features with higher moisture availability, light availability, and soil disturbance than surrounding conditions appeared to behave as linear invasion vectors allowing black locust to access and colonize otherwise undisturbed and isolated natural sites. Black locust distribution was limited to invasion vectors more on cool and shaded slopes whereas it colonised off these features into natural areas on warmer and higher light slopes and lowland open areas. As described in Section 5.2 “Managing Black Locust Invasions”, black locust seed germination and root sprouting on invasion vectors can be reduced by remediating disturbed soils and planting native tree and shrub species to shade sites and cover exposed soils. When black locust is present, planting coniferous tree species and dense thicket-forming shrubs will help slow its establishment and maturation by increasing competition for space, light, and moisture.

Vegetation Species Associations

Following Objective 3.1, I identified native vegetation species associated with high and low risks of black locust invasions. Black locust has established and matured on both open early seral sites as well as the understories of mature deciduous and mixedwood forests in warm and mesic to moist conditions. Early seral sites colonized by black locust included exposed dry slopes with historic and active soil disturbances and scattered moisture-receiving microsites, as well as less steep plateaus, mid-slope benches, and creek valleys with a history of anthropogenic disturbances including logging and rural development and natural disturbances including forest fires. While black locust is described as an exposure-tolerant early-seral species in some literature (Stone 2009; Commonwealth Agricultural Bureau International (CABI) 2019), it appears to be behaving like a partially shade-tolerant mid-seral species on some sites, and has established and matured in the understories of deciduous and mixedwood forests of paper birch, black cottonwood, and trembling aspen. In these forests black locust recruits have also established underneath and alongside moderate density deciduous shrub cover. Black locust has been observed physiologically adapting to and establishing under closed canopy forests in its invasive range (Granata et al. 2020): it is unclear if invasions under native tree canopies will persist and establish as overstory trees mature and die back or if black locust recruits will naturally fail to establish cohort dominance as long as disturbances are minimized (Granata et al. 2020; Motta et al. 2009). In the study area, black locust recruit cover under deciduous tree and shrub cover was highest on sites with warm aspects, loose soils, and sites that received surface water and groundwater flow. Recruit cover was also high on warm and well-lit submesic thinly spaced coniferous and trembling aspen stands and on cool and moist coniferous stands in canopy gaps with disturbed soils. As described in Section 5.2, black locust colonizing the understories of deciduous forests risks replacing aging stands and those exposed to natural and anthropogenic disturbances. Black locust colonization can be contained by protecting forests from future disturbances and planting mid-seral tree and shrub species to increase their propagule availability and their ability to outcompete black locust.

5.2. Managing Black Locust Invasions

Treatments for Containing Invasions

Following Objective 3.2 and based on the results of this study, strategies for containing, limiting, and treating new black locust recruit and shrub invasions into disturbed and natural areas are suggested below. Successful containment of black locust depends on restoring or creating unfavourable conditions for black locust colonization within the dispersal distance of established black locust shrubs and trees. Black locust seeds are gravity dispersed distances of up to 100 m (Warne 2016; Stone 2009; Morimoto et al. 2010). Mature trees deposit larger seed volumes than immature trees and seeds can persist decades in soil seedbanks until dormancy is broken by light, physical disturbances, and fire (Warne 2016; Stone 2009). Mature black locust trees readily send up clonal suckers tens of meters from their bases and suckering increases when trees are disturbed with mechanical treatments, herbicide, or fire (Commonwealth Agricultural Bureau International (CABI) 2019; Stone 2009). Keeping soils undisturbed within 100 m of mature flowering trees will avoid breaking seed dormancy and stimulating seedbank germination. Keeping black locust trees and shrubs undisturbed until targeted, long-term removal is possible will avoid stimulating rootstock suckering and reduce clonal invasions.

Management strategies can be employed to reduce propagule pressure and create and maintain unfavourable conditions for black locust colonization. Propagule pressure from seeds and roots can be reduced by actively monitoring sites for new invasions and removing recruits and small shrubs before they have the opportunity to establish. Soil disturbances created by removing black locust can be minimized by treating small black locust before they have the opportunity to develop large stems and deep root systems. This will also reduce impacts to surrounding native species and increase their ability to recolonize sites. Unfavourable conditions for black locust colonization can be created by planting native tree and shrub species suitable to site conditions near black locust invasions.

Planting native species will help stabilize disturbed soils on invasion vectors, reducing erosion, loose soil, and bare soil and decreasing black locust's ability to colonize sites (Vitková et al. 2015). Planting native species will also reduce germination and root sprouting success on uninvaded sites by creating shade cover and will help outcompete new black locust recruits and shrubs for light and moisture. Long-term native species planting strategies can be designed to contain black locust on both linear invasion vectors and in the understories of mature deciduous and mixedwood forests. It is likely the best vegetative containment strategy for black locust invasions will be to (1) plant a dense hedge of native species within the root dispersal distance of black locust stands to physically outcompete new root sprouts and (2) plant lower-density native plants within the 100 m seed dispersal distance of mature trees to cover and stabilize soils and minimize disturbances which would scarify seeds, increase understory light availability, and stimulate germination. Black locust root advancement and seed dispersal distances will be critical considerations when deciding the width of vegetative buffers to establish around black locust stands. Taller black locust trees will disperse more seed farther and may have more vigorous invading root systems. Clonal or rhizomatous thicket-forming deciduous species including snowberry, rose species, Oregon grape, thimbleberry, red-osier dogwood, and trembling aspen may be critical in halting rootstock advancement and creating understory layers too dense to allow seedling establishment. Species should be selected for suitable site conditions including temperature, light and moisture availability, and soil structure and nutrients. Species should also be selected for suitable site disturbances and seral conditions – early-seral species would be more suitable for outcompeting black locust invasions on disturbed slopes, while mid- and later-seral species would be more suitable for outcompeting black locust invasions in the understories of maturing native forests.

Treatments for New and Established Invasions

Following Objective 3.3, I suggest the following strategies for managing and treating established black locust stands in disturbed and natural areas. Black locust invasions on sites affected by legacy and active anthropogenic disturbances including roads, trails, and rural and resource-use areas are often characterized by dense even-aged stands. Repeated mechanical and herbicide treatments may be suitable for removing these stands as long as the disturbances caused by these treatments can be contained to disturbed sites. Removing black locust on anthropogenic disturbances will reduce propagule pressure into surrounding native forests. Limiting the disturbance caused by removing black locust to the footprints of already disturbed sites will avoid breaking the dormancy of seeds dispersed into surrounding intact forests from mature trees growing on disturbance footprints (Morimoto et al. 2010). Mature black locust trees also readily send up clonal suckers tens of meters from their bases when disturbed with herbicide or mechanical treatments – this allows invasions into nearby areas to increase when mature trees are chopped down (Commonwealth Agricultural Bureau International (CABI) 2019; Stone 2009). Monitoring natural areas surrounding disturbance footprints will allow resprouts from black locust rootstocks triggered by the clearing of mature trees to be removed before invasions have the opportunity to establish outside of disturbance footprints. Germination of buried seeds and rootstock left by black locust on disturbed sites can be reduced by removing soil after black locust stands have been removed. Soil disturbances caused by the removal of above and below ground biomass can be remediated by the addition of topsoil and organic matter. While soil compaction is often undesirable for native species, compaction appears to reduce black locust colonization (Vítková et al. 2015). Mechanical decompaction will be desirable if it improves native species' ability to establish on disturbed sites before black locust is able to recolonize these sites. Following soil remediation, sites can be densely planted with thicket-forming native shrub and tree species to outcompete new black locust invasions. Sometimes removing above and below ground black locust may not be possible due to site accessibility, time or budget constraints or due to the risk of physical or chemical treatments causing greater disturbance than sites can recover from without reverting to early seral conditions. When black locust cannot be fully removed sites may be treated by cutting black locust, establishing artificial shade cover to reduce seedbank germination and rootstock sprouting, and densely planting native shrub and tree species to outcompete new recruits for space, light, and moisture.

Black locust invasions on open slopes affected by natural soil disturbances were often characterized by short black locust trees stressed by heat and cold exposure. While black locust is accessible on these sites, steep slopes and unstable soils make mechanical treatment difficult, and disturbances caused by removing black locust risk destabilising slopes and creating unsuitable conditions for native species recruitment. On these open slopes black locust root mass could be retained and soil disturbances could be minimized by cutting plants to their root crowns and applying targeted herbicide for uptake into plant roots. This would kill the plant while leaving root-mass in the ground to continue stabilizing soil. On open sites with sensitive native species or disturbed and degraded sites where black locust's benefits to slope stability and soil enrichment may outweigh the risks of displacing native species, neither physical nor herbicide treatments may be desirable. On these sites it may be possible to retain black locust and plant native species in the shaded and stabilized microsites they provide with the goal of establishing shrub and tree vegetation cover to outcompete black locust for soil space or overtop and shade it out as native species mature.

Black locust invasions in the understories of warm and well-lit mesic to moist native deciduous and mixedwood forests are often characterized by variable densities of multiple age classes of black locust recruits, shrubs, and short trees intermixed with multiple age classes of native tree and shrub species. At these sites mechanical and herbicide treatments may risk disturbing native species' recruitment and creating unstable open conditions favourable for black locust. Disturbances to surrounding native species can be minimized by treating black locust invasions at their earliest recruit stages when the disturbance required to remove black locust individuals is small. Early treatments will also remove new individuals before they have the opportunity to begin producing seed and clonal root systems and will reduce propagule pressure into surrounding forests. When treating black locust invasions in the understories of intact native forests, soil and vegetation disturbances that increase black locust's ability to recolonize sites or impair native species' ability to establish and recover should be avoided or mitigated.

Treating mature black locust trees intermixed with native tree species is more difficult because mature black locust trees readily send up clonal suckers tens of meters from their bases when disturbed with mechanical or herbicide treatments (Commonwealth Agricultural Bureau International (CABI) 2019; Stone 2009). This may increase recruit and shrub invasion density into surrounding forests when mature trees are mechanically removed or targeted with herbicide. When mature black locust trees occur intermixed with mature native trees species on natural and recovering forested sites, disturbance should be minimized to avoid triggering regeneration from root-crowns and renewed recruitment from soil seedbanks disturbed during tree removal. The best strategy for treating mature black locust trees intermixed with native tree species is to allow these individuals to age and be overtopped while containing new invasions into surrounding forests. This can be accomplished by protecting surrounding sites from disturbances, monitoring mature black locust trees and early and selectively removing new recruits, and ensuring native species are present to fill in canopy gaps created as overstory native tree species naturally mature and die back.

Black locust invasions in the understories of moderate or higher density coniferous forests are usually limited to areas with active soil and canopy cover disturbances. Dense forests of competitive shade-tolerant species are resistant to black locust invasion (Nicolescu et al. 2020). When invasion vectors have allowed black locust to establish in otherwise intact shaded forests, native shrub and tree establishment around black locust should be supported by planting mid-seral coniferous trees and dense-crowned deciduous shrubs and trees. This will help stabilize soils, fill in canopy gaps with native species before they can be colonized by black locust, and increase shade-cover over existing black locust recruits to slow and stop their spread.

Mature stands of black locust trees not intermixed with other mature native tree species often occur in two different forms: moderate canopy cover stands on warm submesic to mesic sites, and closed canopy stands on warm mesic to moist sites. These stands appeared to be between 60 and 80 years old and may have become established from initial black locust plantings or early colonization of sites cleared by logging and stand-replacing fires. The disturbance caused by removing these stands would revert sites to early seral conditions and stimulate black locust regeneration across large areas recovering from historic disturbances. Mature black locust stands on sites without active disturbances are best treated by supporting the establishment of mid-seral native tree species capable of replacing maturing black locust stands. Several management strategies will help maturing black locust stands be replaced by native tree species. Protecting maturing black locust stands from future stand-replacing natural and anthropogenic disturbances will minimize early seral sites available for black locust to recolonize and will support increased abundances of mid-seral native tree species. Propagule availability and dispersal ability for natural recolonization under and around black locust stands can be supported by restoring mid-seral conifers throughout the study area. Increasing the abundance of rare Douglas-fir and western redcedar in the study area will increase these species' ability to naturally establish near black locust stands and in canopy gaps created by decaying trees, even if their ability to recruit directly under black locust is uncertain. Finally, planting native tree and shrub species near and directly underneath maturing black locust stands will help reduce black locust colonization of forested areas adjacent to black locust stands, outcompete black locust establishment in canopy gaps under its own stands, and increase the ability of native species to replace maturing black locust stands.

Several deciduous and coniferous tree species may be considered for planting in the understories of black locust stands to contain colonization at stand edges and re-establish native forests as black locust stands mature. Black cottonwood may be suitable for planting under black locust on warm and mesic to moist sites and appear to grow rapidly when light becomes available in canopy gaps under black locust. Individual black cottonwood shrubs and recruits are very narrow and may not displace black locust recruitment unless planted very densely to maintain high cover while they mature. Trembling aspen may be suitable for planting on submesic to mesic sites and appear best suited of any tree species to growing under dense black locust shade cover, because the suckers observed under black locust stands are clonal suckers supported in low light conditions by mature trees growing in higher light conditions at the edges of stands. Any conifer species suitable to the ICHxw BEC zone and the site conditions black locust are growing on may be suitable to plant under black locust. These species include western redcedar on warm and moist sites, western hemlock on cool and moist sites (although invasion risk appears low on these sites unless disturbed), western white pine on submesic to moist sites, and Douglas-fir on warm and submesic to mesic sites. Trials to test the establishment of native tree species within or adjacent to black locust stands should be undertaken under various edatopic grid and canopy cover conditions.

6. Research Opportunities

There is a need for future research (1) identifying abiotic conditions limiting and enhancing black locust establishment and maturation, and (2) assessing the impacts of black locust invasions on different abiotic site types and native vegetation species communities (3) testing methods of containing and restoring black locust invasions on both disturbed sites and natural areas by modifying abiotic conditions and planting native species to stabilize sites and inhibit colonization, and (4) monitoring native species replacement under black locust stands on disturbed and undisturbed conditions and testing methods of replacing black locust stands with native species by manual removal, site modifications, and native species planting. Research on abiotic limiting and enhancing conditions, at-risk sites, containment methods, and restoration methods will help (1) protect and modify the most important underlying conditions limiting black locust invasions on sites, (2) prioritize sites with the highest invasion risks for protection and restoration, (3) limit the impacts of new invasions on native species and the need to restore established stands after they have already displaced native species, and (4) replace established stands with native tree and shrub species characteristic of mid- and later- seral forests in the Lower Columbia Valley.

Recommendations for addressing Goal 1 are presented in the Discussion under Section 4.1 “Aerial Image Validation”. Further research opportunities related to Goals 2 and 3 are presented below.

6.1. Abiotic Conditions Limiting Black Locust Establishment and Maturation

This study characterized black locust tree, shrub, and recruit cover associations with abiotic conditions including temperature, light availability, and moisture availability represented by insolation and NDMI (Goal 2, Objective 2.2). There is a need to characterize key abiotic conditions limiting and enhancing black locust establishment and maturation using field observations. This will assist identifying high and low risk areas of invasions and prioritizing monitoring, containment, and restoration actions to high-risk sites (Objective 3.1). This will also help determine the most important abiotic factors to modify to contain colonization and restore established black locust stands (Objectives 3.2 and 3.3). Research can be conducted to identify key combinations of abiotic conditions – including light availability, temperature, soil moisture, soil nutrient regimes and soil structure – impacting biological processes including germination and growth that determine black locust colonization density and the maturation form, lifespan, and impacts of black locust stands on sites.

Environmental data used in this study came from remote sensed sources including a 1 m^2 DEM and 20 m^2 Sentinel-2 multi-band satellite imagery. These data indicate light availability, temperature, and moisture availability on plots. These data and are suitable for comparing plot conditions to each-other but do not represent actual measurements of biophysical conditions black locust interacts with during dispersal, germination, establishment, and maturation. True measures of abiotic conditions influencing black locust include: light availability at the topographic position and microsite level, mean temperatures and temperature variability, moisture availability due to topographic position, soil moisture holding capacity, bare soil exposure, soil density, and soil nutrient and chemical composition.

Combinations of these variables will limit black locust colonization on different site types and spatial scales. At large spatial scales these conditions are influenced by aspect, slope, and topographic position. These conditions are also influenced by natural disturbances including fire and mass wasting and anthropogenic disturbances including trails and roads, utility corridors, logging, and rural and residential development. Research that relates abiotic conditions that influence black locust establishment and maturation to site characteristics that may be measured during monitoring may be used to assist restoration planning within invaded landscapes.

Lab studies can be conducted observing black locust's germination and maturation response to different combinations of abiotic factors in microcosm or mesocosm experiments. Field studies can be designed to observe black locust establishment and maturation in sites with different combinations of these conditions. Plots in an exposed stratification class (open sites) could be deployed across sites with a range of moisture availability or soil disturbance conditions, and plots in a shaded stratification class (forested sites) could be deployed across a range of light availability and soil disturbance conditions. Likewise, plots on disturbed soils could be deployed across a range of light and moisture availability conditions. Abiotic limiting or enhancing factors can also be modified and tested in field settings, for example, by modifying bare soil exposure and soil density near mature trees and observing black locust seedbank germination and rootstock sprouting responses.

Understanding the link of abiotic limiting factors to black locust germination and growth responses can be used to (1) assess the likelihood of new invasions succeeding on sites with known abiotic conditions, (2) indicate the invasion density and maturation form of colonizing black locust and (3) indicate the short- and long-term impacts of invasions on different sites. This will help prioritize sites with high colonization and high impact risk for containment and restoration, discussed in Section 6.2 “Invasion Impacts”. Understanding abiotic limiting factors will allow restoration treatments to modify the most important abiotic factors limiting black locust’s ability to invade and impact sites. Sites with high likelihood of colonization near black locust invasions can be modified before black locust has the opportunity to establish, while sites that have been colonized can be modified to reduce invasion impacts and support native species establishment (discussed in Section 6.3 “Containment Strategies”).

6.2. Invasion Impacts

This study identified combinations of abiotic conditions, landscape features, and native vegetation species associated with high and low risks of black locust invasions (Goal 3, Objective 3.1). There is a need to identify the impacts of black locust invasions on different abiotic site types and native vegetation species communities. Identifying black locust invasion impacts will help prioritize sites for monitoring, containment, and restoration and (Objectives 3.2 and 3.3) select suitable native species to contain new invasions replace established black locust stands. Research can identify site types where native vegetation species establishment has been limited following black locust invasions. These site types may be at risk of black locust impacts following future disturbances and may benefit from protection from future invasions and rapid restoration when black locust is detected. Research can also identify site types where native vegetation species have begun re-establishing and maturing following black locust invasions. These site types may be able to naturally recover from future black locust invasions if native species propagule availability is maintained in nearby areas – allowing native species to recruit under black locust – and if sites are protected from future disturbances. This will help minimize black locust regeneration and allow native species colonizing underneath black locust to mature and replace aging black locust stands.

Not all black locust invasions appeared to have the same impacts on native species during their initial invasion stages and later maturation stages, and it was not clear if the appearance of black locust stands in early phases of colonization was an adequate indicator of their longer-term impacts on native vegetation species. In the study area, a range of different black locust invasion densities, plant health and maturation forms, and canopy cover densities were observed, largely due to apparent differences in light availability, moisture availability, and temperature extremes between sites. Black locust colonization density, health, and maturation form had different impacts on native vegetation species displacement during colonization and on their recovery under maturing black locust stands.

On exposed and steep slopes with dry and thin soils, unstable slopes, and extreme summer and winter temperatures, black locust was observed growing as short shrubs and stunted trees. When occurring at low density, invasions of shrubs and stunted trees appeared to displace few native species due to slow black locust growth, short height at maturation, and wide spacing between individuals. However, even low-density invasions may alter or arrest vegetation succession where stunted black locust shrubs or trees persist but are incapable of creating microsites for later-seral shrub and tree species establishment. On submesic to mesic sites with lower slopes and less exposure stress black locust was observed maturing into short trees with moderate canopy cover which allowed native species to establish in their understories as they matured. On mesic to moist sites with moderate to high light availability and more stable temperatures, black locust was observed colonizing most densely and maturing into tall and healthy trees and may have displaced native species during invasions through shading and the depletion of soil moisture. On warm aspects with high light availability and mesic to moist soils black locust was observed colonizing sporadically and occasionally densely under forest understories. These invasions appeared to displace few understory native species during their establishment but showed signs of having rapidly increased in height and cover under canopy gaps caused by disturbances and the maturation and decay of overstory trees.

Exposed Sites

On exposed and steep sites with warm aspects, dry and thin soils, unstable (erodible) material, and apparent summer high and winter low temperature extremes, black locust colonized sites as short shrubs and stunted trees. Colonization density was low in dry areas and higher in microsites with soil disturbance and increased moisture-reception in small gullies and mid-slope benches. Black locust on these sites would have stabilized soils, provided some shade cover, added leaf litter and increased soil moisture retention, and added organic matter and nitrogen from roots and leaf litter deposition. Low colonization density on exposed sites appeared to immediately displace few native species and have low short-term impacts. It is possible black locust on exposed, disturbed sites is capable of arresting further ecosystem succession towards mid- and late seral communities composed of native tree and shrub species, but it is also possible black locust on exposed sites is stabilizing and enriching disturbed sites and facilitating some native species establishment and maturation. On exposed and dry sites addressing the questions below will help determine where black locust invasions should be prevented and removed and where they can be maintained and worked with to obtain the greatest benefits to site stability, soil health, and native species recovery.

Questions:

Is black locust displacing early-seral native tree and shrub species on exposed and dry sites with thin or disturbed soils, or is it colonizing conditions too harsh to be colonized by other native woody vegetation? Other early-seral native tree and shrub species may be capable of stabilizing disturbed sites and building soils. It is unclear if black locust is outcompeting other native species or if it is filling an unoccupied niche using its deep vertical root-system to access submerged water-tables and its horizontal rhizomes to catch surface water runoff and spread across unstable soils.

Do stressed black locust remain arrested and persist long term, eventually decay in place, or slowly continue maturing?

Are stressed black locust on exposed sites arresting or facilitating succession? Do black locust on exposed sites provide more benefits from being left in place than it would benefit and cost sites if they were removed?

Submesic to Moist Mature Stands

On flat to gently sloping sites with warm aspects and submesic to mesic soils, black locust matured into short trees with moderate canopy cover, while on mesic to moist sites with moderate to high light availability and more stable temperatures black locust was observed colonizing in dense shrub stands and maturing into tall and healthy trees. Moderate to dense shrub colonization likely displaced high numbers of native species. Native tree and shrub species presence and cover in black locust stands was highest on submesic to mesic sites with moderate canopy cover and lower on moist sites with high canopy cover until canopy gaps opened as overstory black locust stems decayed.

Questions:

Are native tree and shrub species capable of establishing and maturing in the understories of single-species, single-aged black locust stands as they mature after dense invasions?

Do mature stands replace themselves from clonal root systems as they age, or do they die and facilitate native species establishment, maturation, and stand replacement?

Forested Sites

On warm aspects with high light availability and mesic to moist soils black locust was observed colonizing sporadically and occasionally densely under forest understories. These invasions appeared to have low initial impacts when new but appeared to have increased in cover and replaced overstory trees and understory shrubs when canopy gaps became available from decaying overstory trees and natural and anthropogenic disturbances. Black locust may be outcompeting native mid-seral tree and shrub species in forest understories on suitable conditions or benefiting from poor propagule availability of native species, or it may be benefiting from areas where native species are slow or unable to colonize due to poor natural site suitability, low propagule availability, or disturbances.

Questions:

Do invasions in forest understories displace native mid-seral tree and shrub species? Are invasions in forest understories occurring where native tree and shrub species colonization is low due to limited propagule availability, or are they occurring on sites with less suitable conditions for the establishment and maturation of mid-seral tree and shrub species?

Do invasions in forest understories usually succeed overstory trees or can they remain in place and die without maturing?

6.3. Containment Strategies

This study suggested strategies for containing and restoring black locust recruit and shrub invasions on both disturbed sites and natural areas (Goal 3, Objective 3.2). There is a need to test treatments to contain black locust invasions by remediating disturbed sites and planting native species. Containing black locust will help reduce displacement of native species during invasions (Objective 3.1), limit the need for mechanical and herbicide methods of removing black locust that risk further disturb sites, and limit the need for restoring established black locust stands or waiting for them to mature and be replaced with other species (Objective 3.3). Research can be conducted on methods of modifying abiotic limiting factors and on selection and use of native species plantings to reduce black locust establishment density and maturation success on disturbed sites, along invasion vectors, and within the understories of maturing native forests.

Containing Invasions by Planting Native Species

Once abiotic conditions limiting or determining black locust's ability to invade and impact sites have been identified, limiting factors may be directly or indirectly manipulated with field treatments to contain black locust invasions. Shade cover, soil bulk density and soil erosion, and exposed soil appeared important limiters of invasion presence and invasion density in this study. Research can test methods of increasing shade cover and stabilizing and covering soils by planting native tree and shrub species on both natural and anthropogenic invasion vectors and in forest understories invaded by black locust. Native tree and shrub species have different abilities to stabilize disturbed soils and compete with black locust recruits for light and moisture. Some tree and shrub species have dense stems and dense root masses: for example, trembling aspen, snowberry, Oregon grape, rose species, thimbleberry, red-osier dogwood, and other rhizomatous thicket-forming shrubs. Other species have lower stem densities and less below-ground biomass but have denser and more persistent canopies: for example, most coniferous species. Below-ground biomass from thicket-forming shrubs will be important for stabilizing disturbed soils and outcompeting black locust roots for both soil space and soil moisture. Above-ground biomass will be important for establishing permanent shade-cover to reduce seedbank germination and rootstock sprouting of black locust. Shade cover and ground cover represent clear targets that can be researched in field studies and aimed for in restoration treatments. Field research including monitored restoration treatments can test targets for shade cover and ground cover and find the best locations to plant thicket-forming shrubs and coniferous tree species relative to mature black locust propagule sources and invading recruits and shrubs to slow recruitment and outcompete maturating plants.

Containing Invasions in Forest Understories

Identifying strategies to treat black locust invasions in the understories of native forests and enhance native tree and shrub species establishment and maturation will help ensure native forests are capable of replacing themselves as they age. Black locust colonizing the understories of maturing deciduous and mixedwood forests appears to be occupying a similar role as mid-seral coniferous trees and deciduous understory shrubs. Research is needed to test if black locust is actively outcompeting and displacing native species on suitable sites in the understories of deciduous forests or if it is colonizing sites where abiotic conditions or natural and anthropogenic disturbances are limiting these species' ability to establish and mature. Research can test whether black locust is outcompeting and displacing native conifers and mid-seral shrub species or growing on sites naturally or anthropogenically less suitable by testing the success of removing black locust and planting native species in forest understories. This will determine best management actions for containing black locust in forest understories.

If black locust colonization in forest understories is caused by competition and displacement of native species on sites suitable for their growth, then removing black locust and planting native species will help support their establishment and maturation and reduce the likelihood of black locust invasions becoming dominant when maturing overstories composed of native trees decay and when stands are disturbed. If black locust colonization is caused by lack of suitable conditions for mid-seral tree and shrub species in the understories of maturing forests, then planting conifers and shrubs will be less successful and restoration treatments will need to protect sites from disturbances, modify underlying abiotic conditions to support native conifer and shrub species, and find suitable native species to plant to outcompete black locust colonizing native forest understories. In cases of black locust invasions in forest understories, restoration should protect sites from disturbances to reduce the likelihood of rapid black locust maturation in disturbed stands, remediate legacy disturbances by stabilizing and covering soils to reduce black locust colonization opportunities and increase native species establishment and maturation success. Restoration should also plant native tree and shrub species to outcompete black locust using the methods discussed in Section 5.2 and Section 6.3.

6.4. Removal and Restoration Strategies

This study suggested strategies for restoring established black locust stands on both disturbed sites and natural areas (Goal 3, Objective 3.3). There is a need to develop methods of removing established black locust stands and replacing them with native tree and shrub species. Identifying strategies to restore black locust stands will help identify sites where black locust stands can be left for natural replacement and where active treatments will be needed to re-establish displaced native species. Research can be conducted on the lifespan of black locust stands and the natural rates of native species establishment in their understories. To support active restoration, research can be conducted on manual clearing and replanting methods, methods for removing established black locust without triggering seedbank and rootstock regeneration, and suitable native tree and shrub species to establish under black locust stands on various site conditions to replace stands as they mature.

The long-term impacts of black locust invasions will be determined by black locust stands' lifespan on disturbed and undisturbed conditions and native mid- and later-seral tree species that are able to establish and mature in black locust understories on different site conditions. Studies report individual stems from root colonies living 60 to 120 years and beginning to decay inside after 60 years (Stone 2009). Clonal rootstocks live longer than individual stems, as evidenced by the common practice of coppicing black locust forestry plantations and the habit of black locust to send up new shoots from its root system when mature trees are chopped down during restoration (Stone 2009). Black locust stands that appeared to have established in the 1940's were observed maturing and beginning to decay in some parts of the study area. There is a need for monitoring to identify whether these stands will continue decaying as they age, or if they will experience a second round of regeneration from seedbanks and rootstocks as overstory stems decay and new canopy gaps become available to support black locust understory establishment.

Observations and field research can be conducted on clonal black locust stands lifespans on disturbed and undisturbed sites, and seed and root establishment and maturation under different ages of black locust stands and densities of black locust canopy cover. Research on black locust stands lifespans and understory self-establishment will help determine how long black locust is able to compete for light and moisture with native tree and shrub species able to establish and mature in its own understory and will indicate the timeline for the natural replacement of stands with native species.

Identifying the lifespan of clonal black locust stands both exposed to and protected from disturbances throughout their maturation is a critical first step in identifying the need to deliberately restore established black locust stands in the Lower Columbia Valley. Secondly to understanding black locust stands' natural aging process, identifying techniques to increase stand decay rate without triggering seedbank germination and stem and rootstock regeneration will increase opportunities for native tree and shrub species to establish and mature in the understories of black locust stands without competition from black locust recruits. Finally, identifying techniques of establishing artificial and vegetative cover to prevent seedbank germination and rootstock regeneration will help enable stand logging treatments and provide tools for preventing the regeneration of stans exposed to natural disturbances.

On sites where minimizing soil disturbance is a priority, techniques that reduce black locust cover without triggering the vigorous rootstock regeneration witnessed after cutting, burning, and broadcast herbicide application should be tested. These may include stem girdling, targeted herbicide application via girdling or injection, and fungal inoculation to instigate stem heart rot may cause stems to decay.

On already disturbed sites, logging stands for merchantable timber or fuelwood followed by planting native species may be a suitable restoration treatment for removing black locust stands and reducing dispersal into nearby uninvaded sites. These treatments will mechanically induce both seedbank germination and stem and rootstock regeneration and favourable conditions for increased regeneration by disturbing soils and increasing light availability. Research can be conducted on the density of (1) artificial shade and ground cover and (2) native tree and shrub species stem and canopy cover required to suppress regeneration induced from disturbances to black locust seedbanks and the roots and stems of mature trees. This will help establish initial artificial cover and inform planting targets for species to replace black locust on disturbed sites. These same tools can be deployed to supress colonization and re-establishment when established black locust stands are disturbed by fire or other natural disturbances.

Instead of or alongside removing established black locust, natural regeneration can be supported by planting native tree and shrub species in the understories of maturing stands and around their boundaries. Identifying species able to naturally establish and be planted under mature black locust stands will help replace black locust stands with native mid- and later-seral forest species and minimize the long-term impacts of black locust in the region.

Early- and mid-seral deciduous tree species including black cottonwood and trembling aspen were observed establishing and maturing underneath black locust tree cover. Later-seral conifer species may be more suitable than early-seral deciduous trees to replace black locust stands long-term in the study area as these species naturally succeed under early-seral deciduous trees and tend to live longer (and provide shade). Western white pine and to a lesser extent Douglas-fir were observed establishing and maturing underneath moderate black locust tree cover on submesic to mesic sites. Other conifers including western redcedar, western hemlock, and spruce species were rarely observed under black locust – this may be due to poor propagule availability, black locust stands growing on conditions less suitable for these species, or suppression of establishment by site modifications. Research can determine if black locust stands are growing on natural conditions less suitable for mid-seral conifer recruitment or if they are supressing these species. Conifer establishment and maturation can be compared between invaded sites and uninvaded sites with similar underlying abiotic conditions to determine if black locust stands change conifer establishment and maturation from expected values based on their growth on uninvaded sites. This research will help determine if black locust stands are changing long-term ecosystem successional processes or if these processes are continuing to follow trends expected based on abiotic conditions underlying black locust stands. This research will also be able to suggest conifer species suitable to replace black locust stands by natural recruitment and planting.

7. Conclusions

Goal 1: Assess the effectiveness of aerial imagery as a tool for visually identifying mature black locust stands and new black locust invasions.

Aerial imagery allowed flowering tree-height black locust to be identified but did not help identify non-flowering trees and black locust shrubs and recruits. Using aerial imagery to identify black locust trees will help contain new invasions by identifying areas of high propagule pressure into surrounding native forests. Due to black locust's short seed dispersal distance and its habit of invading in lines and clumps of clonal individuals (Morimoto et al. 2010), new invasions tend to advance from mature trees and dense thickets of shrubs and recruits established from clonal suckering. When assessing invasions in the future, field and remote-sensed data can be used to identify the presence of abiotic conditions and vegetation species associated with new invasions around visible black locust trees. This will allow areas around flowering stands to be assessed a risk-level of containing black locust recruit and shrub invasions not visible on imagery and will help prioritize sites to visit in the field for monitoring and restoration.

Goal 2: Characterize the abiotic conditions and native tree and shrub species associated with black locust invasions in the study area using ground sampling plots, field observations, ecological modelling, and literature review.

Non-parametric multi-dimensional scaling, correlation analysis, and regression analysis were used to identify abiotic conditions (including temperature, light availability, and moisture availability) and native tree and shrub species associated with black locust invasions. Modelling results were combined with literature review and field observations to assess abiotic conditions and native tree and shrub species associated with black locust invasions.

Objective 2.2: Characterize abiotic conditions associated with black locust tree, shrub, and recruit cover within the study area.

Black locust was associated with warm aspects, moderate to high insolation, and submesic to moist conditions and increased in density on sites with natural and anthropogenic vegetation and soil disturbances. Light availability represented by insolation was associated with increasing black locust density. Light availability was highest in the study area on south and west facing mid and upper slopes, in canopy gaps on disturbed and undisturbed sites, and in the understories of deciduous tree and shrub stands and sparse coniferous tree stands on warm aspects. Increasing soil moisture – but not permanently saturated soils – was associated with increasing black locust density and health. Moisture availability was most suitable for black locust within gullies and mass-wasting channels, slope breaks including natural benches as well as trails and roads, surface and sub-surface seeps, and warm and well-lit creek and river banks. Increasing temperature (warmer aspects) was associated with increasing black locust density and health as long as moisture was also available. Soil disturbances and canopy gaps created by mass wasting and trails, roads, and rural and resource-use areas appeared to increase black locust colonization on both warm and cool sites with submesic to moist conditions but did not increase black locust colonization on hot and dry sites.

Objective 2.3: Characterize native tree and shrub species associated with black locust tree, shrub, and recruit cover within the study area.

Black cottonwood, introduced silver maple, trembling aspen, western white pine, and to a lesser extent Douglas-fir were associated with black locust invasions. Black cottonwood and silver maple were strongly associated with black locust and can easily be identified on aerial imagery. The visibility of these species on aerial imagery near flowering black locust indicates high likelihood of understory colonization by black locust shrubs and recruits and indicates high priority sites to follow up with field surveys. Trembling aspen and western white pine were associated with black locust when growing on warm and submesic to moist sites but not when growing on cool and shaded sites, unless stands had open canopies or natural or anthropogenic vegetation and soil disturbances were present. Black locust has colonized the understories of maturing deciduous and mixedwood forests and may be either actively outcompeting and displacing native conifer and shrub species on sites suitable for their growth, benefiting from low propagule availability and reduced competition on sites suitable for these species, or growing on sites where abiotic conditions or natural and anthropogenic disturbances are limiting these species ability to establish and mature.

Black locust stands supported sparse native tree and shrub cover in their understories when short, but appeared to begin supporting tree and shrub recruitment as they gained height and as canopy gaps opened. Black cottonwood recruits and shrubs were present under black locust on moist sites with bare soil patches, and trembling aspen and silver maple recruits and shrubs were present under black locust on sites with stable soils and often slightly higher black locust canopy cover than sites where black cottonwood appeared able to establish. Western white pine and Douglas-fir recruits and shrubs were present under black locust on submesic to mesic sites where stands were moderately dense to open and allowed moderate to high understory light availability from around the sides of mature trees or under canopies that were less dense, apparently due to lack of moisture and stem decay. Both deciduous and coniferous tree species appeared to establish best under black locust where canopy gaps were present or where black locust canopies were naturally thin, and where existing black locust canopies provided enough shade cover and leaf litter deposition to displace grass and herb species. Low propagule availability rather than unsuitable conditions may be limiting some conifer species – especially Douglas-fir and western redcedar – establishment and maturation under black locust stands.

<u>Goal 3:</u> Based on black locust tree, shrub, and recruit associations with abiotic conditions and native tree and shrub species, provide recommendations for containing black locust invasions and restoring established black locust stands in the study area and the Lower Columbia Valley.

<u>Objective 3.1:</u> Identify combinations of abiotic conditions, landscape features, and native vegetation communities associated with high and low risks of black locust invasions.

Black locust was introduced to remediate disturbed sites in the Lower Columbia Valley in the 1940's: close to 80 years after its introduction it is continuing to colonize naturally and anthropogenically disturbed sites as well as the understories of maturing early seral deciduous and mixedwood forests in warm, well-lit, and submesic to moist conditions. Black locust's ability to colonize naturally and anthropogenically disturbed soils (including legacy and active trails, roads, and mass wasting slopes) and warm well-lit sites with moderate to high moisture availability (including gullies, slope breaks, surface and sub-surface seeps, and creek and river edges) has allowed it to follow natural and anthropogenic features and colonize deciduous and mixedwood forests understories in suitable temperature, light, and moisture conditions. Black locust recruit and shrub colonization was moderately dense on exposed and dry slopes with moisture available in micro-sites and most dense on mesic to moist early seral sites. Invasions in the understories of mature forests were less dense and appeared to remain low impact until disturbances or natural canopy gaps allowed black locust to mature and increase in cover. Mature black locust stands appeared to have begun supporting deciduous and coniferous tree establishment in their understories in the last five to ten years due to increasing height and increasing amount of overstory canopy gaps from decaying stems. Black locust's ability to stabilize disturbed soils, establish shade cover, and supplement soils with nitrogen and organic matter may be helping replenish soil organic matter on sites degraded and destabilized in the last century by natural and anthropogenic disturbances and aiding native tree and shrub establishment and maturation in some areas.

<u>Objective 3.2:</u> Suggest strategies for containing and restoring black locust recruit and shrub invasions on both disturbed sites and natural areas.

<u>Objective 3.3:</u> Suggest strategies for restoring established black locust stands on both disturbed sites and natural areas.

Several strategies can be employed to contain and treat new black locust invasions and recover native forests on sites occupied by mature black locust stands. Remediating disturbances on natural and anthropogenic invasion vectors by stabilizing soils and increasing native vegetation cover will help discourage black locust from spreading through canopy gaps and disturbed soils and increase native species' ability to outcompete black locust recruits for light and moisture. Targeting removal actions towards black locust recruits and shrubs invading the understories of minimally disturbed and recovering native forests will help stop background clonal invasions before black locust has the ability to begin propagating aggressively into openings created by aging deciduous trees and natural and anthropogenic disturbances. Removing black locust recruits and shrubs in the understories of maturing deciduous forests will also create space for native mid-seral tree and shrub species to establish and compete with black locust for light and moisture, if sites have suitable underlying abiotic conditions and no background disturbances exist limiting propagule dispersal, germination, and maturation. Planting native tree and shrub species around new black locust invasions will reduce their spread by increasing shade cover, covering exposed soils and stabilizing disturbed soils, and competing with new black locust for moisture. Removing mature black locust stands on actively disturbed sites and sites with legacy anthropogenic impacts (including trails, roads, and historic logging activity) and remediating these sites after black locust has been removed will reduce propagule pressure into surrounding native forests and minimize suitable areas for recolonization. Under maturing black locust stands, planting native coniferous tree species and thicket-forming deciduous trees and shrubs will reduce the likelihood of black locust establishing in its own canopy gaps and help support natural vegetation species establishment and speed and direct succession to native mid- and later-seral forests.

Black locust invasions can be managed to support restoration and conservation in the Lower Columbia Valley by treatments that mitigate the impacts of invasions on native species while working with its ability to stabilize and remediate disturbed sites. Initial black locust invasions displace early-seral native tree and shrub species. Black locust appears capable of colonizing and stabilizing exposed sites subjected to temperature stress, low moisture availability, and soil disturbance. Black locust may arrest further ecosystem succession if it remains in unhealthy and stunted shrub and short tree forms capable of enriching soils and supporting early-seral species that favour open sites, without developing adequate crown cover to shelter exposed sites and facilitate the establishment of native mid-seral tree and shrub species. Black locust colonization in the understories of maturing deciduous forests may be outcompeting and displacing native mid- and later-seral tree and shrub species, or colonization may be most successful where dispersal limitations, underlying abiotic conditions, or natural and anthropogenic disturbances have limited mid-seral native species ability to establish and mature. Black locust stands may be able to be replaced by native tree and shrub species without being actively removed. Native tree and shrub establishment under maturing black locust stands can be supported by allowing stands to age and thin while protecting them from disturbances that recreate early seral conditions and stimulate seedbank and rootstock regeneration. Finally, sites where native species have successfully replaced black locust will retain black locust seeds which will remain viable in the soil seedbank and re-establish when logging, fire, mass wasting, or anthropogenic disturbances clear sites. The impacts of black locust invasions may be mitigated and native forests successfully restored if legacy disturbances are remediated, sites are protected from future disturbance, native tree and shrub species are planted on open and forested sites to stabilize sites and outcompete black locust establishment and maturation, and if successional processes already occurring under maturing black locust stands are guided and enhanced by planting native tree and shrub species capable of forming mid- and later-seral forests in the region.

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