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by

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ABSTRACT

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Keywords: American beech (*Fagus grandifolia* Ehrh.), beech leaf disease, CART analysis, forest pathology, *Litylenchus crenatae,* permanent plot monitoring, southwestern Ontario, symptom severity

The health of American beech (*Fagus grandifolia* Ehrh.) is threatened in North America due to its susceptibility to various pathogens, including beech leaf disease. Little is known about beech leaf disease, and forest health specialists have failed to determine the causal agent responsible or how the disease is spread. The purpose of this study is to determine whether particular site conditions, which may negatively impact the health and vigour of American beech trees, affect the susceptibility of beech to infection by beech leaf disease, by assessing foliar symptom severity relative to environmental conditions occurring at 34 unique beech stands in southwestern Ontario. This study was conducted at various American beech stands occurring throughout the Ontario Ministry of Natural Resources and Forestry's Guelph and Aylmer districts. Plots were constructed at each site to capture symptom severity data for overstorey, sapling, and understorey trees, by recording metrics such as percentage of the total canopy afflicted by dieback, chlorosis, undersized leaves and foliar banding at different severity levels. To assess whether a relationship exists between site conditions and symptom severity, the data collected in the field was run through a CART analysis to produce a decision tree that predicted the characteristics of the sites being studied and describe the stressor-response relationship that exists within the data between American beech trees and the environmental conditions occurring on the sites surveyed. The results revealed that slopes equal to or less than 32.8% are associated with an increased presence of beech leaf disease symptoms among seedlings under 1 m in height. Further, it was determined that shoulders, back slopes, and flat areas, and the occurrence of beech scale infestation intensities equal to or greater than the 'trace' classification are associated with the development of severe beech leaf disease symptoms among saplings with DBH under 10 cm. A stressor-response relationship exists between those site conditions that are less conducive to the growth of American beech seedlings and saplings and increased occurrence and severity of beech leaf disease symptoms. In doing so, the results of this study indicated that the causal agent or vectoring organism responsible may attack stressed trees opportunistically, thus providing insight as to how the spread of beech leaf disease can be controlled.

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INTRODUCTION

American beech (*Fagus grandifolia* Ehrh.) is a deciduous tree species native to eastern North America that is characteristic of the Carolinian forest region of southwestern Ontario. American beech is a species of great economic and ecological value, providing moderate-quality wood for use in a wide variety of products, nesting or foraging habitat for many bird species, and nourishment to a variety of wildlife through the supply of beechnuts. Unfortunately, the health of American beech is threatened in North America due to its susceptibility to various pathogens, including beech leaf disease, a recently introduced disease with an unknown causal agent that has affected hardwood stands in 24 counties in the U.S. and Ontario.

The objective of this study is to determine whether site conditions that negatively impact the health and vigour of American beech trees also affect the susceptibility of beech to infection by beech leaf disease, by assessing foliar symptom severity (in terms of severity of striping and blistering of leaves and proportion of canopy with undersized or chlorotic leaves) relative to various site features (measured in terms of aspect, slope, associated vegetation, landform attributes, etc.) occurring at 34 unique beech stands in southwestern Ontario. Little is currently known about beech leaf disease and its mechanism of spread, and forest health specialists have failed to determine the causal agent responsible. The results of this study may provide insight for the many yet-unanswered questions regarding beech leaf disease, and serve as a precursor for other potential avenues for future research regarding the discovery of a potential causal agent and vectoring organism. This study will indicate whether the causal agent or vector responsible attacks stressed trees opportunistically, which may be useful in determining how the spread of beech leaf disease can be managed for and controlled.

LITERATURE REVIEW

AMERICAN BEECH

Taxonomy and Physiology of American Beech

The genus *Fagus* L., which American beech belongs to, is comprised of 10 species of deciduous trees of the Fagaceae family that are native to temperate regions in North America, Europe, and Asia. Beech trees are characterized by high branching, smooth silver-grey bark, and stout trunks (Denk *et al*. 2002). American beech is native to eastern North America and is the only species of the genus *Fagus* that naturally occurs in the Western Hemisphere, likely having spread throughout North America before the Pleistocene glacial period (Deevey, Jr. 1949; Kapp 1977). This species typically grows up to 20-35 m tall, however, growth in ideal site conditions may permit growth of up to 37 m (Hosie 1979; Tubbs and Houston 1990). American beech develops dark green simple leaves with sparsely-toothed margins and short petioles (Hosie 1979). American beech is a mesophytic species, meaning that a given tree uses more water than many drought-resistant vegetative species (such as oaks or pines) to perform transpiration and conduct growth processes (Tubbs and Houston 1990).

<u>Silvics of American Beech</u>

The natural range of American beech extends from Nova Scotia to southern Ontario in eastern Canada, reaching as far south as northern Florida, Arkansas, and eastern Texas in the United States (OMNRF 2014; Tubbs and Houston 1990). In Canada, the American beech is associated with the Carolinian forest region that is found throughout southwestern Ontario as well as the Great Lakes-St. Lawrence forest region found across southeastern Canada (Nat. Resour. Can. 2017). Within its natural range in the United States, American beech stems achieve the greatest size when growing in the alluvial soils of the Mississippi and Ohio River Valleys, where some beeches aged 300 to 400 years occur (Tubbs and Houston 1990). Within the natural range of American beech, annual precipitation is approximately 760 mm to 1 270 mm, though in regions such as Michigan and most of Canada, lower precipitation often occurs at 580 mm and 640 mm, respectively (Tubbs and Houston 1990). Mean annual temperatures occur between 4°C and 21°C in the species' natural range; however, beech are known to persist at temperature extremes between -42°C and 38°C, with growth becoming inhibited with exposure to prolonged above-average summer temperatures (Cleavitt *et al.* 2008; Tubbs and Houston 1990). It is hypothesized that climate change projections indicate an increase in the frequency and severity of drought events in the Great Lakes-St. Lawrence forest region (Pastor and Post 1988; Solomon and Bartlein 1992), which will cause a reduction in radial growth for northern hardwood forest species including American beech, and may increase the populations of defoliating insects such as gypsy moth (*Lymantria dispar* L.), allowing outbreak levels to be more easily achieved (Ives 1981). A study conducted by Fritts (1962) indicated that ring widths of American beech in Ohio are directly related to moisture supply during August and temperatures between May and July of the preceding growing season, as well as precipitation of the previous winter. Fritts (1962) additionally proposed that daily growth of American beech in central Ohio is greatly reduced when soil moisture and atmospheric humidity is low, resulting in a negative correlation between ring width and temperature as a result of the high temperatures that often accompany dry periods in the region. Further, high July temperatures are more limiting to the radial growth of beech located on poorly-drained sites, whereas high August temperatures are more limiting to those on well-drained sites. The relationship that exists between radial growth and environmental conditions that occur in the previous growing season is likely due to early season conditions that influence bud initiation and potential photosynthetic area of the following year as a result, and late season conditions that affect food accumulation and the food reserves available for growth (Fritts 1962).

American beech populations primarily grow in two principal soil groups: grey-brown podzols and laterite; beeches are rarely found in limestone soils except for populations occurring in the western edge of the species' natural range. American beech is also associated with soil pH levels ranging from 4.1 to 6.0 in timber stands (Fowells 1965; Tubbs and Houston 1990). A study conducted by Duchesne and Ouimet (2009) in Quebec indicated that the current expansion of American beech in the province can be partially attributed to soil base cation depletion of magnesium and calcium caused by atmospheric acid deposition, which creates base-poor soil conditions that are conducive to the growth of American beech at the expense of sugar maple (*Acer saccharum* Marshall) due to a combination of low sensitivity to soil base cation availability and reduced interspecific competition. However, another paper counters the conclusions made by Duchesne and Ouimet (2009) by stating that American beech is in a better position to thrive in the long-term as a late-successional shade-tolerant species, and that multiple interacting factors are likely at play in influencing the expansion of American beech forest in eastern North America beyond soil alkalinity alone (Messier *et al*. 2011). Further, a study conducted by MacDonald *et al*. (1998) regarding the effects of environmental stress on vigor and growth in northern hardwood forests concluded that the most significant predictors of periodic diameter increment for the assessed hardwood trees was the water-holding capacity of soil rather than nitrate or sulphate deposition into soils (Brooks 1994). The authors of this study further suggested that changes to climatic conditions cause greater effects on tree mortality, vigour, and growth in northern hardwood forests than pollutant deposition (Allen *et al*. 1992; LeBlanc *et al*. 1987; LeBlanc 1993; MacDonald *et al*. 1998). A survey conducted by Brooks (1994) yielded similar results, indicating that patterns of mortality and growth are more frequently related to drought, insect defoliation, and stocking rather than acid deposition into soils. Populations are typically greater on dry to mesic soils that are coarse-textured, conditions typically found in the northern extent of the species' range (Tubbs 1978; Tubbs and Houston 1990). Beech trees have been found growing on poorly-drained sites that do not experience prolonged flooding events and on sites where the water table is within 15 cm and 25 cm of the soil surface; however, American beech is less tolerant to these conditions than other species, such as red maple (*Acer rubrum* L.). The root system developed by American beech varies depending on the level of drainage occurring at a site, with shallower root systems occurring on poorly-drained sites (Fowells 1965; Fritts 1962). As a result of their shallow root systems, American beech trees are readily affected by rapid decline in soil moisture, which results in limited radial growth during mid-summer drought events (Fritts 1962). American beech is also among the least tolerant species to flooding during the growing season relative to co-occurring species due to its shallow root system (Tubbs and Houston 1990).

The fruit of beech trees, commonly referred to as 'beechnuts', are bur-like structures that hold two to three nuts. Beechnuts require one growing season to mature and typically ripen between September and November. Seed fall commences after the first heavy frost which causes the burs to open. American beech is monoecious, developing flowers of both sexes on the same tree, and reproduces by seed dispersal and through the sprouting of roots (Farahat and Lechowicz 2013; Tubbs and Houston 1990). Seed production typically proliferates when a beech tree is approximately 40 years old. The majority of seed produced by a given tree drops to the ground directly beneath the parent tree, and seed dispersal is often restricted; small rodents may carry seeds a short distance from the parent tree, but seeds are rarely transported over one kilometre from the parent tree (Asuka *et al.* 2004). Beech seeds germinate between early spring and early summer. Germination is most successful on mineral soil or leaf litter, and is poor on excessively wet sites. Further, germination and survival is more successful on mor humus compared to mull humus (Fowells 1965; Smith and Every 1980). American beech seedlings perform better beneath a moderate canopy or in protected small openings compared to larger open areas, likely due to the increased susceptibility to drying of the soil surface below the depth of shallow seedling roots in open areas. Due to this, American beech express strong survivability in the shade of old-growth stands (Duchesne and Ouimet 2009). Though height growth of seedlings is approximately the same in dense or moderate shade, total dry weight and root development are greatest in moderate shade conditions; height growth, dry weight, and root development are all reduced in open areas relative to shaded areas (Logan 1973). Large seedling populations can occur under extremely dense stands; however, growth is slowed in these conditions.

Reproduction of American beech slows when forest stands are heavily cut using silvicultural methods such as clearcutting, with many young beeches becoming out-competed by light-requiring species such as white birch (*Betula papyrifera* Marshall), yellow birch (*Betula alleghaniensis* Britt.), or white ash (*Fraxinus americana* L.). As a result of clearcutting, fewer beech persist in new stands compared to the original pre-cut stand (Fowells 1965); beech may be nearly eliminated after repeated clearcuts occur on short rotations in a given stand. However, partial cuttings such as single-tree selection cuttings permit the development of shade-tolerant beech reproduction by minimizing competition with species associated with vigorous growth response to increased light (Tubbs and Houston 1990). American beech is incredibly shade-tolerant, partly due to its low respiration rate (Loach 1967) as well as its stomatal response to changes in light intensity; the leaves' stomata rapidly open and close when light intensity suddenly increases or decreases. The stomata of beech are more responsive than those of less tolerant species such as red maple, red oak (*Quercus rubra* L.), or tulip tree (*Liriodendron tulipifera* L.) (Woods and Turner 1971). However, beech may exhibit reduced tolerance when exposed to cold climates and poor soil quality (Tubbs and Houston 1990).

Diseases and Insects Affecting American Beech

Over 70 types of decay fungi have been reported to attack American beech (Hepting 1971); the most important decay fungi to note include *Cerrena unicolor* (Bull.: Fr.) Murrill, *Ganoderma applanatum* (Pers.) Pat., *Fomes fomentarius* (L.: Fr.) J. Kickx, *Phellinus igniarius* (L: Fr.) Quel., *Inonotus glomeratus* (Peck) Murrill, *Kretzschmaria deusta* (Hoffm.) P.M.D. Mart., and shoestring fungus (*Armillaria* spp.) – one of the most important root pathogenic fungi in North America – which attacks and girdles the roots of weakened trees (Tubbs and Houston 1990). The root systems of beech can also be parasitized by *Conopholis americana* (L.) Wallr. and *Epifagus virginiana* (L.) Bart., both of which are broomrapes (Gill 1953).

Various defoliating insects are known to feed on the foliage of American beech, including forest tent caterpillar (*Malacosoma disstria* Hubner), gypsy moth, fall cankerworm (*Alsophila pometaria* Harris), and Bruce spanworm (*Operophtera bruceata* Hulst). Continuous and heavy defoliation of beech can increase susceptibility to attack by shoestring fungus (Tubbs and Houston 1990).

Due to the thinness of the American beech's bark, the species is vulnerable to many sapsucking insects, such as the giant bark aphid (*Longistigma caryae* Harris, T.W.) and beech blight aphid (*Fagiphagus imbricator* Fitch) (Tubbs and Houston 1990). Oyster-shell scale (*Lepidosaphes ulmi* L.) outbreaks result in crown dieback and even stand death in severe cases when heavy and continuous outbreaks occur (Baker 1972). American beech scale (*Xylococculus betulae* Pergande) targets the sprout thickets that emerge after beech bark disease passes through a stand, causing roughened spots to appear on the stems of young trees (Houston 1975).

Beech bark disease, an insect-fungus complex, is perhaps the most notorious disease to target American beech, having been confirmed in Ontario since 1999

(McLaughlin and Greifenhagen 2012). Beech trees become susceptible to beech bark disease after they are attacked by the exotic woolly beech scale (*Cryptococcus fagisuga* Lind.), which causes injury to the thin bark of American beech by creating 1 mm wounds to feed on parenchyma cells, creating small fissures in the bark surface that provide access to fungal inoculation (Ehrlich 1934; Fajvan *et al.* 2019; Houston and O'Brien 2008). Once the bark is infested with the scale, the tree becomes susceptible to infection by bark canker fungi (*Neonectria faginata* (Pers.: Fr.) Fr. Var. Lohman, A.M. Watson, & Ayers; *Neonectria ditissima* (Tul. & C. Tul.) Samuels & Rossman), which form mycelial colonies and lesions on the host tree's stem, eventually weakening the stem, girdling the tree and causing canopy death (Houston and O'Brien 2008). Fortunately, approximately 1% of American beech trees exhibit genetic resistance to beech bark disease (Houston 1983; Koch *et al.* 2010; McLaughlin and Greifenhagen 2012). Trees exhibiting resistance often grow in close proximity, which suggests that a clonal relationship exists among non-diseased neighbouring trees (Koch *et al.* 2010) or that a genetic association exists due to limited seed dispersal distance (Fajvan *et al.* 2019; Tubbs and Houston 1990).

NEMATODES

Foliar Nematode Biology and Population Dynamics

Foliar nematodes belonging to the genus *Aphelenchoides* are widespread pathogens that are associated with over 700 host plant species (Crossman and Christie 1936; Knight *et al.* 1997). *Aphelenchoides ritzemabosi* Schwartz and *A. fragariae* (Ritzema Bos) Christie are foliar nematodes that are associated with temperate climates (Winslow 1960). Adult nematodes of this genus are vermiform and attain a length of approximately 1 mm at maturity (Shurtleff and Averre 2000), and can be distinguished from many other plant-parasitic nematode taxa by their large angular metacorpus, finely-annulated cuticle, offset lip region, lateral field containing two to four lines, and tapered conical tail end (Franklin 1978). Another foliar nematode, *Litylenchus crenatae* Kanzaki, Ichihara, Aikawa, Ekino & Masuya of the family Anguinidae, is associated with Japanese beech (*Fagus crenata* Blume), and is characterized by its dimorphism in adult females, lateral field containing six or more lines, pointed tail tip, presence of a quadricolumella, female post-uterine sac, and male posterior bursa that reaches near the tail tip (Kanzaki *et al.* 2019).

Both feeding and reproduction occur within infested leaf tissue; nematodes feed within the mesophyll and epidermis of foliage using their stylets to pierce neighbouring cells (Volvas *et al*. 2005). Eggs are laid in the healthy green sections of leaf tissue (Wallace 1959). Observations made by Stewart (1921), Wallace (1959), and French and Barraclough (1961) indicated that *A. ritzemabosi* can complete their lifecycle in 14 days if temperatures do not fall below 15°C (French and Barraclough 1961): five days are required for embryonic development, and maturation occurs over an additional five days; this rapid generation time indicates that foliar nematode populations can rapidly increase within foliar tissue, with thousands of nematodes per gram of leaf tissue developing over two months (Kohl 2011). Various studies have concluded that foliar nematodes of various species exhibit similar patterns of population dynamics during a given growing season, with the highest populations occurring in July, followed by a decline in late August and September and then another increase in October (Kohl *et al.* 2010; Warfield *et al.* 2004).

However, the experiment conducted by Kohl *et al.* (2010) indicated that disease severity of the host plants studied did not increase until the start of September; this suggests that foliar nematodes do not migrate from infected leaves to non-infected leaves until late in the growing season when temperatures start to decrease. Alternatively, this disparity between population increase and symptom severity increase may be due to a reduction in reproductive output during warmer summer months (Kohl *et al.* 2010).

Infection Behaviour and Parasitizing Potential

Foliar nematodes affect the leaves of host plants by migrating up plant stems and entering the stomata of foliage. Due to their migratory requirements, infection more often occurs on plant surfaces that have been recently moistened by rain, dew, or overhead irrigation (Kohl 2011). Nematodes primarily feed endoparasitically, which collapses the spongy parenchyma and palisade leaf cells (Volvas *et al.* 2005; Winslow 1960), causing angular lesions to form on infested foliage that often turn brown-black or chlorotic before becoming necrotic with age (Daughtrey *et al.* 1995). Nematodes may also feed ectoparasitically on the buds, stems, and flowers of host plants (Franklin 1978; Shurtleff and Averre 2000).

Modes of Travel and Migration

Foliar nematodes such as *Aphelenchoides fragariae, A. ritzemabosi,* and *A. besseyi* Christie migrate over plant surfaces via water films to enter leaf stomata (Kohl 2011). Yamada and Takakura (1987) determined that *A. fragariae* populations increased in the leaves of lilies during the rainy season. Further, a study by Szczygiel and Hasior (1972) confirmed that populations of *A. ritzemabosi* and *A. fragariae* increased in field-grown strawberry plants during early spring and late fall when relative humidity was greatest. A study by Wallace (1959) concluded that *A. ritzemabosi* adults move more rapidly in thick water films that immersed the epidermal hairs found on the undersides of chrysanthemum leaves. However, foliar nematodes may also spread via direct contact between an infected leaf and uninfected plant tissue (Jagdale and Grewal 2006; Kohl 2011), even through seeds and dehisced infected leaves that fall onto healthy plant tissue (Lehman 1996). Due to the results of Jagdale and Grewal's (2006) experiment which indicated that nematodes were only present on the outer surface of the hosta foliage studied, it is suspected that *A. fragariae* migrate on the surfaces of plants. Further, 25% to 46% of nematodes were alive at conditions with 90% relative humidity compared to 66% to 77% at 100% relative humidity, which suggests that high moisture is needed for nematodes to survive and conduct upward migration (Jagdale and Grewal 2006, Wallace 1959). A study conducted by Adamo *et al.* (1976) on *A. besseyi* concluded with the suggestion that vertical migration of this species on rice plants is favoured by rough surfaces and an inverse water gradient; the nematodes' rate of climb on non-absorbent and non-textured surfaces of capillary tubes was nil, whereas it was high on the rough and absorbent surface of a matchstick. It was also determined that the stems of rice seedlings were ineffective migratory structures when wetted from below, however, migration of *A. besseyi* readily occurred when moisture was continuously supplied to the stem. Further, it was found that the vertical ascent of nematodes in water films was texture-dependent, with rate of climb being nearly nil on smooth surfaces regardless of moisture conditions. Due to the species' equal migration habits downwards and upwards, it was further suggested by the authors that directional movement of *A. besseyi* was not influenced by gravity, thereby indicating that geotaxis is not involved in migration (Adamo *et al.* 1976). The results of Kohl *et al.*'s

(2010) experiment indicated that increased distance between canopies of host species causes a decrease in infections by inhibiting *A. fragariae* dispersal; the steep disease gradient developed from this study suggested that canopy spacing of 10 cm among nursery-grown lantana results in 45% to 50% fewer infected plants compared to 0-cm spacing when canopies were touching and dispersal appeared most efficient, which suggests that host plant spacing can yield a significant effect on nematode dispersal.

<u>Overwintering Survival</u>

Foliar nematodes can tolerate eight hours of exposure to temperatures ranging from -80°C to 40°C in leaf tissues (Jagdale and Grewal 2006). Adults and fourth-stage juveniles of the *Aphelenchoides* genus overwinter in an anhydrobiotic state for several months to three years (Daughtrey *et al.* 1995) within desiccated tissues of the host plant's dried leaves and dormant buds (French and Barraclough 1961; Jagdale and Grewal 2006). However, eggs of various nematode species, including *A. fragariae,* are incapable of overwintering, unlike juveniles and adults (Jagdale and Grewal 2006; Lewis and Mai 1960). It is hypothesized that overwintering survival is improved when bare soil is dry as opposed to moistened, particularly at moisture levels exceeding 30% field capacity (French and Barraclough 1961; Szczygiel and Hasior 1971; Wallace 1959). In Jagdale and Grewal's (2006) study of the pathogenicity and overwintering survival of *A. fragariae* on hostas, their results indicated that 35% to 79% of the nematodes found in dormant buds were located within the two outermost layers of the buds.

EXPERIMENTAL DESIGN AND USE OF STATISTICS

Monitoring and Impact Analysis System

To establish a system for monitoring the occurrence and spread of beech bark disease in Michigan's northern hardwood forest, the University of Michigan and Michigan Department of Natural Resources devised a monitoring and impact analysis system (named the 'Michigan Beech Bark Disease Monitoring and Impact Analysis System', or BBDMIAS) to measure the current condition and future changes to overstorey vegetation as a result of disturbances such as beech bark disease (Petrillo *et al.* 2005). A modified version of this system would be useful for determining change in forest composition over time in hardwood stands afflicted with beech leaf disease. The system outlined by Petrillo *et al.* (2005) consists of 202 extensive plots (composed of a matrix of 30 sampling points where basal area is measured, as well as tree damage data and abundance of beech bark disease indicators on American beech trees) and 62 more detailed intensive plots (subsets of the extensive plots, wherein data is collected on all tree species, including standing dead trees) which were established throughout Michigan's eastern Upper Peninsula as well as the western and northern Lower Peninsula. The plots set up were permanent, as those partaking in the study wished to re-evaluate the metrics taken from each plot after three years to determine the impact caused by beech bark disease over time (Petrillo *et al.* 2005).

Petrillo *et al.* (2005) outlined three main objectives of the study: to identify the extent of Michigan's beech trees that are affected by beech bark disease, to collect baseline data on the current health condition of American beech and northern hardwood stands containing beech before they become affected by beech bark disease, and to monitor changes in the condition of beeches and northern hardwood forests over time. Each tree in the extensive and intensive subplots that were candidate trees for measurement were given numbered metal tags placed on the buttress root of the tree. For each beech tree sampled in the extensive plot, the variables measured included tree status, DBH, tree tag number, live crown ratio, crown density, crown dieback, foliage transparency, crown light exposure, tree vigour or condition, and percent beech scale coverage. For each tree (over 12.5 cm DBH) sampled in the intensive subplots, the variables measured include tree status DBH, tree tag number, live crown ratio, crown density, crown dieback, foliage transparency, crown light exposure, tree vigour or condition, crown class or position, tree damage, and (where applicable) percent beech scale coverage (Petrillo *et al.* 2005).

CART Analysis

Classification and regression tables are useful for analyzing complex ecological data that can be defined using non-linear relationships and high-order interactions (De'ath and Fabricius 2000; Ryo and Rilig 2017). Classification and regression tree analysis (otherwise known as a CART analysis) is a useful statistical method for determining the relative importance of different variables for identifying homogeneous groups that exist within a given dataset; this is accomplished using a decision tree that can predict the characteristics of the values being studied (De'ath and Fabricius 2000; Song and Lu 2015). Trees explain variation of a single response variable by repeatedly splitting data into homogeneous groups using combinations or categorical or numeric variables, with the data separated into two mutually-exclusive groups with each split (De'ath and Fabricius 2000; SAS Institute 2017). Decision trees can be represented graphically to improve understanding of the statistical output: the root node (representing undivided data) occurs at the top of the graph, while the leaves (each of which represents a final group) are shown beneath the node. Trees also provide an excellent method of describing and predicting patterns and processes (De'ath and Fabricius 2000; Rokach and Maimon 2008). Advantages of using decision trees for ecological data analysis include sufficient flexibility to handle a wide range of response types, invariance to monotonic transformations of explanatory variables, ease of construction, and providing the ability to handle missing values in response and explanatory variables; thus, use of decision trees in a CART analysis represents a suitable alternative to traditional statistical methods such as log-linear models, multiple regressions, and variance analysis (De'ath and Fabricius 2000).

BEECH LEAF DISEASE

Known and Potential Host Species

In North America, beech leaf disease primarily affects American beech. However, in 2016 it was also observed on European beech (*Fagus sylvatica* L.) and Oriental beech (*F. orientalis* Lipsky) at Holden Arboretum in Geauga County, Ohio (EPPO 2018; Ewing *et al.* 2019; Pogacnik 2018), and was found on European beech again in commercial nursery stock in Lake County, Ohio in 2017 (Crane 2019; EPPO 2018; Ewing *et al*. 2019). Chinese beech (*F. engleriana* Seemen ex Diels) and Japanese beech are currently considered potential host species as well (EPPO 2018).

Range of Disease and History of Spread

Beech leaf disease was first discovered by Lake Metropark Biologist John Pogacnik in 2012 in Lake County, Ohio (Pogacnik 2018). A year after the initial discovery was made, beech leaf disease spread to the neighbouring Ashtabula and Geauga Counties in 2013. In 2014, Cuyahoga County became the fourth in Ohio with confirmed presence of beech leaf disease, followed by Portage County in 2015, then Medina and Trumbull Counties in 2016. During 2016, it was also discovered that beech leaf disease had spread to the state of Pennsylvania in Erie and Crawford Counties. By 2017, beech leaf disease was confirmed in Ontario in Elgin County, and had spread to Summit and Stark Counties in Ohio as well as Mercer, Lawrence, Warren, and Elk Counties in Pennsylvania and Chautauqua County in New York. By 2018, spread of the disease continued into Mahoning County, Ohio and Potter County, Pennsylvania. During the same year, beech leaf disease was also confirmed in an additional five counties in Ontario: Chatham-Kent, Middlesex, London, Oxford, and Norfolk (OMNRF 2018). As of 2018, at least 24 counties in Ontario and the U.S contain American beech trees infected with beech leaf disease (Ewing *et al.* 2019; Martin *et al.* 2019; OMNRF 2018).

Between 2012 and 2016, beech leaf disease has spread at a rate of 506 ha per year in Lake County, Ohio (Crane 2019; DiGasparro 2019; Ewing *et al.* 2019). Given this rate of spread, it is suggested that the disease is currently undergoing a rapid expansion phase that is similar to that of other invasive pathogens and insects, such as emerald ash borer (*Agrilus planipennis* Fairmaire) (DiGasparro 2019). Due to a lack of understanding as to what the causal agent of this disease is, it is unknown as to when and how the causal agent was introduced into Ohio, though it is likely that a non-native organism is responsible.

<u>Symptoms and Differential Infection on Beech of Various Sizes</u>

Symptoms of infection are only apparent on the leaves and buds of beech trees and are present from spring onwards after buds begin to emerge and leaf-out occurs (DiGasparro 2019; Pogacnik and Macy 2016; Pogacnik 2018). Early foliar symptoms include the development of dark green striping or banding between lateral veins (with bands never crossing leaf veins) and reduction of leaf size (Ewing *et al.* 2019; Martin *et al.* 2019; Pogacnik 2018). Banded areas of the leaves later become slightly raised and thick or leathery in texture, as illustrated in Figure 1; (DiGasparro 2019; Martin *et al.* 2019; OMNRF 2018) leaf curling may also develop in more severe cases. In the early stages of infection, the striped appearance of affected leaves is most apparent when looking up at the tree's canopy from below (Martin *et al.* 2019; Pogacnik and Macy 2016; Pogacnik 2018); this is illustrated in Figure 2. Progression of symptoms leads to bud abortion, reduced leaf production, and premature leaf drop (Pogacnik and Macy 2016), all of which contribute to a reduction in canopy cover in affected stands, as well as reduce photosynthetic potential (DiGasparro 2019). In the most severe cases, leaves near the tips of branches appear shriveled and curled and exhibit chlorotic yellow banding, similarly to what is shown in Figure 3; this is often accompanied by reduced bud and leaf production (Gasparro 2019).

Figure 1. Characteristic foliar blistering symptoms.

Figure 2. Early-stage interveinal banding, visible from beneath the canopy.

Figure 3. Late-stage leaf deformation and chlorosis.

In Japan, the foliage of Japanese beech, European beech, copper beech (*Fagus sylvatica* f. *purpurea* [Aiton] C.K. Schneid.), Siberian alder (*Alnus hirsuta* Turcz.), montane alder (*A. maximowiczii* Call.), and Japanese hop-hornbeam (*Ostrya japonica* Sarg.) have developed leaf galls when leaves have become infested with *Litylenchus crenatae;* the foliage of Japanese beech were additionally afflicted by interveinal striping after becoming infested with this nematode (EPPO 2018; Kanzaki *et al.* 2019).

Symptom progression varies greatly depending on the size of the host tree. In a given affected stand, initial symptoms often appear among smaller beech trees growing in the understorey (Ewing *et al.* 2019). Among sapling-sized beech trees, progression from early-stage symptoms to severe late-stage symptoms is rapid, with mortality sometimes occurring in only one year. Conversely, larger overstorey beech trees exhibit slower disease progression, with symptoms often occurring in the lower branches first before progressing upwards into the canopy (Pogacnik and Macy 2016). Mortality is estimated at two to five years for beech saplings and six years for larger beech trees (Martin *et al.* 2019). Where the disease is established, the proportion of symptomatic trees in a given area can exceed 90% (EPPO 2018; Pogacnik and Macy 2016).

<u>Theories on Causal Agents Responsible</u>

Despite the widespread nature of beech leaf disease and the potentially massive economic losses that may result if it eradicates American beech – with losses estimated at $225 million in Ohio alone (Crane 2019) – the causal agent is currently undiagnosed. Due to its rapid spread and the observed variability of environmental conditions on sites where the disease occurs, it is unlikely that beech leaf disease is an abiotic disorder; rather, a biotic agent is theorized as being responsible for infection and spread of the disease (Ewing *et al.* 2019). Unfortunately, DNA and molecular testing that has occurred since 2012 on symptomatic beech leaves in Ohio have provided no evidence that a fungus, bacteria, virus, or phytoplasma is responsible (OMNRF 2018). However, an association between symptomatic beech leaves and the occurrence of nematodes exists, which suggests that nematodes act as vectors for the causal agent or are inflicting damage to foliage and buds to create the symptoms present on affected plants. The nematodes infesting symptomatic leaves, which were first discovered by plant pathologist Dave McCann, belonged to a species that was not yet identified at the time of discovery, but were similar to a bush-dwelling species found in New Zealand that cause similar symptoms to the leaves of native trees (McCarty 2018; Popkin 2018). In June of 2018, Dr. Qing Yu of Agriculture Canada confirmed that nematodes of the genus *Litylenchus* is present in symptomatic American beech leaves from southwestern Ontario. As of 2019, the nematode species has been defined as *Litylenchus crenatae*, and is confirmed to be occurring in both symptomatic stands in North America and in Japan, where the native Japanese beech tree is parasitized (Kanzaki *et al.* 2019; OMNRF 2018).

Although the evidence suggests that nematodes play a role in the infection and spread of beech leaf disease, it is unlikely that feeding behaviour by nematodes is solely responsible, due to the nature of the symptoms; feeding by foliar nematodes often results in the development of discoloured or necrotic spotting on leaves rather than the interveinal bands seen on infected beech leaves (Daughtrey *et al.* 1995; Popkin 2018). The scientific community dealing with the issue of beech leaf disease has largely come to the consensus that *Litylenchus crenatae* is associated with beech leaf disease, however, it is still unknown as to whether the nematode serves as a vector for the causal agent or what type of causal agent the organism may be (EPPO 2018). As of yet, no Koch's Postulate has succeeded in proving pathogenicity of *L. crenatae,* according to Dr. Sharon Reed of the Ontario Forest Research Institute (pers. comm., April, 2019). Ewing *et al.* (2019) state that the interveinal banding and crinkling of foliage exhibited by infected beech trees are consistent with the symptoms that occur among other vascular plants infected by viruses or phytoplasmas.

Suggestions for Future Research on Beech Leaf Disease

Regarding beech leaf disease and the nature of how it is spread, very little is known. It is clear from my literature review that there is no definitive explanation as to what the causal agent of beech leaf disease is or how it can be managed, though Ewing *et al.* (2019) cited the use of next-generation sequencing and leaf microbiome analysis to aid in the determination of a causal agent. Further, there appears to be no existing studies that analyze the relationship that exists between site conditions and symptom severity in American beech stands. Though Ewing *et al.* (2019) have established that it is unlikely that beech leaf disease is caused by an abiotic disorder due to the observed variability of environmental conditions on sites where the disease currently occurs, no one has yet studied whether symptom severity worsens on sites characterized by environmental conditions that are unfavourable to the growth of beech. This lack of study indicates that there are gaps in the research that fail to address the question of whether the causal agent or vectoring organism responsible, such as *Litylenchus crenatae*, attacks host trees opportunistically. By conducting research that will address this topic, new avenues of research can be established which may enhance management objectives and control recommendations to effectively mitigate the spread of beech leaf disease in North America.

OBJECTIVE

The objective of this study is to determine whether particular site conditions which may negatively impact the health and vigour of American beech trees (such as waterlogged or poorly-drained sites) affect the susceptibility of beech to infection by beech leaf disease, by assessing foliar symptom severity (in terms of severity of striping and blistering of leaves and proportion of canopy with undersized or chlorotic leaves) relative to various site features (in terms of aspect, slope, associated vegetation, landform attributes etc.) occurring at 34 unique beech stands in southwestern Ontario, specifically within the Ontario Ministry of Natural Resources and Forestry's Guelph and Aylmer districts. Little is currently known about beech leaf disease and its effects on the mortality of infected trees, and forest health specialists have failed to determine what causal agent is responsible or how the disease is spread. Therefore, I hope that the results of this study will provide insight for these yet-unanswered questions regarding beech leaf disease, and serve as a precursor for other potential avenues for future research regarding the discovery of a potential causal agent of beech leaf disease. Additionally, I hope that this study will indicate whether the causal agent responsible attacks stressed trees opportunistically, which may be useful in determining how the spread of beech leaf disease can be controlled. If my findings indicate that conditions more likely to cause stress to American beech are correlated to higher severity of beech leaf disease symptom severity, it may be reasonable to suggest that opportunistic parasitic nematodes are involved in the vectoring of the disease, and opportunistically attack weakened trees with reduced vigour.

HYPOTHESES

This study is designed using the null hypothesis that there is no significant relationship that exists between beech leaf disease symptom severity and the presence of site conditions that are less conducive to the growth of American beech. The alternative hypothesis is that there is a significant positive relationship that exists between beech leaf disease symptom severity and the presence of site conditions that are less conducive to the growth of American beech. Therefore, I predict that a greater occurrence of site conditions that negatively impact vigour of American beech corresponds to greater severity of beech leaf disease symptoms present at a given site.

MATERIALS AND METHODS

For this study, 34 permanent overstorey vegetation plots were identified and set up in various conservation areas, provincial parks, and woodlots throughout southwestern Ontario, specifically within the Ontario Ministry of Natural Resources and Forestry's Guelph and Aylmer districts. A map illustrating the location of the sites used for constructing monitoring plots is shown in Figure 4.

Figure 4. Map of permanent beech leaf disease monitoring plot site locations (Source: Google Earth 2019).

For this survey, 17 locations were selected and two 0.04 ha (11.28 m-radius) overstorey vegetation plots were constructed at each location; each plot was located in

Elgin, Norfolk, Middlesex, Oxford, Chatham-Kent, and Niagara Counties. Within each 0.04 ha plot, five additional subplots were constructed: one sapling plot (3.6-m radius, measured from the centre of the overstorey vegetation plot) and four understorey vegetation plots (1-m radius, measured from each cardinal point of the boundary of the 0.04 ha plot). Between July 30 and August 14, 2019, various measurements were taken from each plot to determine beech leaf disease symptom severity under a variety of environmental and biological conditions. A diagram illustrating the plot design used at each of the 34 sites assessed is shown in Figure 5.

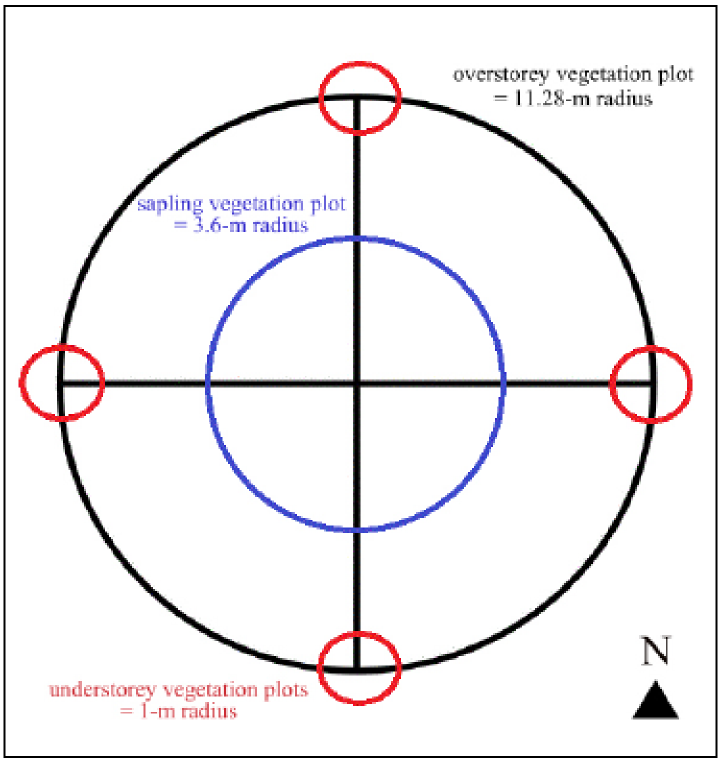

Figure 5. Diagram of permanent plot design for each monitoring plot location.

Once each plot was established, various site conditions were determined. Plot coordinates were taken from plot centre using a Garmin global positioning system unit. Live and dead tree basal area was then determined using a wedge prism, with an ultrasound vertex instrument used to assist in tallying 'borderline' trees; the number of 'in' living and dead trees was tallied to determine this value. Using the ultrasound vertex instrument, percent slope was determined from plot centre. Slope aspect was determined using a compass from plot centre. Landform was determined as belonging to one of the following categories using visual analysis: ridgetop, spur ridge, nose slope, head slope, side slope, cove, draw, or flat. Slope shape was determined as belonging to one of the following categories using visual analysis: convex, concave, or flat. Slope position was determined as one of the following categories using visual analysis: summit, shoulder, back slope, foot slope, floodplain, flat, or gently-rolling hill.

Within the boundary of the overstorey vegetation plot, every tree greater than 10 cm DBH was tagged using numbered aluminum tags that were nailed to a buttress root, with numbering commencing with the outermost tree closest to the northern cardinal point of the plot boundary to the east and ending with the innermost tree closest to the northern cardinal point of the plot boundary to the west. Each tree was then assessed for species, DBH, crown class designation (dominant, codominant, intermediate, or suppressed), and overall estimated exact percent of crown dieback.

For any American beech (*Fagus grandifolia*) trees greater than 10 cm DBH that were rooted within 11.28 m of plot centre, additional measurements were taken: estimated percentage of dead main branches in the canopy (using cover classes between 1 and 6), estimated percentage of dead fine branches in the canopy (using cover classes between 1 and 6), position of dead main and fine branches in the canopy (upper canopy, lower canopy, or both), percentage of leaves in the canopy that are normal, striped, and shrunken or curled (using cover classes between 1 and 6), position of normal, striped, and shrunken or curled leaves in the canopy (upper canopy, lower canopy, or both), estimated exact percentage of undersized leaves in the canopy, estimated exact percentage of chlorotic leaves in the canopy, mean beech scale (*Cryptococcus fagisuga*) intensity on the north and south sides of the stem (using an intensity scale of 0 to 5) at breast height (1.3 m), mean scale intensity on the entire stem (using an intensity scale of 0 to 5), mean intensity of fruiting bodies of *Neonectria ditissima* or *Neonectria faginata* on the north and south sides of the stem at breast height (using an intensity scale of 0 to 5), and mean intensity of fruiting bodies of *Neonectria ditissima* or *Neonectria faginata* on the entire stem (using an intensity scale of 0 to 5). Other remarks related to health issues present on assessed American beech trees, such as the presence of anthracnose or defoliation, was also recorded.

Within the boundary of the sapling vegetation subplot, every tree less than 10 cm DBH and greater than 1 m in height was tagged using numbered aluminum tags that were nailed to a buttress root or loosely tied around the base of the stem using twist-tie garden wire, with numbering commencing with the outermost tree closest to the northern cardinal point of the plot boundary to the east and ending with the innermost tree closest to the northern cardinal point of the plot boundary to the west. Each tree was then assessed for species, DBH, and overall estimated exact percent of crown dieback.

For any American beech trees less than 10 cm DBH and greater than 1 m in height that were rooted within 3.6 m of plot centre, additional measurements were taken: estimated percentage of dead main branches in the canopy (using cover classes between 1 and 6), estimated percentage of dead fine branches in the canopy (using cover classes between 1 and 6), percentage of leaves in the canopy that are normal, striped, and shrunken or curled (using cover classes between 1 and 6), estimated exact percentage of undersized leaves in the canopy, estimated exact percentage of chlorotic leaves in the canopy, mean beech scale (*Cryptococcus fagisuga*) intensity on the north and south sides of the stem (using an intensity scale of 0 to 5) at breast height, mean scale intensity on the entire stem (using an intensity scale of 0 to 5), mean intensity of fruiting bodies of *Neonectria ditissima* or *Neonectria faginata* on the north and south sides of the stem at breast height (using an intensity scale of 0 to 5), and mean intensity of fruiting bodies of *Neonectria ditissima* or *Neonectria faginata* on the entire stem (using an intensity scale of 0 to 5). Other remarks related to health issues present on assessed American beech trees, such as the presence of anthracnose or defoliation, was also recorded.

Within the boundary of each understorey vegetation subplot, every woody plant less than 1 m in height was identified by species, with a tally conducted for the number of individuals of each species that was rooted within 1 m of the overstorey vegetation plot's boundary marker. For any American beech tree seedlings rooted within the subplot, an assessment of the presence of beech leaf disease symptoms was made by determining whether any leaves showed signs of striping, shrinking, or curling; any seedlings exhibiting symptoms were marked with a 'Y', those that did not were marked with an 'N' on the data sheet. Estimated percentage of vegetative cover was also determined at each subplot (using cover classes between 1 and 6). Using a spherical crown densiometer, forest overstorey density was determined in the field at each cardinal point of the subplot by tallying the number of dots on the face of the densiometer that represent canopy openings.

Once the tallies were completed, the values determined were multiplied by 1.04 to obtain the percentage of overhead area that was not occupied by canopy; the difference between 100 and the determined value was then calculated to obtain percent estimated overstorey density at each cardinal direction within the understorey vegetation plots.

An explanation of the codes used to designate categories of cover classes is shown in Table 1. An explanation of the codes used to designate categories of canopy position for dead branches and symptomatic beech foliage is shown in Table 2. An explanation of the codes used to designate categories of beech foliage symptom severity is shown in Table 3. An explanation of the codes used to designate categories of mean scale and *Neonectria* fruiting body intensity is shown in Table 4.

Table 1. Cover class designations used at each vegetation plot and subplot in the field.

Cover Class Code	Percent Range/Description
1	0
2	< 10
3	10-25
4	25-50
5	50-75
6	75-100
7	recently dead (fine twigs present)
8	dead for a long time

Table 2. Canopy position designations used for American beech trees assessed in the overstorey vegetation plots.

Canopy Position Code	Canopy Position (equally divide tree canopy into two parts)
1	lower canopy
2	upper canopy
3	both lower and upper canopy

Table 3. Beech leaf disease foliar symptom severity designations used for data collection for American beech trees assessed in the overstorey and sapling vegetation plots.

Symptom Severity Code	**Description of Symptoms Present**
1	NORMAL: leaves are typical size and shape; healthy
2	STRIPED: leaves exhibit interveinal dark striping or bubbling; striping per leaf may be variable, but less than 2/3 of the leaf shows a striping pattern
3	SOLID STRIPES, SHRINKING, OR CURLING: over 2/3 of the leaf shows a striping pattern or solid darkening, leaves are thick and leathery, shrinking and/or curled edges evident

Table 4. Mean scale and *Neonectria* canker fruiting body intensity designations used for American beech trees assessed in the overstorey and sapling vegetation plots.

Mean Intensity Code	**Description of Intensity**
0	no infestation
1	trace (1-10 single scale colonies)
2	light (numerous single scale colonies scattered over the bole)
3	moderate (accumulation of scale colonies producing a clumping appearance)
4	moderate-heavy (clumps of scale colonies building to the point of appearing to stream down the bole)
5	heavy (scale accumulation on the bole has increased to the point where portions appear white-washed, or vertical accumulation lines create the appearance of streaming down the bole)

Materials used in this study included a compass (to determine slope aspect and establish the cardinal points of each plot boundary), a wedge prism with a basal area factor (BAF) of 2 m^2/ha (to determine live and dead basal area of the plot), a diameter tape (to determine DBH of overstorey and sapling trees within each plot), a 30-m. distance tape (to measure and mark plot size for the overstorey, sapling, and understorey vegetation plots), binoculars (to assess the canopies of large overstorey trees and assign symptom severity values), 256 metal pig-tail markers (to establish permanent overstorey plot boundaries in each cardinal direction from plot centre and temporary sapling subplot boundaries in each cardinal direction from plot centre), 64 1.5 m-tall PVC pipes (to establish a permanent marker for plot centre and the north boundary for each overstorey vegetation plot), a spherical crown densiometer (to determine forest overstorey density at each cardinal point of every understorey vegetation plot), and a Haglof Vertex IV ultrasound instrument system (to assist in tallying 'borderline' trees for basal area tallies and confirming cardinal point delineation for plot set-up).

Multiple classification trees were produced using non-parametric data input into IBM's SPSS statistical analysis software, which aids in the determination of the relative importance of different variables for identifying homogeneous groups that exist within the dataset. This is accomplished using a decision tree that predicts the characteristics of the sites being studied and identifies potential relationships between particular site conditions and increased severity of beech leaf disease symptoms by helping to describe the stressor-response relationship that exists within the data between the surveyed sapling- and seedling-stage American beech trees and the environmental conditions occurring on the observed sites From the data collected at every sapling vegetation plot, the following dependent variables were individually considered for statistical analysis: the percent value of all surveyed beech trees in a given plot that presented any beech leaf disease symptoms ('bldprs'), the percent value of all surveyed beech trees in a given plot that presented interveinal foliar banding ('strpc'), and the percent value of all surveyed beech trees in a given plot that presented foliar curling, shrinking, or shriveling ('cssc'). From the data collected at every understorey vegetation plot, one dependent variable was considered for statistical analysis: the percent value of all surveyed beech trees in a given plot that presented any beech leaf disease symptoms ('bldprs'). The output of the statistical analysis executed by IBM SPSS software additionally provided a table and a histogram for each tested dependent variable, depicting the normalized importance of each considered independent variable: slope percent ('spc'), slope aspect ('sa'), slope shape ('ss'), slope position ('spo'), landform type ('ldf'), average densiometer reading ('dens'), mean scale intensity class ('scalc'), and total basal area ('ba').

Due to the limited scope of the statistical analysis for this project, data collected from the overstorey vegetation plots was omitted so that only saplings under 10 cm DBH and seedlings under 1 m in height were considered. Metrics assessed from smaller American beech specimens are the focus of this study due to the greater accuracy of field analysis of symptom severity, in addition to the known greater infection potential experienced by beech trees that grow in the understorey of Carolinian forests. Additionally, it has been observed that sapling- and seedling-sized American beech develop more rapid progression of symptoms and a possess a greater risk of mortality over a shorter time period. Given the greater risk of severe symptom manifestation and mortality among American beech trees persisting in the forest understorey, it seems most logical that data collected from these specimens are given preference in the analysis of the relationship between site conditions and beech leaf disease symptom severity.

Data collected in the field was imported into IBM SPSS from a Microsoft Excel spreadsheet (found in Appendices I and II). Once imported, the variable measures (nominal, ordinal, or scale) were defined according to the data type being represented under each variable type. To build the classification tree, 'tree' was selected from the 'classify' drop-down menu under the 'analyze' tab. After selecting 'tree', the dependent and independent variables were identified for each run. For each of the runs made on IBM SPSS software, the same settings were applied to the dataset within the program. Among the 'growing method' options provided, 'CRT' (meaning 'classification and regression tree') was selected. Split-sample validation was applied with random assignment case allocation and a training sample value of 90% due to the relatively small size of the dataset being tested. Further, due to the size of the dataset used for statistical analysis, the minimum number of cases for parent and child nodes was set to one to ensure that the program's output would properly reflect the statistical significance of the input data without producing an infeasible output.

An explanation of the codes used to abbreviate the various types of slope positions, slope shapes, and landform types observed in the plot assessments and considered in the statistical analysis is shown in Table 5.

Table 5. Slope position, slope shape, and landform type designations used to abbreviate the output of the classification trees.

Variable Code	Code Meaning	Independent Variable Type
back	back slope	slope position
fts	foot/toe slope	slope position
rolh	rolling hill	slope position
shld	shoulder	slope position
flat	flat	slope position
smit	summit	slope position
foot	foot slope	slope position
vex	convex	slope shape
cave	concave	slope shape
fl	flat	slope shape
side	side slope	landform type
nose	nose slope	landform type
terr	terrace	landform type
ridt	ridgetop	landform type
flt	flat	landform type

The tables and figures produced from the statistical analysis are illustrated in the Results section and in Appendices III through X. The results of the classification tree analysis primarily focus on the interpretation of the classification tree output and the independent variable importance charts produced from the SPSS software. The 'independent variable importance' value measures how much the model-predicted value changes for different values of the independent variable, and the 'normalized importance' percentage value is calculated by dividing the largest importance values. The importance charts given in Figures 6, 8, 10, and 12 are derived from the values presented in the importance tables (shown in Appendices III, V, VII, and IX), with the independent variables on the vertical axis sorted in order of descending value. However, these figures do not indicate the direction of the relationship between these variables and the predicted probability of symptom occurrence. Although inferences can be made about the directions of these relationships based on current literature, a model with more easily-interpretable parameters must be used to statistically determine this. When analyzing the classification trees produced from IBM's SPSS software, the terminal nodes are of the greatest interest in statistical analysis because they represent the best classification predictions for the model.

The metrics given at each branch of the classification tree that connect the terminal nodes to the root node represent individual 'decisions' within the model that lead to the 'outcome' represented by the terminal nodes. These decisions are identified in the Results section and analyzed in the Discussion section to ultimately determine how they influence the relevant dependent variable; this procedure identifies possible relationships between particular site conditions and increased presence or severity of beech leaf disease symptoms by helping to describe the stressor-response relationship that exists within the data between American beech trees and the environmental conditions occurring on the sites surveyed.

RESULTS

Forest health metrics evaluated from a total of 619 individual American beech trees from 25 sapling vegetation plots and 88 understorey vegetation plots in the Guelph and Aylmer districts of southwestern Ontario were statistically analyzed on SPSS using the classification tree method. A summary table of the metrics considered from the American beech trees assessed in the sapling and understorey vegetation plots is shown in Appendices I and II, respectively.

MODEL 1: ‘BLDPRS’ FOR UNDERSTOREY VEGETATION

Using the percent value of surveyed trees in a given plot that presented symptoms of beech leaf disease (‘bldprs’) as the dependent variable in the analysis of data collected from all understorey vegetation plots, Figure 6 suggests that site factors including slope percent, slope position, and forest overstorey density have the greatest effect on the presence of beech leaf disease symptoms on American beech seedlings under 1 m in height.

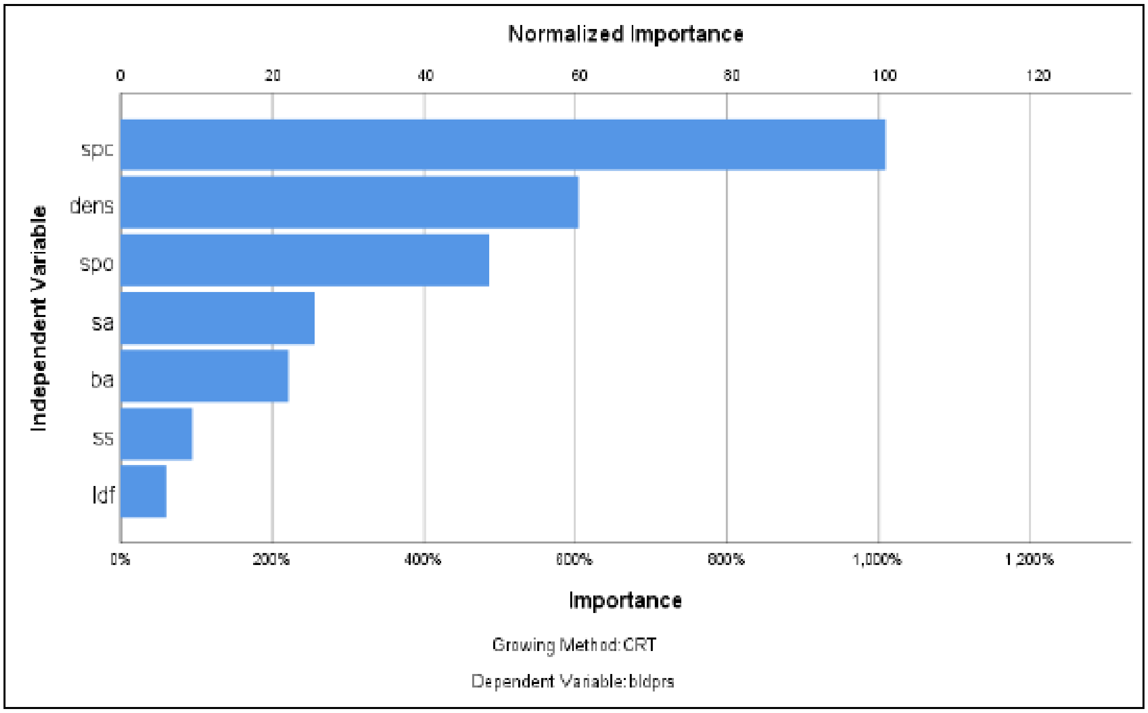

Figure 6. Independent variable importance chart for understorey vegetation with 'bldprs' as the dependent variable (Source: IBM SPSS 2020).

Regarding the data collected from all understorey vegetation plots, using the percent value of surveyed trees in a given plot that presented symptoms of beech leaf disease ('bldprs') as the dependent variable, the nodes of interest are nodes 3, 6, 9, 10, 11, 12, 13, and 14. The Gain Summary for each of the following terminal nodes is shown in Appendix IV. The following information has been derived from the classification tree illustrated in Figure 7.

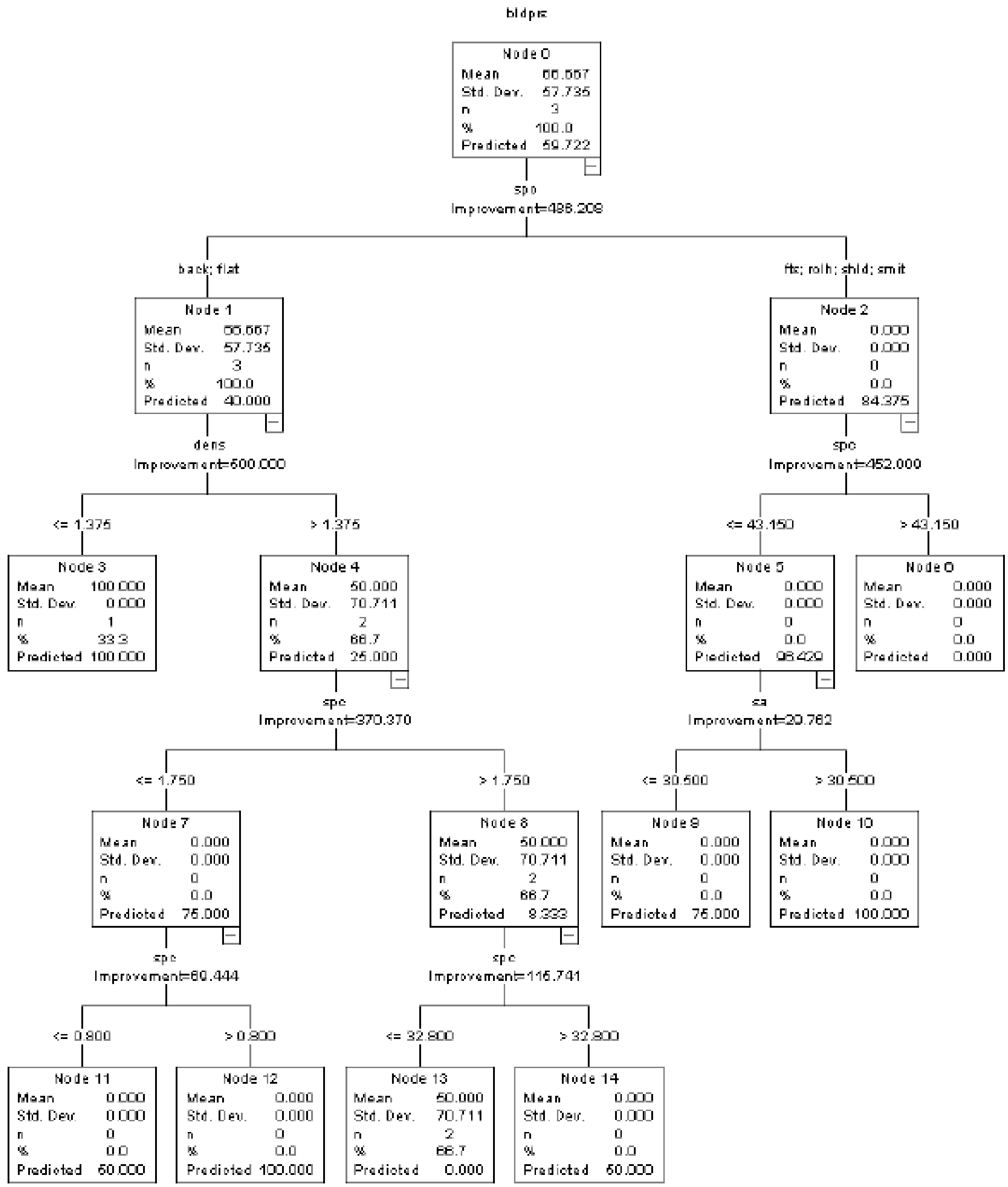

Figure 7. Classification tree for understorey vegetation with ‘bldprs’ as the dependent variable (Source: IBM SPSS 2020).

There are two cases in Node 3, accounting for 11.1% of the total number of cases in this model. This terminal node is attributed to sites on back slopes or flat ground with an average densiometer reading equal to or less that 1.375.

There is one case in Node 6, accounting for 5.6% of the total number of cases in this model. This terminal node is attributed to sites on foot and toe slopes, rolling hills, shoulders, or summits with a slope greater than 43.15%.

There is one case in Node 9, accounting for 5.6% of the total number of cases in this model. This terminal node is attributed to sites on foot and toe slopes, rolling hills, shoulders, or summits with slope equal to or less than 43.15% and slope aspect equal to or less than 30.50 degrees.

There are six cases in Node 10, accounting for 33.3% of the total number of cases in this model. This terminal node is attributed to sites on foot and toe slopes, rolling hills, shoulders, or summits with slope equal to or less than 43.15% and slope aspect greater than 30.50 degrees.

There is one case in Node 11, accounting for 5.6% of the total number of cases in this model. This terminal node is attributed to sites on back slopes or flat ground with an average densiometer reading greater than 1.375, and slope equal to or less than 0.8%.

There is one case in Node 12, accounting for 5.6% of the total number of cases in this model. This terminal node is attributed to sites on back slopes or flat ground with an average densiometer reading greater than 1.375, and slope greater than 0.8%.

There are five cases in Node 13, accounting for 27.8% of the total number of cases in this model. This terminal node is attributed to sites on back slopes or flat ground with an average densiometer reading greater than 1.375, and slope equal to or less than 32.8%.

There is one case in Node 14, accounting for 5.6% of the total number of cases in this model. This terminal node is attributed to sites on back slopes or flat ground with an average densiometer reading greater than 1.375, and slope greater than 32.8%.

The output of the classification tree for Model 1 produced two predictions of particular interest due to the number of cases represented and their consequent statistical significance: terminal nodes 10 and 13. When comparing the metrics given at each branch of the classification tree that connects the terminal node of interest to the root node, it was observed that similar decisions related to slope percent occurred for the predictions given in nodes 10 and 13; the classification tree predicted that slopes equal to or less than 32.8% are significant determiners of foliar symptom presence among American beech seedlings. The observed independent variable of significance ('spc') was further corroborated by the output of the independent variable importance chart for Model 1.

MODEL 2: 'BLDPRS' FOR SAPLING VEGETATION

Using the percent value of surveyed trees in a given plot that presented symptoms of beech leaf disease ('bldprs') as the dependent variable in the analysis of data collected from all sapling vegetation plots, Figure 8 suggests that site factors including forest overstorey density, slope aspect, basal area, and slope percent have the greatest effect on the presence of foliar symptoms on American beech saplings with a DBH under 10 cm.

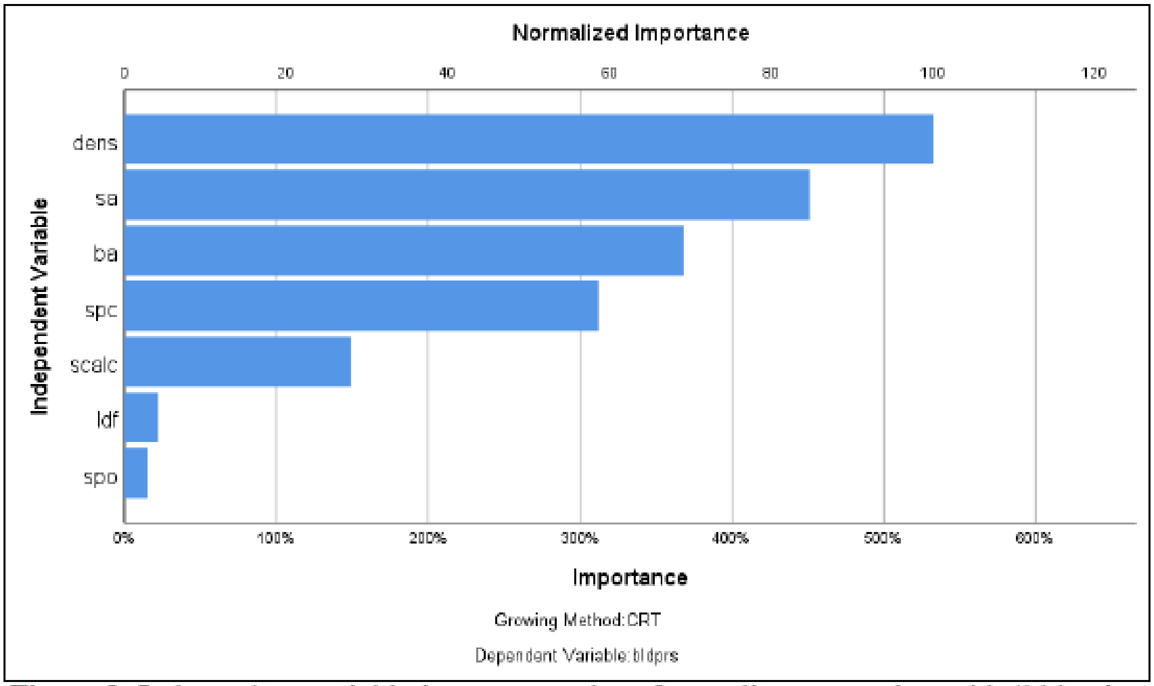

Figure 8. Independent variable importance chart for sapling vegetation with 'bldprs' as the dependent variable (Source: IBM SPSS 2020).

Regarding the data collected from sapling vegetation plots, using the percent value of surveyed trees in a given plot that presented symptoms of beech leaf disease ('bldprs') as the dependent variable, the nodes of interest are nodes 3, 4, 8, 10, 11, 12, 13, 15, and 16. The Gain Summary for each of the following terminal nodes is shown in Appendix VI. The following information has been derived from the classification tree illustrated in Figure 9.

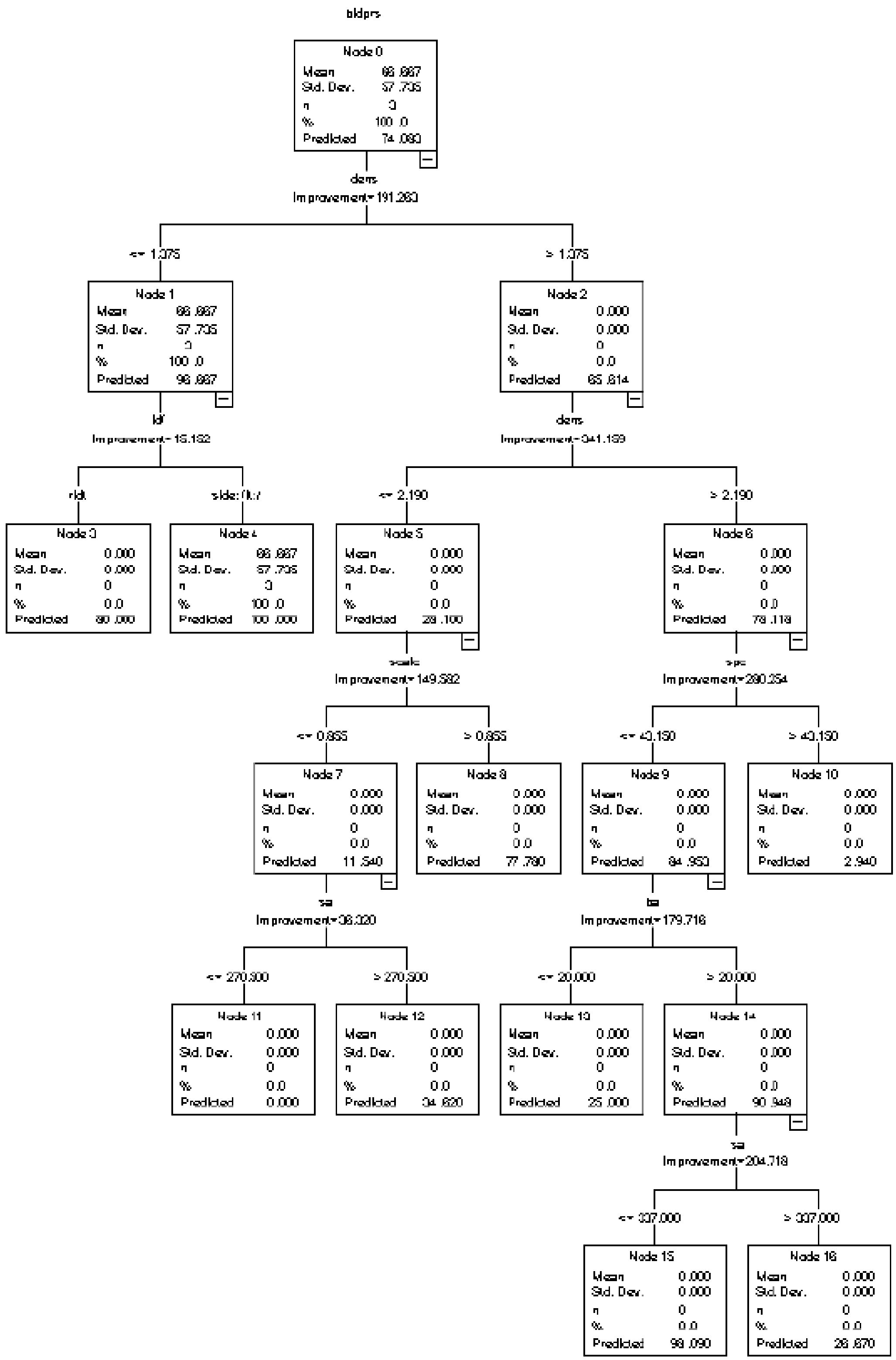

Figure 9. Classification tree for sapling vegetation with 'bldprs' as the dependent variable (Source: IBM SPSS 2020).

There is one case in Node 3, accounting for 4.5% of the total number of cases in this model. This terminal node is attributed to sites with an average densiometer reading equal to or less than 1.375 that also occur on ridgetops.

There are 5 cases in Node 4, accounting for 22.7% of the total number of cases in this model. This terminal node is attributed to sites with an average densiometer reading equal to or less than 1.375 that also occur on side slopes or flat ground.

There is one case in Node 8, accounting for 4.5% of the total number of cases in this model. This terminal node is attributed to sites with an average densiometer reading between 1.375 and 2.190, where the mean scale intensity on saplings growing on-site is greater than 0.85.

There is one case in Node 10, accounting for 4.5% of the total number of cases in this model. This terminal node is attributed to sites with an average densiometer reading greater than 2.190 where slope is greater than 40.15%.

There are two cases in Node 11, accounting for 9.1% of the total number of cases in this model. This terminal node is attributed to sites with an average densiometer reading between 1.375 and 2.190, where the mean scale intensity on saplings growing on-site is equal to or less than 0.85 and slope aspect is equal to or less than 270.50 degrees.

There is one case in Node 12, accounting for 4.5% of the total number of cases in this model. This terminal node is attributed to sites with an average densiometer reading between 1.375 and 2.190, where the mean scale intensity on saplings growing on-site is equal to or less than 0.85 and slope aspect is greater than 270.50 degrees.

There is one case in Node 13, accounting for 4.5% of the total number of cases in this model. This terminal node is attributed to sites with an average densiometer reading greater than 2.190 where slope is equal to or less than 40.15% and basal area is greater than 20.00 m^2/ha.

There are nine cases in Node 15, accounting for 40.9% of the total number of cases in this model. This terminal node is attributed to sites with an average densiometer reading greater than 2.190 where slope is equal to or less than 40.15%, basal area is greater than 20.00 m^2/ha, and slope aspect is equal to or less than 307.00 degrees.

There is one case in Node 16, accounting for 4.5% of the total number of cases in this model. This terminal node is attributed to sites with an average densiometer reading greater than 2.190 where slope is equal to or less than 40.15%, basal area is greater than 20.00 m^2/ha, and slope aspect is greater than 307.00 degrees.

The output of the classification tree for Model 2 produced two predictions of particular interest due to the number of cases represented and their consequent statistical significance: terminal nodes 4 and 15. When comparing the metrics given at each branch of the classification tree that connects the terminal node of interest to the root node, it was observed that there are no significant relationships between various measured site conditions and an increased presence of sapling-sized American beech with observable foliar symptoms of beech leaf disease, as similar findings could not be compared among the decisions associated with the terminal nodes of greatest significance.

MODEL 3: 'STRPC' FOR SAPLING VEGETATION

Using the percent value of surveyed trees in a given plot that presented foliar banding symptoms ('strpc') as the dependent variable in the analysis of data collected from all sapling vegetation plots, Figure 10 suggests that site factors including forest overstorey density, slope position, basal area, landform type, and slope percent have the greatest effect on the presence of early or moderate beech leaf disease symptoms on American beech saplings with a DBH under 10 cm.

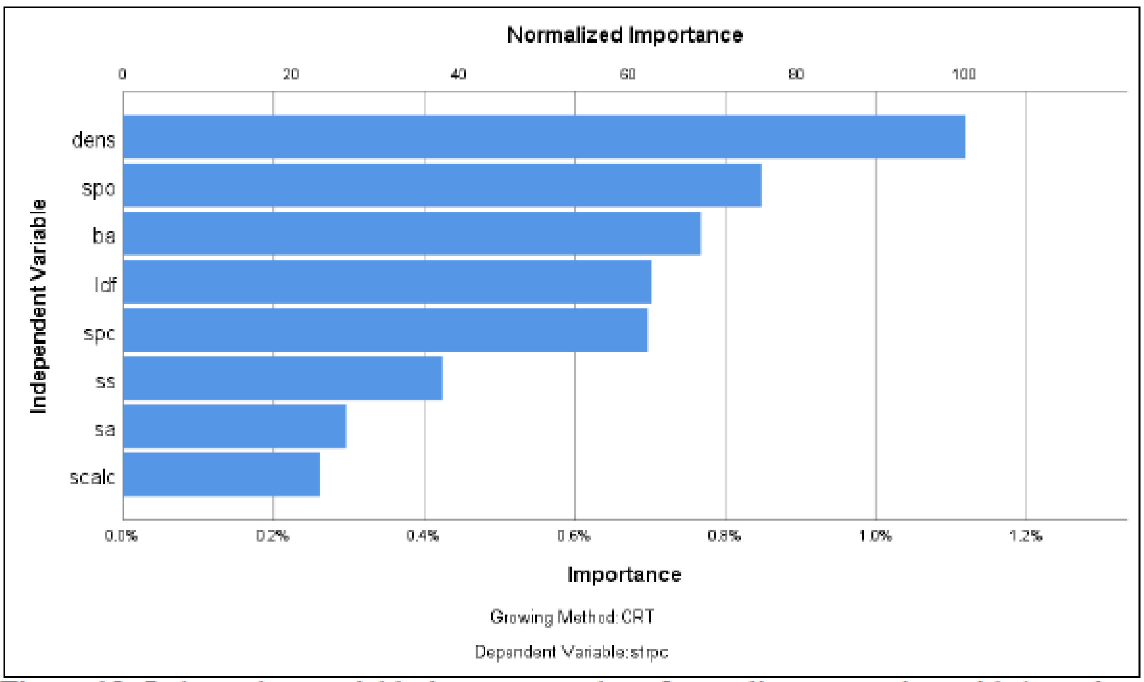

Figure 10. Independent variable importance chart for sapling vegetation with 'strpc' as the dependent variable (Source: IBM SPSS 2020).

Regarding the data collected from sapling vegetation plots, using the percent value of surveyed trees in a given plot that presented foliar banding symptoms ('strpc') as the dependent variable, the nodes of interest are nodes 8, 9, 10, 11, 15, 16, 17, 18, 19, 20, 21, 23 and 24. The Gain Summary for each of the following terminal nodes is shown in Appendix VIII. The following information has been derived from the classification tree illustrated in Figure 11.

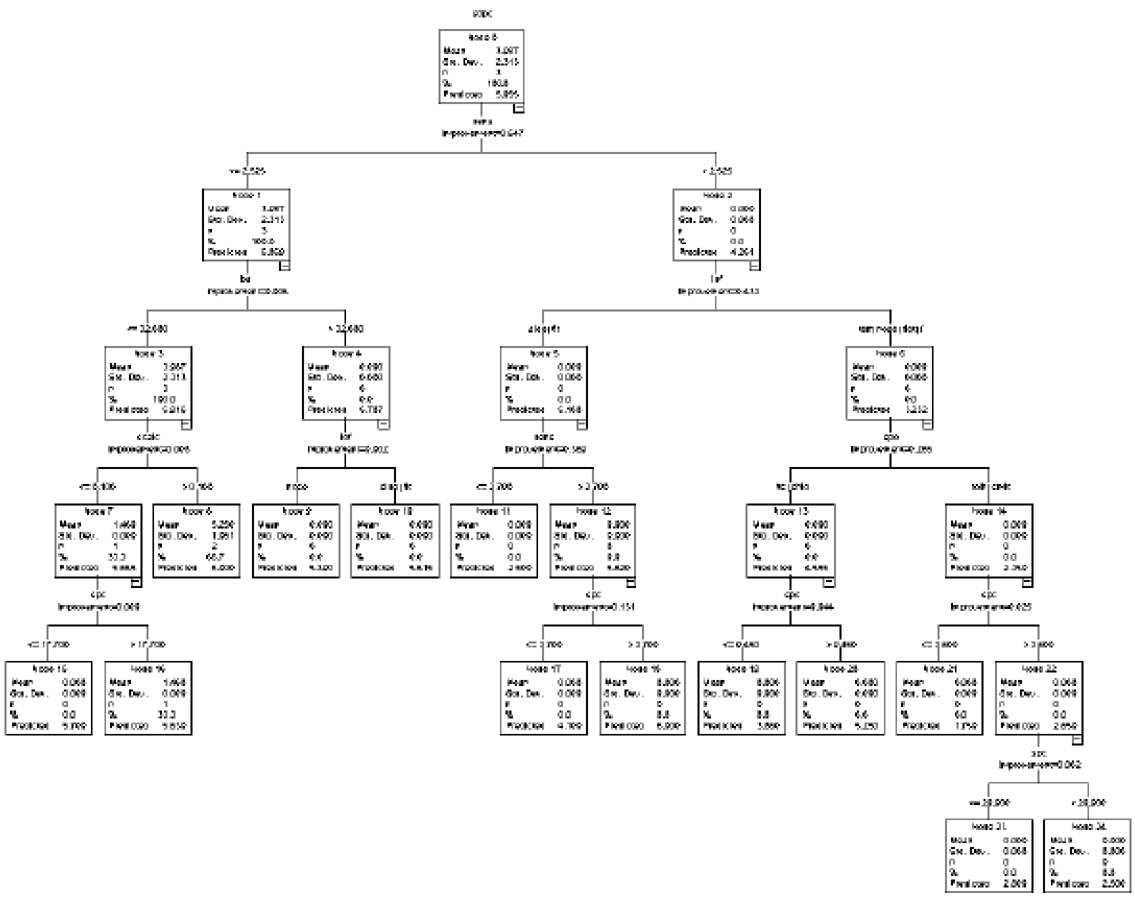

Figure 11. Classification tree for sapling vegetation with 'strpc' as the dependent variable (Source: IBM SPSS 2020).

There are eight cases in Node 8, accounting for 27.3% of the total number of cases in this model. This terminal node is attributed to sites with an average densiometer reading equal to or less than 2.525 where basal area is equal to or less than 32 m^2/ha and the mean scale intensity on saplings growing on-site is greater than 0.1.

There is one case in Node 9, accounting for 4.5% of the total number of cases in this model. This terminal node is attributed to sites with an average densiometer reading equal to or less than 2.525 where basal area is greater than 32 m^2/ha and the site is situated on a nose slope.

There are two cases in Node 10, accounting for 9.1% of the total number of cases in this model. This terminal node is attributed to sites with an average densiometer reading equal to or less than 2.525 where basal area is greater than 32 m^2/ha and the site is situated on a side slope or flat ground.

There is one case in Node 11, accounting for 4.5% of the total number of cases in this model. This terminal node is attributed to sites on side slopes or flat ground with an average densiometer reading between 2.525 and 2.790.

There is one case in Node 15, accounting for 4.5% of the total number of cases in this model. This terminal node is attributed to sites with an average densiometer reading equal to or less than 2.525 where basal area is equal to or less than 32 m^2/ha, the mean scale intensity on saplings growing on-site is equal to or less than 0.1, and slope is equal to or less than 17.7%.

There is one case in Node 16, accounting for 4.5% of the total number of cases in this model. This terminal node is attributed to sites with an average densiometer reading equal to or less than 2.525 where basal area is equal to or less than 32 m^2/ha, the mean scale intensity on saplings growing on-site is equal to or less than 0.1, and slope is greater than 17.7%.

There is one case in Node 17, accounting for 4.5% of the total number of cases in this model. This terminal node is attributed to sites on side slopes or flat ground with an average densiometer reading greater than 2.790 and slope equal to or less than 3.70%.

There are four cases in Node 18, accounting for 18.2% of the total number of cases in this model. This terminal node is attributed to sites on side slopes or flat ground with an average densiometer reading greater than 2.790 and slope greater than 3.70%.

There is one case in Node 19, accounting for 4.5% of the total number of cases in this model. This terminal node is attributed to sites with an average densiometer reading greater than 2.525 on a terrace, nose slope, or ridgetop where the slope position is characterized as a foot and toe slope or shoulder, and slope is equal to or less than 2.45%.

There is one case in Node 20, accounting for 4.5% of the total number of cases in this model. This terminal node is attributed to sites with an average densiometer reading greater than 2.525 on a terrace, nose slope, or ridgetop where the slope position is characterized as a foot and toe slope or shoulder, and slope is greater than 2.45%.

There is one case in Node 21, accounting for 4.5% of the total number of cases in this model. This terminal node is attributed to sites with an average densiometer reading greater than 2.525 on a terrace, nose slope, or ridgetop where the slope position is characterized as a rolling hill or summit, and slope is equal to or less than 3.60%.

There is one case in Node 23, accounting for 4.5% of the total number of cases in this model. This terminal node is attributed to sites with an average densiometer reading greater than 2.525 on a terrace, nose slope, or ridgetop where the slope position is characterized as a rolling hill or summit, and slope is between 3.60% and 20.90%.

There is one case in Node 24, accounting for 4.5% of the total number of cases in this model. This terminal node is attributed to sites with an average densiometer reading greater than 2.525 on a terrace, nose slope, or ridgetop where the slope position is characterized as a rolling hill or summit, and slope is greater than 20.90%.

The output of the classification tree for Model 3 produced two predictions of particular interest due to the number of cases represented and their consequent statistical significance: terminal nodes 8 and 18. When comparing the metrics given at each branch of the classification tree that connects the terminal node of interest to the root node, it was observed that there are no significant relationships between various measured site conditions and an increased presence of sapling-sized American beech with early or moderate symptoms of beech leaf disease in the form of interveinal foliar banding, as similar findings could not be compared among the decisions associated with the terminal nodes of greatest significance.

MODEL 4: 'CSSC' FOR SAPLING VEGETATION

Using the percent value of surveyed trees in a given plot that presented foliar curling, shrinking or shriveling symptoms ('cssc') as the dependent variable in the analysis of data collected from all sapling vegetation plots, Figure 12 suggests that site factors including slope position, basal area, landform type, and mean scale intensity have the greatest effect on the presence of severe beech leaf disease symptoms on American beech saplings with a DBH under 10 cm.

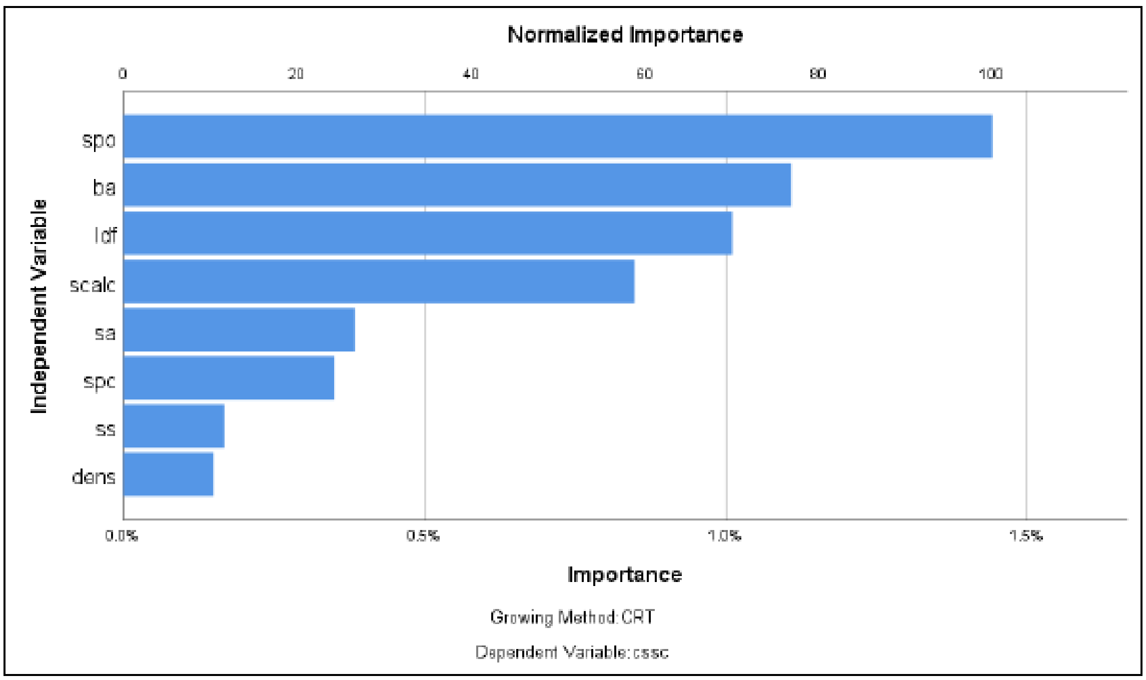

Figure 12. Independent variable importance chart for sapling vegetation with 'cssc' as the dependent variable (Source: IBM SPSS 2020).

Regarding the data collected from sapling vegetation plots, using the percent value of surveyed trees in a given plot that presented foliar curling, shrinking or shriveling symptoms ('cssc') as the dependent variable, the nodes of interest are nodes 3, 7, 8, 12, 13, 14, 16, 17, 19, 20, 21, and 22. The Gain Summary for each of the following terminal nodes is shown in Appendix X. The following information has been derived from the classification tree illustrated in Figure 13.

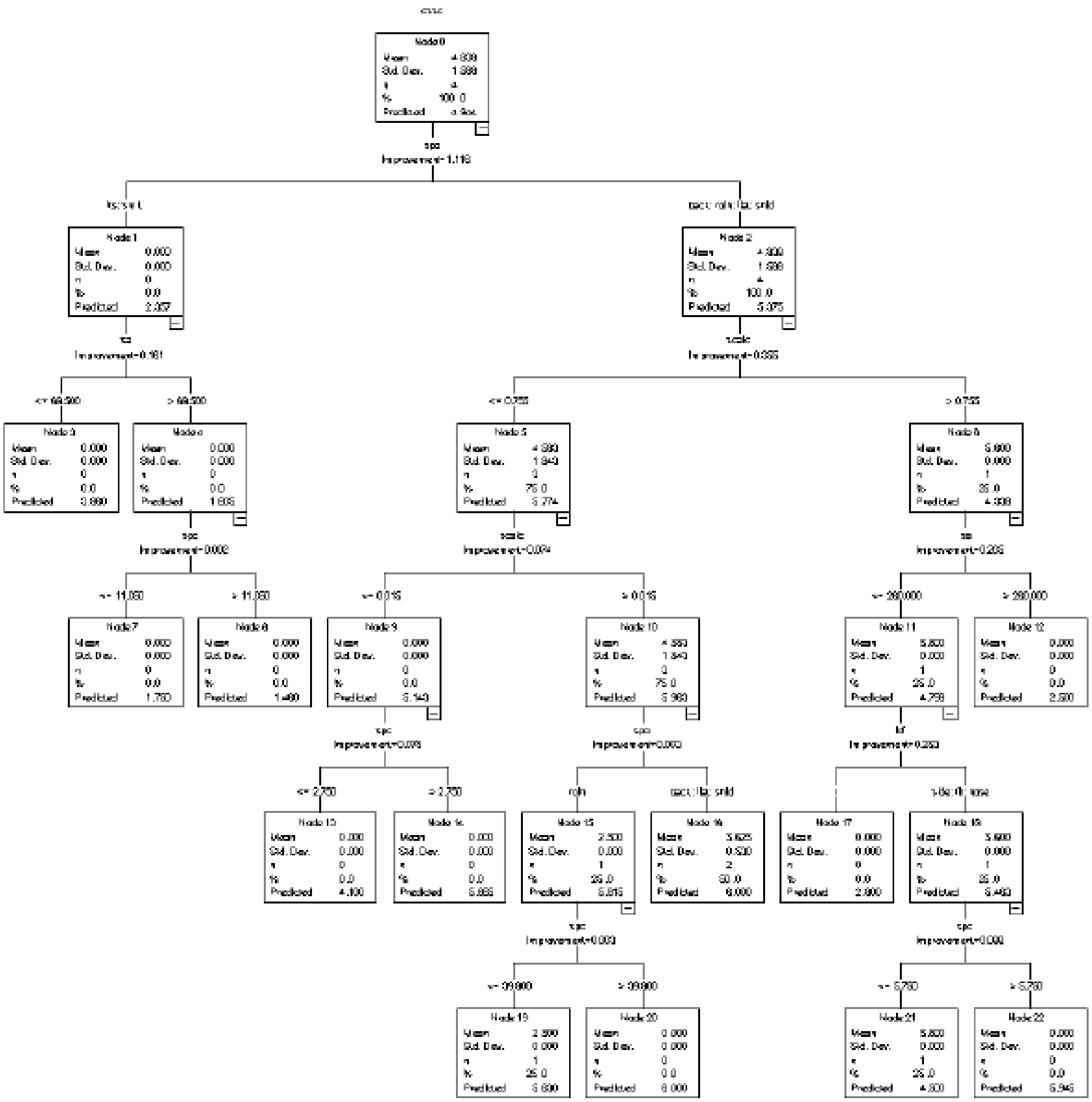

Figure 13. Classification tree for sapling vegetation with 'cssc' as the dependent variable (Source: IBM SPSS 2020).

There is one case in Node 3, accounting for 4.8% of the total number of cases in this model. This terminal node is attributed to sites on foot and toe slopes or summits where slope aspect is equal to or less than 69.50 degrees.

There is one case in Node 7, accounting for 4.8% of the total number of cases in this model. This terminal node is attributed to sites on foot and toe slopes or summits where slope aspect is greater than 69.50 degrees and the slope is equal to or less than 11.05%.

There is one case in Node 8, accounting for 4.8% of the total number of cases in this model. This terminal node is attributed to sites on foot and toe slopes or summits where slope aspect is greater than 69.50 degrees and the slope is greater than 11.05%.

There is one case in Node 12, accounting for 4.8% of the total number of cases in this model. This terminal node is attributed to sites on back slopes, rolling hills, shoulders, or flat ground, where the mean scale intensity on saplings growing on-site is greater than 0.755 and slope aspect is greater than 260.00 degrees.

There is one case in Node 13, accounting for 4.8% of the total number of cases in this model. This terminal node is attributed to sites on back slopes, rolling hills, shoulders, or flat ground, where the mean scale intensity on saplings growing on-site is equal to or less than 0.015 and the slope is equal to or less than 2.75%.

There are two cases in Node 14, accounting for 9.5% of the total number of cases in this model. This terminal node is attributed to sites on back slopes, rolling hills, shoulders, or flat ground, where the mean scale intensity on saplings growing on-site is equal to or less than 0.015 and the slope is greater than 2.75%.

There are eight cases in Node 16, accounting for 38.1% of the total number of cases in this model. This terminal node is attributed to sites on back slopes, shoulders, or flat ground where the mean scale intensity on saplings growing on-site is greater than 0.015.

There is one case in Node 17, accounting for 4.8% of the total number of cases in this model. This terminal node is attributed to sites on back slopes, rolling hills, shoulders, or flat ground, where the mean scale intensity on saplings growing on-site is greater than 0.755, slope aspect is greater than 260.00 degrees, and the landform type is not characterized as a side slope, nose slope, or flat ground.

There is one case in Node 19, accounting for 4.8% of the total number of cases in this model. This terminal node is attributed to sites on rolling hills where the mean scale intensity on saplings growing on-site is between 0.015 and 0.755 and slope is equal to or less than 39.80%.

There is one case in Node 20, accounting for 4.8% of the total number of cases in this model. This terminal node is attributed to sites on rolling hills where the mean scale intensity on saplings growing on-site is between 0.015 and 0.755 and slope is greater than 39.80%.

There is one case in Node 21, accounting for 4.8% of the total number of cases in this model. This terminal node is attributed to sites on back slopes, rolling hills, shoulders, or flat ground, where the mean scale intensity on saplings growing on-site is greater than 0.755, slope aspect is greater than 260.00 degrees, the landform type is characterized as a side slope, nose slope, or flat ground, and slope is equal to or less than 5.75%.

There are two cases in Node 22, accounting for 9.5% of the total number of cases in this model. This terminal node is attributed to sites on back slopes, rolling hills, shoulders, or flat ground, where the mean scale intensity on saplings growing on-site is greater than 0.755, slope aspect is greater than 260.00 degrees, the landform type is characterized as a side slope, nose slope, or flat ground, and slope is greater than 5.75%.

The output of the classification tree for Model 4 produced two predictions of particular interest due to the number of cases represented and their consequent statistical significance: terminal nodes 16 and 22. When comparing the metrics given at each branch of the classification tree that connects the terminal node of interest to the root node, it was observed that similar decisions related to slope position and mean scale intensity occurred for the predictions given in nodes 16 and 22; the classification tree predicted that back slopes, shoulders, and flat areas are significant determiners of severe symptom presence among American beech saplings in the form of foliar curling, shrinking, or shriveling. Additionally, the classification tree predicted that mean scale intensity values greater than

0.755 among American beech saplings growing within the given sapling vegetation plot is a significant determiner of severe symptom presence among saplings. The observed independent variables of significance ('spo' and 'scalc') were further corroborated by the output of the independent variable importance chart for Model 4.

It is observed from each of the classification trees produced from the four model runs that slope shape as an independent variable ('ss') is not associated with any of the branches that connect to the discussed terminal nodes. However, the independent variable importance charts produced for models 1, 3, and 4 on SPSS indicate that slope shape is of minor importance among all independent variables considered for the relationships analyzed within the entire datasets that were input into these models.

DISCUSSION

The data collected in the field from each vegetation monitoring plot was used to form a classification tree analysis, which allows for the determination of the relative importance of different variables for identifying homogeneous groups that exist within the dataset; this has been accomplished using a decision tree that predicts the characteristics of the sites being studied. The output of the classification tree provided many predictions from each of the model runs, but those of greater interest in this study are Nodes 10 and 13 from the understorey vegetation dataset concerning the 'bldprs' dependent variable, Nodes 4 and 15 from the sapling vegetation dataset concerning the 'bldprs' dependent variable, Nodes 8 and 18 from the sapling vegetation dataset concerning the 'strpc' dependent variable, and Nodes 16 and 22 from the sapling vegetation dataset concerning the 'cssc' dependent variable. These eight nodes are the most statistically significant for analysis due to the number of cases represented in these nodes. Among all of the terminal nodes produced from the four model runs, 80.95% were associated with two or fewer cases, and therefore present less of a meaningful prediction based on the data input into the SPSS software.

For each of the discussed terminal nodes representing an outcome of their respective models, the metrics given at each branch of the classification tree that connects the terminal node to the root node were analyzed to determine how they influence the relevant dependent variable in an attempt to identify a relationship between particular site conditions and increased severity of beech leaf disease symptoms; this strategy helps to describe the stressor-response relationship that exists within the data between American beech trees and the environmental conditions occurring on the sites surveyed. Among the majority of relationships examined within each of the four model runs conducted, no statistically significant relationships were found. However, comparison of the classification trees produced from each model indicated three statistically significant relationships between site factors and beech leaf disease symptom presence and severity in models 1 and 4.

SITE FACTORS INFLUENCING SYMPTOM PRESENCE AMONG SEEDLINGS

Slope Percent

Statistical analysis of the data collected from all understorey vegetation monitoring plots revealed that similar decisions related to slope percent occurred for the predictions given in nodes 10 and 13 from Model 1, where slopes equal to or less than 32.8% are significantly related to foliar symptom presence among American beech seedlings. This value calculated by the classification tree output on SPSS corresponds to a range of slope classes of 'level' to 'very strong' (SCWG 1998; Meyer 2010). This range of slope classes is typically associated with lower slope positions that receive more water from upslope, and thus experience poorer drainage and greater soil moisture over extended time periods relative to upper-slope positions (MacMillan and Pettapiece 2000; Meyer 2010). On gentle and level slope classes, mottling and gleying may occur; this is indicative of periodic or prolonged saturation and subsequent oxidation of ferrous iron and deposition of hydrated ferric oxides (SCWG 1998; Meyer 2010). However, American beech stands are not generally associated with soils of the Gleysolic Order. In Tubbs' (1978) writing on northern hardwood ecology, he asserts that healthy American beech populations typically occur on dry to mesic coarse-textured soils that are well-drained. Though beech trees can occur on poorly-drained sites, they are relatively intolerant to the conditions experienced in those areas compared to other northern hardwood species. Additionally, specimens that grow on poorly-drained terrain develop shallower root systems, making those individuals more easily impacted by sudden and rapid decline in soil moisture; subsequently, American beech trees with shallow root systems often experience limited radial growth. Regarding the tolerance of American beech to moist soil conditions as it pertains to seedlings specifically, it has also been found that germination of beech seeds is less successful on wet sites relative to drier mineral soils and leaf litter (Fowells 1965; Smith and Every 1980); this suggests that newly-established surviving seedlings exert more energy for growth and undergo greater stress during development when exposed to moist soil conditions, resulting in reduced vigour during early growth stages.

Differences in topographic position may also influence mesoclimates, as valley bottoms and level areas are typically colder at night relative to sites on extreme or steep slopes due to air drainage from steeper surrounding slopes (Meyer 2010; White 2015). Though the literature indicates that American beech is a shade-tolerant species due to its low respiration rate and stomatal responsiveness to changes in light intensity (Loach 1967), Tubbs and Houston (1990) maintain that beech exhibit reduced tolerance to shady conditions when exposed to colder climates and poor soil quality, which may result from the mesoclimates experienced at sites situated on gentle lower slopes.

Eluviated brown chernozems, which are characterized by slight to moderate acidity in the upper soil horizons underlain by clay illuviation (SCWG 1998), are often found on lower concave slopes where sediments have been deposited from upslope (Meyer 2010). Additionally, humic folisols largely composed of well-decomposed H horizons typically develop on lower, gentle slopes and in valley bottoms, and are associated with rooting channels, which Gish and Jury (1983) found to increase solute dispersion in soil (SCWG 1998). The writings of Tubbs and Houston (1990) indicate that American beech trees achieve the greatest size when grown in alluvial soils, which are typically fine-textured and largely composed of clay, silt, and organic matter (Meyer

2010). Further, the works of Tubbs and Houston (1990) and Fowells (1965) suggest that populations of American beech are most plentiful in grey-brown podzols (now considered 'podzolic grey-brown luvisols' according to the Canadian System of Soil Classification (SCWG 1998)) characterized by a silty B horizon overlying clay, as well as laterite soil groups that are rich in iron and aluminum (Tardy 1997).

The soil properties most closely related to the establishment and growth of American beech populations as described by Fowells (1965) and Tubbs and Houston (1990) are somewhat consistent with the soil properties associated with topographical features related to the range of slope classes under study (such as the typical pH levels, soil texture, and presence of organic matter), which suggests that the original prediction that a greater occurrence of conditions that negatively impact vigour of American beech corresponds to greater severity of beech leaf disease symptoms is refuted. However, other features associated with moderate slopes are likely to negatively impact the vigour of American beech and thus render them more susceptible to infection by opportunistic pathogens, perhaps including beech leaf disease as stated in the prediction. The work of both Fowells (1965) and Smith and Every (1980) indicate that germination of American beech seeds is less successful on wet sites compared to dry mineral soils, suggesting that those seedlings that successfully germinate under unfavourable soil moisture conditions (similar to those associated with level ground and gentle to moderate slopes) undergo restricted root growth and greater growth stress during early seedling development, and exhibit an overall reduction in vigour as a result (Meyer 2010). Further, the influence of steep slopes on the mesoclimates of sites on relatively level ground or low slopes can stimulate colder nocturnal temperatures according to Meyer (2010) and White (2015), which can negatively impact the vigour of beech seedlings by altering foliar stomatal responsiveness to light conditions, resulting in reduced tolerance to shady conditions that are often experienced by American beech saplings under 1 m in height (Tubbs and Houston 1990). The results of this study indicate that American beech seedlings experience a significantly higher likelihood of presenting foliar symptoms of beech leaf disease on sites where slopes are equal to or less than 32.8%, thereby suggesting that there may be a link between unfavourable site conditions related to soil moisture and nocturnal mesoclimates and beech leaf disease infection potential among seedlings. Therefore, these findings partly support the original prediction that a greater occurrence of conditions that negatively impact vigour of American beech corresponds to greater severity of beech leaf disease symptoms.

SITE FACTORS INFLUENCING SYMPTOM PRESENCE AMONG SAPLINGS

Statistical analysis of the data collected from all sapling vegetation monitoring plots revealed that there are no significant relationships that exist between any site factors and an increased presence of American beech saplings with observable foliar symptoms of beech leaf disease.

SITE FACTORS INFLUENCING EARLY OR MODERATE SYMPTOM PRESENCE AMONG SAPLINGS

Statistical analysis of the data collected from all sapling vegetation monitoring plots revealed that there are no significant relationships that exist between any site factors and an increased presence of American beech saplings with early or moderate foliar symptoms of beech leaf disease in the form of interveinal banding.

SITE FACTORS INFLUENCING SEVERE SYMPTOM PRESENCE AMONG SAPLINGS

Slope Position

Statistical analysis of the data collected from all sapling vegetation monitoring plots revealed that similar decisions related to slope position occurred for the predictions given in nodes 16 and 22 from Model 4, where the occurrence of shoulders, back slopes, and flat areas are significantly related to severe foliar symptom presence among American beech saplings in the form of foliar curling, shrinking, or shrivelling. ‘Shoulders’ are considered a transitionary position between a summit and a back slope, where the slope is always convex; shoulders typically experience the greatest erosion loss on a mountain or hill due to their high slope positions. ‘Back slopes’ constitute the midportion of a landmass and can either be convex or concave (Dr. Reed, pers. comm., July 30, 2019). Slope erosion commonly occurs at high positions due to the gravitational force that acts on soil particles to initiate downward movement (Keller 1985; Meyer 2010) and can result in root exposure among trees growing on the eroded slopes as the soil surface is removed over time. Soil erosion and consequent root exposure that typically occurs at shoulder sites is thought to be associated with beech sprouting, according to Takahashi *et al.* (2010) and Ramage and Mangana (2017); the work of Takahashi *et al.* (2010) indicates that young American beech trees under 2 m in height in southern Quebec regenerate by vegetative sprouting from parent tree roots at upper- and mid-slopes, while regeneration by seed is more common at lower slope positions. Held (1983) and Jones and Raynal (1986) theorized that stressful events such as root injury sustained from freezing and thawing lead to increased occurrence of American beech root sprouts, particularly in the species' northern distribution range. Holmes and Likens (2016) further assert that American beech trees that undergo stressful biotic events such as infection by bark canker fungi responsible for beech bark disease are more likely to produce root sprouts as a stress response rather than release seeds. Sprouting is a common occurrence among temperate hardwood trees, and is a known induced response to injury or sudden and stressful changes in environmental conditions (Del Tredici 2001). Due to the literature supporting the concept that root sprouting by hardwood trees such as American beech is stimulated by stressful environmental factors, as well as the work of Takahashi *et al.* (2010) that found a relationship between high slope positions and an increased frequency of beech regeneration by vegetative root sprouting, it can be theorized that American beech are ill-adapted to the erosional activity of shoulders and back slopes due to the resulting stress response that they typically produce when exposed to such conditions. As a result, it can be assumed that stressed American beech saplings will endure reduced vigour when exposed to the environmental conditions associated with sites characterized by shoulders and back slopes. By negatively impacting the health and vigour of vulnerable beech saplings, the juvenile trees would become increasingly susceptible to opportunistic pathogens and pests. The results of this study indicate that American beech saplings experience a significantly higher likelihood of expressing severe foliar symptoms of beech leaf disease if growing on a shoulder or back slope, thereby suggesting that there may be a link between the conditions associated with high slope positions and beech leaf disease infection potential among saplings. These findings support the original prediction that a greater occurrence of site conditions that negatively impact vigour of American beech corresponds to greater severity of beech leaf disease symptoms.

Due to lower-slope sites receiving subsurface water from upslope, soils on upper- and mid-slope positions such as shoulders or back slopes also hold less water over shorter time periods relative to soils found on lower-slope sites. Both shoulders and back slopes experience rapid movement of water through soil, which reduces the water content and creates well-draining soil conditions (Meyer 2010). Takahashi *et al.*'s (2010) findings support the accepted theory that American beech saplings are sensitive to low soil moisture. At shoulders (and back slopes to a lesser extent), soil depth is often shallow and lacks a C horizon due to erosion, with low water-holding capacity that is unfavourable to the development of juvenile beech trees. These authors also found that the maximum DBH of mature American beech measured on lower slopes were slightly larger than those on upper slope sites in the Gault Nature Reserve in southern Quebec (Takahashi *et al*. 2010), indicating that radial growth may be slowed among saplings growing on shallow, drier soils associated with shoulders and back slopes relative to lower slope positions (such as foot and toe slopes) due to a lack of adequate adaptation to these particular site conditions. The adverse effects on radial growth and water uptake caused by soil conditions on back slopes and shoulders suggest that the vigour of juvenile American beech is reduced relative to beech saplings growing on lower slope positions associated with site conditions to which American beech is better adapted, further supporting the theory that there is a relationship between the conditions associated with high slope positions and beech leaf disease infection potential among saplings. Therefore, these findings also support the original prediction that a greater occurrence of site conditions that negatively impact vigour of American beech corresponds to greater severity of beech leaf disease symptoms.

'Flat' areas occur where the entire area is flat; if adjacent to hills or bodies of water, these areas can experience flooding during high water periods (Dr. Reed, pers. comm., July 30, 2019). As discussed in the previous paragraphs related to the results given from Model 1, sites on level ground receive excess water from surrounding slopes through gravitational force and exhibit poor soil drainage and pronounced soil moisture as a result (MacMillan and Pettapiece 2000; Meyer 2010). As a consequence, the presence of poorly-drained soils impacts root development of juvenile beech, resulting in the growth of shallow root systems that prevent American beech saplings from easily overcoming sudden changes in water availability and inhibiting radial growth (Fritts 1962). Additionally, germination success is reduced on wetter sites associated with flat areas and floodplains (Fowells 1965; Smith and Every 1980), which indicates that excessive soil moisture inhibits the growth and vigour of juvenile American beech. Level areas also experience colder nocturnal temperatures relative to surrounding slopes (Meyer 2010; White 2015), which may impact foliar stomatal response to light and limit shade tolerance among saplings growing in flat areas (Tubbs and Houston 1990). These various site conditions associated with level areas suggest that juvenile American beech trees face greater biotic stresses when growing in mesic conditions associated with level sites compared to well-draining lower slopes or foot and toe slopes. However, other findings suggest that vigour is more pronounced in flat areas relative to shoulders and back slopes. Takahashi *et al.* (2010) determined that American beech found at moist sites in flat areas near the base of slopes were predominantly regenerated by seed rather than vegetative cloning, thus indicating that the parent trees growing on level ground are under less environmental stress than those at high slope positions that reproduce via root sprouting. However, the results of the 2010 study failed to measure survivability of the young American beech that resulted, so no conclusion could be drawn on the effects of level sites on the vigour of American beech during the more vulnerable seedling and sapling stages. The results of this study generally indicate that American beech seedlings experience a significantly higher likelihood of presenting severe foliar symptoms of beech leaf disease if growing on flat ground relative to foot and toe slopes or gentle rolling hills, thereby suggesting that there may be a link between the conditions associated with level sites (particularly those related to soil moisture and nocturnal mesoclimates) and beech leaf disease infection potential among saplings. Therefore, these findings further substantiate the study's prediction that a greater occurrence of conditions that negatively impact vigour of American beech corresponds to greater severity of beech leaf disease symptoms.

Mean Scale Intensity

Statistical analysis of the data collected from all sapling vegetation monitoring plots revealed that similar decisions related to mean scale intensity occurred for the predictions given in nodes 16 and 22 from Model 4, where the occurrence of mean scale intensity code values greater than 0.755 are significantly related to severe foliar symptom presence among American beech seedlings in the form of foliar curling, shrinking, or shriveling. This value, calculated by the classification tree output on SPSS, corresponds to a scale intensity value greater than 'trace', wherein more than one to 10 single scale colonies occur on a given American beech sapling in a sapling vegetation plot, on average (Dr. Reed, pers. comm., July 30, 2019).

Though the exotic woolly beech scale is not able to directly kill host trees, this scale insect is responsible for reducing the vigour and growth of American beech, thereby reducing their resistance to fungal infection and making them susceptible to infection by *Neonectria faginata* and *Neonectria ditissima* (McLaughlin and Greifenhagen 2012) through the creation of miniscule wounds on the thin and vulnerable bark of beech stems (Ehrlich 1934; Fajvan *et al.* 2019; Houston and O'Brien 2008). The feeding damage to beech bark caused by the woolly beech scale allows for fungal inoculation to occur; once the bark canker fungi colonize the host tree's stem, the stem becomes weakened and girdled, with canopy death resulting (Houston and O'Brien 2008).

There is a current lack of literature that quantifies the change in susceptibility to opportunistic pathogens and insect pests experienced by American beech that are infested with woolly beech scale or afflicted by beech bark disease. However, the damage sustained from woolly beech scale and resulting bark canker fungi are known to negatively influence the health and vigour of host trees, which would thereby render them more susceptible to other opportunistic pathogens relative to healthy American beech occurring in otherwise identical growth conditions. The results of this study indicate that American beech saplings experience a significantly higher likelihood of expressing severe foliar symptoms of beech leaf disease if beech scale colonies occur on the stem, thereby suggesting that there may be a link between damage inflicted by woolly beech scale feeding and beech leaf disease infection potential among saplings. These findings support the original prediction that a greater occurrence of conditions that negatively impact vigour of American beech corresponds to greater severity of beech leaf disease symptoms.

LIMITATIONS AND SOURCES OF ERROR

The various metrics measured at each vegetation monitoring plot in the field failed to include any related to soil conditions such as texture, acidity, moisture, or parent material. Therefore, any conclusions drawn in this study related to the relationships between soil conditions and beech leaf disease symptom severity were drawn from inferences based on literature pertaining to soil characteristics associated with the topographic features identified at each site. Any future related surveys conducted in the field should include the sampling and measurement of soil parameters to validate the assumptions made in this study.

Despite the extreme caution exercised in the field when collecting data in the vegetation monitoring plots, there is always the potential for human error in surveying. Although the statistical analysis of this study attempted to mitigate inaccuracies in the data by only considering seedlings and saplings that are more easily observable in an outdoor surveying environment relative to tall overstorey trees, the observations considered in the Results section may not provide a completely accurate representation of the severity of foliar symptoms among the American beech trees studied.

Further, the independent variable importance charts illustrated in the Results section do not indicate the direction of the relationships between the variables under study and the predicted probability of symptom occurrence. Although inferences can be made about the directions of the identified relationships based on current literature, a model with more easily-interpretable parameters must be used to statistically evaluate this. Therefore, the corroboration of the results given from the classification trees in each model may not be the most statistically accurate avenue.

CONCLUSION

The findings of this study generally indicate that the presence of environmental conditions that are likely to cause stress to American beech seedlings and saplings are correlated to a higher likelihood of infection by beech leaf disease, as well as a higher risk of expressing severe foliar symptoms among sapling-sized trees. Though the study was not able to determine the causal agent responsible for beech leaf disease or indicate how the disease is transmitted among beech trees, the results provide support to the theory that the causal agent or vectoring species is opportunistic and is more likely to inflict damage on weakened specimens occurring in unsuitable growth conditions that reduce vigour. Regarding the popular theory that a parasitic nematode such as *Litylenchus crenatae* is responsible for either vectoring the unknown causal agent or directly inflicting damage by feeding on foliage and buds of beech trees, the results of this study suggests that any parasitic nematode associated with beech leaf disease infection is an opportunistic organism that is more easily able to colonize host trees that are weakened and less able to fight off an attack.

The results of the study have revealed that particular environmental conditions associated with many current American beech stands in southwestern Ontario are potentially conducive to the development of beech leaf disease due to the stress response that may be expressed by juvenile American beech that are poorly adapted. Fortunately, recognition of this issue provides opportunities to create or enhance management objectives to promote health and vigour of American beech populations and mitigate the spread of beech leaf disease in North America, by ensuring that any new plantings of American beech occur on sites to which they are properly adapted. The results further emphasize the need to develop practical control measures for beech scale infestations, as this study identified a relationship between woolly beech scale colonization and the presence of severe foliar beech leaf disease symptoms among saplings; by protecting vulnerable American beech saplings from being infested by scale insects, they may remain vigorous enough to overcome a secondary attack from the mystery causal agent of concern.

Despite the discoveries made in this study, much more work is left to be done to identify the causal agent responsible for this fatal foliar disease and fully understand its mechanism of spread. The use of a transmission electron microscope to examine infected foliar tissue for the presence of viral bodies or phytoplasmas may be fundamental to answering all of the unknowns surrounding beech leaf disease, and for developing the most effective control measures possible to adequately protect the nation's valuable remaining American beech stands.

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APPENDICES

APPENDIX I

Beech Leaf Disease Symptom Severity Metrics Taken from Sapling Vegetation Monitoring Plots

Slope %	Slope Aspect	Landform Type	Slope Shape	Slope Position	Avg. Densiometer Reading	Avg. Scale Intensity (0-5)	Total Basal Area	% BLD Presence	Avg. Cover Class Code for Striped Foliar Symptoms 'strpc' (1-8)	Avg. Cover Class Code for Severe Foliar Symptoms 'cssc' (1-8)
35.5	320	side	vex	back	2.75	1	42	100	2.50	2.50
53	193	side	vex	back	0	0.50	24	100	6	6
9.2	55	terr	vex	fts	2.67	0.14	38	92.86	3.86	3.86
37.3	42	nose	vex	rolh	3.00	0.42	30	100	2.50	2.50
49	210	side	vex	rolh	3.13	0.03	38	2.94	6	6
2.7	280	flt	fl	flat	1.88	0.65	30	34.62	6	6
1.6	/	flt	fl	flat	3.25	0	24	100	4.10	4.10
3.9	/	flt	fl	flat	0.50	0	22	100	5.70	5.70
9.7	162	ridt	vex	shld	3.50	0.75	34	100	5.25	5.25
2.7	224	ridt	vex	smit	4.13	0.13	24	100	1.75	1.75
2	/	flt	fl	flat	0	1.00	32	100	4.50	4.50
0.2	/	flt	cave	flat	1.33	0.80	42	100	5.60	5.60
30.6	340	side	vex	rolh	0	0.25	34	100	5.63	5.63
31.5	299	side	vex	rolh	0.50	0	/	100	5.63	5.63
19.4	82	/	vex	fts	0	0.08	18	100	1.46	1.46
3	19	ridt	vex	shld	0.82	0.20	32	80	6	6
7.8	349	flt	fl	flat	2.83	0.33	26	26.67	6	6
40.2	330	nose	vex	back	0.25	0.50	24	0	6	6
15.5	1	side	cave	back	2.83	1.00	20	25	6	6
30.1	110	nose	vex	back	1.42	0.33	32	0	6	6
4.5	85	/	cave	rolh	2.83	0.80	38	100	2.80	2.80
9.5	200	nose	vex	back	1.75	1.00	44	77.78	5.89	5.89
0	94	flt	fl	flat	2.38	0.53	28	94.12	6	6
1.9	261	flt	fl	flat	2.00	0.71	22	0	6	6
5.8	325	flt	fl	flat	6.50	0.41	26	95.83	6	6

Source: OFRI 2019.

APPENDIX II

Beech Leaf Disease Symptom Severity Metrics Taken from Understorey Vegetation Monitoring Plots

Slope %	Slope Aspect	Landform Type	Slope Shape	Slope Position	Avg. Densiometer Reading	Total Basal Area	% BLD Presence
35.5	320	side	vex	back	2.75	42	50
9.2	55	terr	vex	fts	2.67	38	100
37.3	42	nose	vex	rolh	3.00	30	100
49	210	side	vex	rolh	3.13	38	0
2.7	280	flt	fl	flat	1.88	30	0
1.6	/	flt	fl	flat	3.25	24	100
3.9	/	flt	fl	flat	0.50	22	100
9.7	162	ridt	vex	shld	3.50	34	100
2.7	224	ridt	vex	smit	4.13	24	100
0.2	/	flt	cave	flat	1.33	42	100
31.5	299	side	vex	rolh	0.50	/	100
3	19	ridt	vex	shld	0.82	32	75
7.8	349	flt	fl	flat	2.83	26	0
40.2	330	nose	vex	back	0.25	24	100
15.5	1	side	cave	back	2.83	20	0
30.1	110	nose	vex	back	1.42	32	0
4.5	85	/	cave	rolh	2.83	38	100
9.5	200	nose	vex	back	1.75	44	100
0	94	flt	fl	flat	2.38	28	50
1.9	261	flt	fl	flat	2.00	22	0
5.8	325	flt	fl	flat	6.50	26	0

Source: OFRI 2019.

APPENDIX III

Independent Variable Importance for Understorey Vegetation Model Given 'bldprs' as the Dependent Variable

Independent Variable	Importance	Normalized Importance (%)
spc	1009.77	100
dens	604.26	59.8
spo	486.21	48.2
sa	256.45	25.4
ba	220.93	21.9
ss	94.52	9.4
ldf	60.15	6.0

Source: IBM SPSS 2020.

APPENDIX IV

Gain Summary for Terminal Nodes for Understorey Vegetation Model Given 'bldprs' as the Dependent Variable

Node	Number of Cases in Node	Percentage of Total Cases in Node (%)
3	2	11.1
6	1	5.6
9	1	5.6
10	6	33.3
11	1	5.6
12	1	5.6
13	5	27.8
14	1	5.6

Source: IBM SPSS 2020.

APPENDIX V

Independent Variable Importance for Sapling Vegetation Model Given 'bldprs' as the Dependent Variable

Independent Variable	Importance	Normalized Importance (%)
dens	532.42	100
sa	451.30	84.8
ba	368.46	69.2
spc	312.24	58.6
scalc	149.58	28.1
ldf	21.93	4.1
spo	15.15	2.8

Source: IBM SPSS 2020.

APPENDIX VI

Gain Summary for Terminal Nodes for Sapling Vegetation Model Given 'bldprs' as the Dependent Variable

Node	Number of Cases in Node	Percentage of Total Cases in Node (%)
3	1	4.5
4	5	22.7
8	1	4.5
10	1	4.5
11	2	9.1
12	1	4.5
13	1	4.5
15	9	40.9
16	1	4.5

Source: IBM SPSS 2020.

APPENDIX VII

Independent Variable Importance for Sapling Vegetation Model Given 'strpc' as the Dependent Variable

Independent Variable	Importance	Normalized Importance (%)
dens	1.12	100
spo	0.85	75.9
ba	0.77	68.7
ldf	0.70	62.7
spc	0.69	62.2
ss	0.43	38.0
sa	0.30	26.5
scalc	0.26	23.4

Source: IBM SPSS 2020.

APPENDIX VIII

Gain Summary for Terminal Nodes for Sapling Vegetation Model Given 'strpc' as the Dependent Variable

Node	Number of Cases in Node	Percentage of Total Cases in Node (%)
8	6	27.3
9	1	4.5
10	2	9.1
11	1	4.5
15	1	4.5
16	1	4.5
17	1	4.5
18	4	18.2
19	1	4.5
20	1	4.5
21	1	4.5
23	1	4.5
24	1	4.5

Source: IBM SPSS 2020.

APPENDIX IX

Independent Variable Importance for Sapling Vegetation Model Given 'cssc' as the Dependent Variable

Independent Variable	Importance	Normalized Importance (%)
spo	1.44	100
ba	1.11	76.8
ldf	1.01	70.1
scalc	0.85	58.8
sa	0.38	26.7
spc	0.35	24.3
ss	0.17	11.7
dens	0.15	10.3

Source: IBM SPSS 2020.

APPENDIX X

Gain Summary for Terminal Nodes for Sapling Vegetation Model Given 'cssc' as the Dependent Variable

Node	Number of Cases in Node	Percentage of Total Cases in Node (%)
3	1	4.8
7	1	4.8
8	1	4.8
12	1	4.8
13	1	4.8
14	2	9.5
16	8	38.1
17	1	4.8
19	1	4.8
20	1	4.8
21	1	4.8
22	2	9.5

Source: IBM SPSS 2020.