Deer Impacts on Forested Communities and Canada Yew Populations at Apostle Islands National Lakeshore, Wisconsin

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ABSTRACT

Abundant white-tailed deer (*Odocoileus virginianus*) present a significant management problem in forested landscapes of North America. Conserving vulnerable communities requires quantifying herbivory levels and the density of the herbivore populations. The current study was conducted in 2006 to investigate the status of white-tailed deer throughout Apostle Islands National Lakeshore and their impacts on forest communities as well as Canada yew (*Taxus canadensis*) populations. Deer densities were estimated using fecal pellet surveys across islands of known deer occupancy. Using a defecation rate of 34.4 pellet groups deer^{-1} day^{-1}, population estimates on Sand (8.23 deer km^{2}) and York (7.68 deer km^{2}) islands were considerably greater than Basswood (1.82 deer km^{2}) and Oak (1.56 deer km^{2}) islands. The variation in deer density reflects measurable differences in forage availability and browse quality between islands. Browse intensity and electivity indices revealed that northern white cedar or hemlock were selected for browsing by deer on Basswood and Oak islands, yet when Canada yew was abundant (on other islands) they were selected against. Dimensional analyses of browsed and unbrowsed stems were used to assess annual browse biomass production and utilization of Canada yew by white-tailed deer. A species-specific allometric relationship of stem diameter and shoot biomass was developed for Canada yew and used to predict the total browse biomass consumed at the stem level. Estimates of annual browse production and utilization from York and Sand islands revealed that deer herbivory accounted for 53% and 74%, respectively, of new browse biomass losses. Deer

populations and herbivory levels on Sand and York islands are not sustainable for continued growth and reproduction of Canada yew populations, which are regionally uncommon. Landscape composition and species susceptibility to herbivory should be important considerations in the management of deer populations across Apostle Islands National Lakeshore.

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INTRODUCTION:

White-tailed deer (*Odocoileus virginianus*) population dynamics have thrilled ecologists and wildlife managers since the foundation of these disciplines in the beginning of the 20th century. In recent decades, white-tailed deer in North America have expanded their geographic range and increased in abundance beyond concentrations believed to exist prior to European colonization (McCabe and McCabe, 1997; Rooney, 2001). Deer densities above 10 animals km^{-2} are now common throughout temperate regions (Russell et al., 2001). Expanding populations have resulted in serious concern over cascading implications on natural ecosystems as well as economic losses in forestry, agriculture, and transportation.

As an overabundant and selective herbivore, white-tailed deer are functioning as ecosystem engineers (Cote' et al., 2004) by altering patterns of forest regeneration and succession (Frelich and Lorimer, 1985; Waller and Alverson, 1997; Augustine et al., 1998), affecting the growth and survival of understory shrubs and herbs (Allison, 1990*a,b*; Balgooyen and Waller, 1995; Augustine and Frelich, 1998; Rooney and Waller, 2003), facilitating the success of invasive species (Knight et al., 2009) and shifting populations of insects, birds, and other mammals (Casey and Hein, 1983; deCalesta, 1994; McShea and Rappole, 1997; Belant and Windels, 2003; Ostrowski, 2009). The widespread and extensive plant-herbivore interactions imposed by deer on overall community structure may be shifting forests toward alternate stable states or paths of succession (Stromayer and Warren, 1997; Augustine et al., 1998).

While herbivore management continues to challenge ecologists and wildlife managers across white-tailed deer range, the primary causes of overabundant herds are directly linked to anthropogenic sources. Wisconsin's long and rich history of records on land and deer management functions as a catalyst for continued research on the direct and indirect effects of deer on ecosystem function. To fully understand the challenges faced with managing overabundant deer populations and identify conservation efforts, we must first examine how natural systems have been altered.

Most of northern Wisconsin's forested landscape has changed dramatically since the 19th century. The pre-settlement northern forests were largely mature, late-successional communities composed of mixed conifer-hardwoods that were characterized by eastern white pine (*Pinus strobus*), hemlock (*Tsuga canadensis*), northern white-cedar (*Thuja occidentalis*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), and tamarack (*Larix laricina*) as the conifers and sugar maple (*Acer saccharum*), basswood (*Tilia americana*), yellow birch (*Betula alleghaniensis*), red oak (*Quercus rubra*) and ironwood (*Ostrya virginiana*) as the deciduous species (Curtis, 1959; Finley, 1976). It is generally believed that these mature forests were marginal habitat for sustaining deer populations in both summer and winter ranges (Christensen, 1959). McCabe and McCabe (1997) suggested that deer densities in northern Wisconsin were lower than 4 animals km^{-2} prior to settlement, and during this period deer had to compete for resources with other herbivores such as woodland caribou, moose, elk, and bison (Scott, 1939; Schorger, 1942).

Widespread logging in the northern forests began in the 1840s and paved the way for Wisconsin to become the leading lumber-producing state in 1899 (Curtis, 1959). Subsequent settlement and unregulated hunting led to major declines in native large mammal populations throughout the state. By the 1880s white-tailed deer were the only native ungulates remaining in viable numbers, and wolf (*Canis lupus*) populations throughout the region were rapidly declining from state-sponsored bounties. With the removal of a top predator, deer populations could increase rapidly to levels beyond the carrying capacity of available food (McCullough, 1997; Cote' et al., 2004). As the white pine, hemlock, and cedar were cut, early succession hardwood saplings increased in abundance and created favorable habitat for deer survival and reproduction (Christensen, 1959). The early-succession forests that followed logging provided abundant, high-quality forage that increased habitat carrying capacity for deer throughout their range. Increased forage quality and quantity is the most evident variable contributing to the rapid growth of the deer population, yet game laws and protection of deer through restricted hunting seasons has also been a causal factor. The Wisconsin deer herd has grown from an estimated 390,000 animals in 1960 to 1.4 million in 2009 (Wisconsin Department of Natural Resources, 2010) in response to landscape-scale changes in their environment and reductions in predatory pressure.

Decades of research have demonstrated that deer are keystone herbivores (Waller and Alverson, 1997) that directly and indirectly alter forest community composition and structure through selective feeding on a preferred subset of species.

Aldo Leopold (1933) was the first to propose a classification system of deer foods that reflects preference, food availability, and apparent quality. When the food supply is depleted, the preferred plant species become overeaten and deer feed on less-preferred staple foods. During the winter deer feed primarily on woody browse such as terminal stems, buds, and evergreen needles, which are lower in nutrient quality and digestibility than summer foods. In the northern forests, deer prefer northern white-cedar (*Thuja occidentalis*), hemlock (*Tsuga canadensis*), red maple (*Acer rubrum*) and Canada yew (*Taxus canadensis*) over all other winter forage species (Dahlberg and Guettinger, 1956; Beals et al., 1960). Unlike other preferred winter forage, Canada yew has a low growth form that prevents it from expanding beyond the foraging height of herbivores. Although there has been much research on the impacts of deer overabundance, there are still many research questions as well as conservation and management issues that must still be addressed. One plant-herbivore interaction that is seldom investigated is the impact of white-tailed deer on Canada yew.

Canada yew is a sprawling evergreen shrub native to the understory of boreal and conifer-hardwoods forests throughout northeastern North America (Curtis, 1959; Martell, 1974). The diffuse, ascending shoot system of Canada yew facilitates the development of layering networks of primary and secondary branches that create a unique growth pattern (Allison, 1992). Canada yew was once a common and characteristic shrub of the northern conifer-hardwood region (Curtis, 1959; Martell, 1974). Since the deer herd began to increase in the 1930s, yew's frequency and abundance has been severely reduced (Curtis, 1959; Beals et al., 1960; Allison, 1990 *a,b*), although small patches can still be found along steep ravines and other isolated locations with limited deer access (Stachowicz and Allison, 1995). Canada yew is currently listed as vulnerable, imperiled, or critically imperiled in 12 states and one province throughout the northeastern range of the species (NatureServe, 2009).

Deer have been frequently cited as a primary reason for the continued decline in Canada yew across its range (Leopold et al., 1947; Curtis, 1959; Beals et al., 1960; Martell, 1974; Allison, 1990*a,b*; Waller and Alverson, 1997), yet one of the challenges faced with studying such an interaction is locating study systems where Canada yew is still a dominant component of the vegetation and deer populations exist at varying densities. Natural experiments, such as those found on island chains, provide researchers with discrete or continuous spatial variation in deer densities that create opportunities to study deer impacts across a gradient in deer browse. One such area is Apostle Islands National Lakeshore (APIS) in northern Wisconsin.

With many of the region's finest old-growth northern conifer-hardwood forests and a rich cultural history, APIS is an area of unparalleled ecological research opportunity. The islands and natural communities of APIS provide an invaluable means for evaluating deer impacts and developing a management program for the conservation of browse-sensitive species such as Canada yew. APIS has been an area of great concern over expanding deer populations and their impacts on vegetation since the early 20th century (Wisconsin Conservation Department, 1954; Beals et al., 1960;

Allison, 1990a,b; Balgooyen and Waller, 1995; Smith, 2007). The current status of deer on Apostle Islands National Lakeshore and their impacts on plant communities and populations has again raised concern among park managers and regional biologists.

Many of the islands within the archipelago support dense populations of Canada yew and were not known to contain deer populations until recently. Judziewicz and Koch (1993) reported that deer were absent or undetectable on all of the islands within the National Lakeshore except Basswood and Oak islands, which maintain low population levels. Currently, deer are found on most of the islands nearest the Bayfield peninsula; these include Basswood, Oak, Sand, and York. Aerial observations indicates that York Island may have been colonized as early as the winter of 2003 (Tom Doolittle, *personal communication*).

The Canada yew-dominated communities found on these islands are regionally rare, serving as reminders of early vegetation in Wisconsin (Beals et al., 1960) and qualifying Apostle Islands as an area of regionally significant vegetational value. The Apostle Islands' proximity to mainland areas of high sustained deer densities coupled with effective dispersal of white-tailed deer, short distances among islands, and the abundance of a unique, highly preferred browse species sum to create a situation of concern over the conservation of an already imperiled species and ecological community. It can be hypothesized that once the population densities on occupied islands approach carrying capacity, the probability of immigration to surrounding islands will increase. These implications raise concern over the spread of an ecosystem engineer in an area of high conservation value.

In light of the increased trend in deer occupancy across APIS and concern over regionally significant plant populations and communities, the current study was designed to:

1) Estimate the population density of white-tailed deer on occupied islands within Apostle Islands National Lakeshore.
2) Evaluate factors that may contribute to deer population trends on occupied Islands.
3) Investigate the impact of deer on winter browse species.
4) Examine the impact of deer on biomass production and removal of Canada yew (*Taxus canadensis*).

Islands were sampled from the beginning of May through the end of July 2006 to form a snapshot of the deer activity during the previous winter. The results from this investigation may aid park managers and regional biologists in developing monitoring strategies and activation points for preserving the integrity of these historically and botanically significant communities.

STUDY SITE

The Apostle Islands National Lakeshore is an archipelago that stretches off the tip of the Bayfield peninsula in western Lake Superior and includes a narrow mainland band near the Red Cliff Indian Reservation (Figure 1). This chain of islands is made up of 22 moderately small islands, 21 of which are part of the National Lakeshore. Prior to 1970, the islands supported seasonal populations of fur traders, farmers, loggers, commercial anglers, and a small tourist trade. Since 1970, these lands and waters have been protected and managed by the federal government, and in 2004 approximately 80% of the park was designated the Gaylord Nelson Wilderness Area.

The islands forming the Apostle Islands National Lakeshore range in size from Gull Island with 1 ha (3 acres) to Stockton Island with 4,087 ha (10,054 acres) (Judziewicz and Koch, 1993). The topography within the archipelago is relatively uniform. Most islands are low and flat, rising less than 61 m above lake level. Oak Island is the most topographically unique, rising 146 m above lake level and containing numerous steep ravines and undulating hills (Beals and Cottam, 1960; Judziewicz and Koch, 1993).

The post-glacial period deposited thick iron-rich till and drift hills of poorly-drained red sandy clay on much of the islands (Beals and Cottam, 1960; Judziewicz and Koch, 1993). Climatically, the region surrounding Apostle Islands has a humid continental condition that is characterized by cold, long winters and reasonably warm but short summers. Compared to the Bayfield Peninsula, the climate on the islands is moderated by the maritime influence of Lake Superior, which produces warmer winters, later arrival of spring, cooler summers, and longer lasting falls (Judziewicz and Koch, 1993).

Floristically, the Apostle Islands are part of the hemlock-white pine-northern hardwood forest, with some boreal and sub-arctic characters (Curtis, 1959; Judziewicz and Koch, 1993). The pre-settlement vegetation was 90% upland mixed conifer-hardwood forest dominated by hemlock (*Tsuga canadensis*), eastern white pine (*Pinus strobus*), sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and paper birch (*Betula papyrifera*). In areas with high wind and poorly drained soils, balsam fir (*Abies balsamea*) and northern white-cedar (*Thuja occidentalis*) were important colonizing and stabilizing species. The understory in the pre-settlement forest was dominated by Canada yew (Curtis, 1959; Beals et al., 1960; Judziewicz and Koch, 1993).

Prior to the establishment of the National Lakeshore, logging played a significant role in shaping the current vegetation on the islands; most have undergone repeated logging since the late 19^{th} century. After the major logging operations subsided, settlers attempted to farm the impoverished landscape. A few remnant patches were spared from logging or agriculture by their proximity to the lighthouse stations. These areas serve as some of the upper Midwest's best examples of pre-settlement vegetation.

SITE SELECTION

Five islands (Figure 2-6; Table 1) were selected for study based on deer occupancy, presence or absence of Canada yew, and their vegetative compositions. All of the islands sampled form an inner ring around the Bayfield Peninsula. Sand and York Islands contain abundant Canada yew and a well-established deer population. Basswood and Oak Islands are relatively devoid of Canada yew and also contain deer, but at a much lower density then the previous two. Raspberry Island contains abundant Canada yew, but no history of deer occupancy.

Using ArcView 8.01 Geographical Information System (GIS), vegetative covertype data for Apostle Islands National Lakeshore (Ventura and He, 1993) were modified for stratification of the sampling area. The original classification scheme was based on three primary species occupying the greatest overstory percent cover on a given island. For simplification and logistical concerns, the original covertype data for selected islands were compressed by recoding the first dominant and second dominant species only. For example, if two polygons were classified by the three dominants to produce RM-PB-SM (red maple-paper birch-sugar maple) and PB-RM-QA (paper birch-red maple-quaking aspen), then the recoding procedure would produce one category for both polygons, PB-RM (paper birch-red maple) with no distinction between first-order and second-order dominance.

The modified covertype shapefile was used to divide selected islands into four to five transects running east to west and passing through all dominant forest covertype strata. Scarce and/or culturally disturbed areas were omitted from sampling. Systematically selected sampling sites were established along transects at 150-300 meter intervals, unless otherwise needed to ensure that all dominant covertypes were adequately sampled (Figures 2-6; Table 1).

Global Positioning System (GPS) coordinates for each site were derived in advance using the measurement tool package in ArcView. The coordinates were uploaded to a Garmin Map76S hand-held GPS receiver to navigate to and locate sampling sites in the field. Sampling sites were established during the spring survey and permanently marked by driving a two-foot section of red rebar with an aluminum site location tag into the ground at the plot center. The spring survey was designed to capture deer density estimates (pellet survey), browse by deer during the previous winter, and dimension analysis data on browse species.

FIELD METHODS & DATA COLLECTION

Deer Population Survey

Deer density was assessed using a 5.12 m radius plot (82 m^2) established at each site along a transect line (Figures 7). Deer density was estimated by recording the number of deer pellet-groups within each plot (Eberhardt and VanEtten, 1956; Neff, 1968). A pellet-group was defined as any grouping of approximately 68 pellets (Rogers, 1987). If "trails" of pellets were left, or if fewer than 68 pellets were observed, then fractions of groups were reported. It should be noted that pellets within each grouping were not physically counted; a gestalt estimate for 68 was used. If the plot landed on a deer trail, then the plot was moved north until the trail was outside of the sampling area. This technique was used because of the difficulty in firmly identifying individual pellet-groups once they have been disturbed, shuffled, or stepped on by deer walking on trails. The data generated from the pellet count surveys were converted to density of overwintering deer km^{-2} based on a 195-day deposition period and either 13 or 34 pellet groups $deer^{-1}$ day^{-1} (Eberhardt and van Etten, 1956; Rogers, 1987, respectively). Snowshoe hare pellets were noted as present or absent within each plot.

Deer Browse Survey

The estimates of deer density were used to determine the impact of herd size on winter browse species and to investigate food preference. Using the center of the pellet plot as the southeast corner, a 2 x 5 m nested plot (totaling 10 m^2) was established for measuring browse and dimensional analysis data (Figure 7). Within each plot the numbers of individuals for each winter browse species and all branching stems for each individual between 0.25 and 2 meters tall (white-tailed deer molar region) were counted. Each branch was scored as either browsed or available for consumption. A branch was considered browsed if the terminal or lateral stems showed evidence of deer utilization; a branch was considered available if the terminal and lateral stems contain buds or new growth. To further clarify the foraging behavior of the current deer herd, previous winter deer browse was recorded separately from past browse (Beals et al., 1960; Frelich and Lorimer, 1985; Rooney et al., 2002). The number of individuals and stem counts were determined for all winter browse species (with the exception of *Taxus canadensis*, see below) located within each sampling plot (Table 2).

Sampling Taxus canadensis

The sprawling nature of Canada yew (*Taxus canadensis*) created difficulties in estimating browsed and available stems using the above methodology. Undisturbed populations of Canada yew form large networks of virtually impenetrable vegetation that can rise 1.5-2.5 meters above the forest floor. To alleviate the arduous task of sampling such an area, a series of five consecutive 1 x 1 m quadrats (totaling 5 m^2) were established in the north direction when Canada yew is observed within the browse plot. The center of the pellet plot served as the southeast corner of the first 1 x 1 m quadrat (Figure 7). If there was no yew in the north direction, then the next cardinal direction (rotating clockwise from north) containing Canada yew was selected for sampling.

Canada yew spreads vegetatively, therefore it is difficult to determine an individual (genet) without destructively exposing the connective root system. For the scope of this study an individual shoot (ramet) was defined as a single emergent shoot that appeared disconnected from neighboring plants at or above the soil surface. From within each quadrat, all primary rooted shoots of Canada yew were counted to determine the density of Canada yew m^{-2}. Browsed and available stem measurements were taken from a random sub-sample of one rooted shoot per quadrat. Additionally, basal diameter, height, length, and a random sample of diameter-at-point measures were taken from each shoot. Selection of a shoot was determined by locating the rooted stem that was nearest to the southeast corner of each quadrat frame. If the base of a main branch fell in the plot but the terminal end was outside, then those stems attached to the main base were used for browse estimates. Differentiation between browsed and available stems followed the same procedures previously stated.

Dimensional Analysis of Taxus canadensis

Measures of productivity and biomass removal were accomplished by collecting dimensional analysis data from within the molar region of deer to determine (1) the proportion of browsed to available stems, (2) the maximum diameter at the point of browse (DPB), (3) determine diameter-length-biomass relationship, and (4) estimate the annual growth removed by deer.

Dimensional analysis data, including browsed to available stems and DPB, were collected on Canada yew in the field. The DPB was obtained by measuring the diameter of a stem tip that had been browsed by deer. A digital caliper, accurate to 0.1 mm, was used to collect a random sample of two DPB measurements from two different stems in each 1 m^2 plot for a total of 10 DPB measurements per site. Using all the DPB measures collected across Sand and York Islands, it was determined by terminal bud scars that the maximum diameter stem browsed by deer on Canada yew was not older than 3 years. Unbrowsed stems of Canada yew that were between 2-4 years old were collected in late fall from Raspberry Island and kept in an environmental chamber at 2°C until they were analyzed. To lessen the impact of removing large numbers of Canada yew stems at various diameters, 50 branches were selected and each was used to measure incremental diameter-length-biomass parameters at 1-year intervals across all terminal, lateral, and sub-lateral stems. The annual extension growth increments on Canada yew are indicated by terminal bud scars on the stem that are often clearly visible as far back as 5 years. Samples were mounted on paper sheets and examined using a high-resolution scanner prior to dissection. Diameter and length measurements were taken using a digital caliper on each 1-year old stem prior to drying in an oven at 60°C. The biomass for each sample was determined after drying using an analytical balance. Dimensional data on Canada yew was used to develop an allometric regression equation for predicting annual biomass production and removal by deer.

DATA ANALYSIS

Deer Population Estimates

The number of pellet groups observed within each plot was used to estimate the mean pellet density per plot by island:

$$(Eq. 1)\ \overline{x}_i = \frac{x_1 + x_2 + x_3 + \ldots x_n}{n}$$

where x is the number of pellet groups observed per plot, n is the number of plots sampled per island and $\overline{x}_i$ is an estimate of the mean number of pellet grouped per island. Pellet density estimates by island were then used to estimate deer density per km^2 by the following equation:

$$(Eq. 2)\ D = \frac{\overline{x}_i s k}{f d}$$

where $\overline{x_i}$ is the estimate of mean pellet density per plot by island, s is the number of sampling plots per hectare, k is the number of hectares per km^2, f is the defecation rate of white-tailed deer and d is the deposition period (Eberhardt and VanEtten, 1956; Rogers 1987). Deer density was estimated for each island using two defecations rates, 13 pellet groups $deer^{-1}$ day^{-1} (Eberhardt and VanEtten, 1956) and 34 pellet groups $deer^{-1}$ day^{-1} (Rogers, 1987), with a deposition period of 195 days.

Deer Browse Analysis

Forage available and browsed by deer was analyzed using several different methods. Since Canada yew measurements were not taken from within the 10 m^2 browse plots, estimates of available and browsed stems were extrapolated using density estimates from five consecutive 1 m^2 rollover plots (Figure 7) and stem counts from five permanently tagged Canada yew shoots at each site. The density of Canada yew per 1 m^2 for each site, TD_s, was determined by:

$$(Eq. 3)\ TD_s = \frac{\sum d_s}{5}$$

where $\sum d_s$ is the sum of all primary rooted shoots in five consecutive 1 m^2 quadrats at the s^{th} site. An estimate of the mean number of available, TA_s, and browsed, TB_s, stems for Canada yew at each site was calculated by:

$$(Eq. 4)\ TA_s = TD_s\left(\frac{\sum a_s}{5}\right)10 \quad \text{and} \quad (Eq. 5)\ TB_s = TD_s\left(\frac{\sum b_s}{5}\right)10$$

where $\sum a_s$ is the sum of all stems available for browse and $\sum b_s$ is the sum of all stems browsed from five permanently tagged Canada yew shoots at the s^{th} site. The available and browsed estimates were multiplied by a factor of 10 to scale the estimate up to a 10 m^2 sampling area.

Winter forage available for deer was calculated by island:

$$(Eq. 6)\ \overline{A_\iota} = \frac{\sum a_i}{n}$$

where $\sum a_i$ is the sum of all available stems, across all species, recorded on the ι^{th} island and n is the number of sites sampled. All species recorded during the browse survey were then divided into groups of first, second, third and fourth choice deer foods (Table 3), according to Dahlberg and Guettinger (1956) and Beals et al. (1960). The relative density of each food choice, RD_j was calculated by island:

$$(Eq. 7)\ \ RD_j = \frac{\sum a_{ij}}{\sum a_i}$$

where $\sum a_{ij}$ is the sum of all available stems recorded on the i^{th} island within the j^{th} preference ranking and $\sum a_i$ is the sum of all available stems recorded on the i^{th} island.

The severity of browsing (also referred to as browse intensity) on each island was used to estimate the percentage of stems that had been utilized by deer across all sites on an island. Browse intensity at a site, BI_s, was calculated by:

$$(Eq. 8)\ \ BI_s = \frac{\sum b_s}{\sum a_s} \times 100$$

where $\sum b_s$ is the sum of all browsed stems and $\sum a_s$ is the sum of all available stems recorded at the s^{th} site on an island. Browse intensity was evaluated on a scale of 0 (lowest) to 100 (highest). The mean browse intensity for an island, $\overline{BI}_i$, was then calculated by the following equations:

$$(Eq. 9)\ \ \overline{BI}_i = \frac{\sum BI_s}{n}$$

where n is the number of sites sampled across an island. Browse intensity was also evaluated by genera, BI_{gi}, to determine relative use:

$$(Eq. 10)\ \ BI_{gi} = \frac{\sum b_{gi}}{\sum a_{gi}}$$

where $\sum b_{gi}$ is the sum of all browsed species and $\sum a_{gi}$ is the number of available stems belonging to g genus across the i^{th} island.

To further evaluate browse preference by deer for a particular species, electivity indices were calculated for each species according to the following equation (Jacobs, 1974; Jenkins, 1979):

$$(Eq. 11)\ \ E_{ij} = \ln\left[\frac{(r_{ij})(1-p_{ij})}{(p_{ij})(1-r_{ij})}\right]$$

where r_{ij} is the proportion of stems browsed on island i that belong to species j, and p_{ij} is the proportion of stems available on island i that belong to species j. An electivity index greater than 0 implies preference for a species and a value less than 0 implies selection against a species. Electivity indices were calculated for each island separately to evaluate forage preference between islands dominated and not dominated by Canada yew. The significance of each E_{ij} was tested by calculating:

$$(Eq. 12)\ \ X^2 = \frac{E_{ij}^2}{[1/x_{ij} + 1/(m_j - x_{ij}) + 1/y_{ij} + 1/(n_j - y_{ij})]}$$

where x_{ij} and y_{ij} are the number of stems from species j that were browsed and available, respectively, on island i, and m_i and n_i are the total number of stems browsed and available respectively on island i. X^2 was compared with a χ^2 distribution with one degree of freedom (Jenkins, 1979).

Dimensional Analysis of Taxus canadensis

The diameter-point-browse measurements taken from the field were used to determine the distribution, mean, and maximum diameter that deer utilize Canada yew. The mean diameter-point-browse for a site, $\overline{db_s}$, was first calculated by:

$$(Eq. 13)\ \ \overline{db}_s = \frac{\sum db_s}{10}$$

where db_s are diameter-point-browse measures collected at the s^{th} site on an island. The island mean was then calculated by the following equation:

$$(Eq. 14)\ \ \overline{DB}_i = \frac{\sum \overline{db}_s}{n}$$

where n is the number of sites on an island. A two-sample t-test assuming unequal variance was used to test for a significant difference in mean diameter-point-browse measures between Sand and York islands using Minitab 15 (2007) statistical software. The mean diameter-point-browse measures estimated for an island were then used to evaluate whether more than one year's annual growth was being removed at a browse point. The diameter-age relationship of stems analyzed in the laboratory was determined by segregating stems by age and calculating the mean diameter for each age:

$$(Eq. 15)\ \ \overline{D}_a = \frac{\sum d_a}{n}$$

where $\sum d_a$ is the sum of all diameters recorded for an age increment, a, and n is the number of stems measured. Additionally, the diameter-point-browse measures were used to calculate biomass removal using a simple linear regression to model the relationship between incremental diameter and biomass measures collected from laboratory samples of Canada yew.

$$(Eq. 16)\ \ biomass = \alpha + \beta(diameter)$$

After inspecting the normality plot, a frequency histogram of the residuals, and a scatterplot of the residuals verses fitted values (Appendix A), the original model did not meet the assumptions of a least-squares regression. Using a Box-Cox transformation analysis, the diameter and biomass values were transformed to a $\log_{10}$ scale to improve the assumptions of normality and homoscedasticity (Appendix A). The following operational equation was used to predict Canada yew biomass at a given diameter:

$$(Eq. 17)\;\; log_{10}(biomass) = \alpha + \beta[log_{10}(diameter)]$$

To correct for potential bias and underestimation resulting from back-transforming logarithmic biomass values to arithmetic scale (Sprugel, 1983; Jenkins et al., 2004), a correction factor (CF) was developed using the biomass and diameter values collected from laboratory samples. The correction factor was calculated by using the standard error of estimate (SEE) from the regression (Sprugel, 1983). The SEE was determined by the following formula:

$$(Eq. 18)\;\; SEE = \sqrt{\frac{\sum\left(\log y_i - \widehat{\log y_i}\right)^2}{N-2}} \times 2.303$$

where $\log y_i$ are the observed $\log_{10}$ biomass (y_i) values for a given $\log_{10}$ diameter, $\widehat{\log y_i}$ are the predicted $\log_{10}$ biomass values calculated from the regression equation above, *N* is the number of biomass values and 2.303 is to convert it to base- e .

A correction factor (CF) was then calculated according to the formula:

$$(Eq. 19)\;\; CF = e^{(SEE^2/2)}$$

All back-transformed biomass predictions where then multiplied by the CF to correct for bias and potential underestimates resulting from conversions of logarithmic prdictions to arithmetic values.

Resource Pressure on Taxus canadensis

The regression model was used to predict the browsable biomass produced annually by Canada yew and the amount removed by deer. An estimate of the annual browsable biomass produced on an individual shoot of Canada yew for a given site, AB_s, was calculated using the mean number of available stems, TA_s and the mean biomass of age-1 stems, $(\overline{D}_1)$:

$$(Eq. 20)\ \ AB_s = TA_s(\overline{D_1})$$

The mean browsable biomass produced on an individual shoot of Canada yew across an island, $\overline{AB}_i$, was determined using the following equation:

$$(Eq. 21)\ \ \overline{AB}_i = \frac{\sum AB_s}{n}$$

where $\sum AB_s$ is the sum of available stems of Canada yew across n sites on the i^{th} island. To estimate biomass consumed by deer, the regression model was used to predict the browsable biomass at each diameter-point-browse measure collected in the field. The mean biomass removed per browse event for a site was calculated by:

$$(Eq. 22)\ \ \overline{bb}_s = \frac{\sum bb_s}{10}$$

where $\sum bb_s$ represents the sum of the predicted browse biomass measures at the s site on an island. During field collections, the total number of browsed stems on an individual shoot of Canada yew was segregated into current browse and cumulative browse. The current and cumulative browse biomass removed from a shoot of Canada yew at a given site was estimated using the following equation:

$$(Eq.23)\ \ BC_s = \overline{bb}_s(TB_s)$$

where $\overline{bb}_s$ is an estimate of the mean browse biomass removed from a single stem and TB_s represents the mean number of stems browsed (current or cumulative) per shoot of Canada yew at a site. The mean browse biomass removed from an individual shoot of Canada yew across n sites on the i^{th} island was estimated by:

$$(Eq.24)\ \ \overline{BC}_i = \frac{\sum BC_s}{n}$$

Taxus browse pressure, TP, was calculated by dividing the proportion of browse biomass removed during the previous winter by the annual browse biomass produced on an individual shoot:

$$(Eq.25)\ \ TP = \frac{\overline{BC}_i}{\overline{\overline{AB}}_i}(100)$$

RESULTS

Deer Population Estimates

Deer pellets were found at 121 out of 179 plots sampled (67.6%) across all island locations and confirmed that deer populations were established on Sand, York, Basswood, and Oak Islands. The mean pellet density per 82 m^2 sampling plot varied from 4.42 (± *SE* 0.43) on Sand Island to 0.84 (± *SE* 0.20) on Oak Island (Table 4; Figure 8) with no pellets observed on Raspberry Island during the sampling period. Pellet density differed considerably between plots, ranging from 14 to 0 pellet groups per plot. Basswood and Oak Islands contained lower pellet density among plots when compared to Sand and York Islands. From all sampling locations on Basswood Island, 53.2% contained 0 pellet groups, 34.0 % had 1-2 groups, and 12.8% held 3 or more groups. On Oak Island, 46.3% contained 0 pellet groups, 49.3% had 1-2 groups, and 4.4% had 3 or more groups. Comparatively, Sand and York Island plots had 4.3% and 5.3% with 0 pellet groups, 21.3% and 26.3% with 1-2 groups, and 74.4% and 68.4% with 3 or more groups respectively.

Sand Island was unsurpassed in density of deer per km^2 and was followed by York, Basswood, and Oak in order of decreasing density (Table 4). Using a defecation rate of 13 pellet groups $deer^{-1}$ day^{-1} (Eberhardt and VanEtten, 1956), the estimated population of deer km^{-2} for Sand and York Islands were 21.52 and 20.09; the estimated island totals were 258 and 26 animals per island, respectively (Table 4; Figure 8). Alternatively, Basswood and Oak Islands maintained significantly lower population levels

(4.77 and 4.04 deer km^{-2}, with island totals of 37 and 84) than did Sand and York (Table 4; Figure 8). The deer density estimates using a defecation rate of 34.4 pellet groups $deer^{-1}$ day^{-1} (Rogers, 1987) were considerably lower, yielded between 1.56 and 8.23 deer km^{-2} and island totals ranging from 10-99 animals (Table 4; Figure 8).

Deer Browse Analysis

The mean number of browse stems available at a 10 m^2 sampling plot varied considerably between islands dominated and not dominated by Canada yew. While Sand and York Islands contained an abundance of yew in the shrub layer, this species was rarely observed on Basswood and Oak. From the 65 plots sampled on Sand and York Islands, 98% contained Canada yew. On Basswood and Oak Islands only one plot contained yew and this individual was below the molar region of deer, thus it was not counted or considered available. The values for the mean number of browse stems available on Sand and York Islands were significantly greater than those found on Basswood and Oak Islands (Figure 9). For example, York Island plots contained an average of 8429 ± *SE* 1227 available stems per plot and Oak Island contained 286 ± *SE* 50 (Figure 9). Canada yew accounted for 95% of the available stems on Sand and York Islands combined.

When overall forage availability was examined using a preference rating system (Dahlberg and Guettinger, 1956; Beals et al., 1960), the relative density of first choice winter forage available for deer on Sand and York islands was between 49% and 69% greater than Basswood and Oak (Table 5). Forage availability and food preference suggest that an abundance of first choice foods is a primary driver in elevated deer populations on Sand and York Islands relative to Basswood and Oak Islands.

The proportion of twigs browsed differed significantly from islands dominated by and not dominated by Canada yew. An analysis of deer browsing pressure on Sand and York Islands show significantly higher cumulative and current browsing intensity when compared to Basswood and Oak Islands (Figure 10). Partitioning island level browse intensity by species revealed patterns in the relative impact on forage species and selection by deer. Browse species common to all the islands sampled included mountain maple, yellow birch, and beaked hazel. Most species were browsed at varying levels across islands, yet the browse intensity patterns observed for deciduous species were variable with the exception of mountain maple and yellow birch (Figures 11-12). Mountain maple presented consistently higher browse intensity levels then most deciduous species. Yellow birch on the other hand exhibited high levels of browse intensity on Sand and York Islands, but low levels on Basswood and Oak Islands (Figures 11-12).

The species for which browse intensity varied the most between islands dominated and not dominated by Canada yew were cedar and hemlock. Examining browse intensity on coniferous species only reveals that islands without Canada yew show elevated pressure on white cedar and hemlock (Figure 11), while islands with Canada yew exhibit low levels of browse intensity on the same species (Figure 12). A plot-by-plot comparison of sites on Sand and York Islands demonstrates that when hemlock and/or cedar were observed with Canada yew, browse intensity measures were significantly greater on Canada yew (Figure 13). By using browse intensity as a metric to evaluate the relative impact of deer browse pressure, it is evident that there was greater browsing pressure on Canada yew as compared to other conifer species when all were present (Figure 12).

The calculated electivity for browse species observed at Apostle Islands National Lakeshore was used to evaluate deer preference for a particular species rather than simply the use of browse intensity on that species. The electivity index illustrates whether a particular species was selected for (positive value) or against (negative value) by deer. Several species with measurable browse levels were not considered significant ($p > 0.05$) using the electivity analysis because they accounted for a small percentage of the deer's diet; these include red maple, sugar maple, green ash, ironwood, pin cherry, thimbleberry, and mountain ash (Table 6).

Trends in browse intensity and electivity values were broadly similar between islands and their Canada yew dominance. For example, deer on Basswood Island showed strong selection for ($p < 0.001$) mountain maple, big-toothed aspen, red oak, basswood, and white cedar (Table 6). Furthermore, yellow birch, fly honeysuckle, and hemlock were selected against ($p < 0.001$; Table 6). Sand Island electivity values indicate strong selection for mountain maple, red-osier dogwood, and Canada yew, as well as selection against serviceberry, paper birch, beaked hazel, white-cedar, and hemlock. Changes in preference exist between islands dominated and not dominated by Canada yew, with the most significant change seen in white cedar and hemlock. On Sand and York Islands there was strong selection for Canada yew and against white cedar and hemlock. When Canada yew was not present, deer exhibited selection for white cedar or hemlock (Table 6). This suggests that although cedar and hemlock are highly preferred browse species for deer in winter, when Canada yew is abundant, deer will selectively choose yew over the aforementioned species.

Dimensional Analysis of Taxus canadensis

Diameter-at-point-browse (DPB) dimensional data from 642 field observations of Canada yew on Sand and York Islands (combined) ranged from 0.6 to 3.1 mm, with a mean of 1.63 mm (*SE* ± 0.02 mm; Figure 14). When the DPB measures were separated by island it revealed distributional differences between Sand and York. The mean DPB for Sand Island was 1.71 mm (*SE* ± 0.02 mm) and provided to be significantly greater (*t*-value = 7.05) than York Island at 1.44 mm (*SE* ± 0.03 mm). The age-diameter relationship determined from the categorization of 48 unbrowsed stems of Canada yew from Raspberry Island confirmed that deer were removing greater than 1-year's worth of growth from each stem browsed (Table 7). An additional examination into pollen cone location from 3 years of annual growth revealed that 83% of pollen cones were found on age-1 stems on Raspberry Island.

Age-determined incremental diameter and biomass measures collected from 1049 laboratory segments of Canada yew were fitted with a $\log_{10}$-$\log_{10}$ allometric model (Figure 15) to produce the following equation:

$$\log_{10} Biomass(g) = -1.09g + 3.03g/mm\ (\log_{10} mm\ diameter)$$

Diameter at seasonal growth increments proved to be an effective predictor of distal stem biomass in Canada yew, with an R^2 value of 0.89 ($p < 0.001$; Table 8). The scatter plot of residuals demonstrated that there was no large or systematic bias toward over or underestimating biomass at diameter values within the range used to develop the model (Appendix A).

The incremental diameter values generated during laboratory analysis of Canada yew stems were imported into the allometric model to determine the standard error of estimate (*SEE*) from the regression. A correction factor (*CF*) of 1.069 was calculated using the *SEE* and this value corresponds with published *CF* values for other woody species (Jenkins et al., 2004). All biomass predictions were back-transformed and multiplied by 1.069 to correct for bias and potential underestimates resulting from logarithmic conversions.

Resource Pressure on Taxus canadensis

Laboratory analysis of age-1 Canada yew stems were used to determine the amount of browseable biomass produced during the previous growing season on an individual shoot of yew at Sand and York Island sites. Each shoot may contain numerous branches that contribute to annual browseable biomass production. The diameter of age-1 stems ranged from 0.48-2.49 mm, with a mean of 1.06 ± *SE* 0.01 mm. Additionally, the estimated biomass of age-1 stems ranged from 0.007-0.533 g, with a mean of 0.099 ± *SE* 0.003g. Using the mean biomass of age-1 stems, the amount of browseable biomass produced annually on an individual shoot of Canada yew ranged 1.52 to 26.16 g of tissue. The mean biomass produced on an individual yew shoot for Sand and York Islands were 5.52 ± *SE* 0.38 g and 10.4 ± *SE* 1.31 g respectively (Table 9).

DPB measures collected in the field on Sand and York Islands were used to predict the yew biomass consumed by deer per browse event using the allometric regression equation and *CF*. The biomass removed from a browse event across all sites on Sand and York Islands ranged from 0.019 to 2.74 g, with a mean of 0.55 ± *SE* 0.03 g and 0.33 ± *SE* 0.04 g for Sand and York Islands respectively. The mean current and cumulative browse biomass removed from and individual shoot on Sand and York Islands were calculated using the mean number of browsed stems from an individual shoot and the browse biomass removed during an individual browsing event (Table 9). From this analysis, there was no apparent difference between cumulative and current biomass removal rates between Sand and York islands. If taken within the framework of browseable biomass production, removal rates validate the degree of browsing pressure deer exhibit on Canada yew populations. Patterns in browse pressure or relative use on Canada yew indicate that 74% and 53% of new browse biomass produced on Sand and York Islands, respectively, were removed by the current deer population (Table 9).

DISCUSSION

Deer Population Estimates

Prior to the establishment of Apostle Islands National Lakeshore, the Wisconsin Conservation Department issued a special any-deer season in 1954 to “balance the herd with the annual production of winter forage” (Wisconsin Conservation Department, 1954). During that time the conservation department was attempting to reduce the deer population and achieve proper stocking since natural predators no longer existed. In 1954 alone there were 411 deer taken off 12 islands with verified deer populations. One of those was Rocky Island, from which 124 individuals were removed in a single hunting season. From 1954-1964 approximately 1700 animals were removed from Apostle Islands during these special hunting periods. Fifty-nine years have passed since the first any-deer season and again we are confronted with concern over balancing the herd.

Research at Apostle Islands National Lakeshore revealed that deer densities on Sand and York islands were approximately 7.6 and 8.2 deer/km^2 respectively (Table 4). In contrast, populations on Basswood and Oak were between 1.5 and 1.8 deer/km^2 (Table 4). The deer management goal set forth by the Wisconsin Department of Natural Resources (Wisconsin DNR) in Deer Management Unit 3 (Douglas/Ashland/Bayfield counties) is 3.9 deer/km^2, with an estimated deer density of 8.5 deer/km^2 in the fall and 5.8 deer km^2 during the winter of 2008 (Wisconsin DNR, 2010). Prior to European settlement, deer populations in northern Wisconsin were believed to be lower than 4 deer/km^2 (McCabe and McCabe, 1997). The population density of white-tailed deer in the United States and more specifically Wisconsin has increased significantly during the 20th century (Wisconsin DNR, 2010).

There has been a considerable amount of controversy surrounding deer management goals and population regulation. From biologists and naturalists to farmers and foresters, studies have demonstrated damage to tree seedlings, herbaceous plants, crops and reductions in species richness and diversity. Previous studies in the northern temperate region of the eastern United States revealed that white-tailed deer populations greater than 3-5 animals/km^2 can severely affect the survival and reproduction of several woody and herbaceous plant species (Mladenoff and Stearns, 1993).

On the other hand, hunters will argue that there are too few deer to support demand. Studies on protected lands have found that high deer densities tend to be observed in areas where populations are not subjected to hunting pressure (Anderson and Loucks, 1979; Alverson et al., 1988; Frost et al., 1997). The increasingly polarized nature of deer management has forced land management organizations like Apostle Islands National Lakeshore to develop deer management programs that strive to preserve the uniqueness of the park while satisfying all their constituencies. Although areas of Apostle Islands National Lakeshore are open to public hunting, there remote location and accessibility have proven difficult for regional hunters. Our estimates of high deer populations on Sand and York Islands may be a result of limited hunting pressure coupled with a lack of predators and an abundant, highly preferred browse species (see next section). Regrettably, increased local hunting pressure alone may not be enough to impact the rapidly growing herds on Sand and York Islands.

There are several alternative methods for estimating deer populations, yet the Apostle Islands has presented researchers with many challenges with these methods. Winter aerial surveys have been used to detect the presence/absence of deer on islands, but population level estimates have been difficult to obtain due to forest cover, scale of the survey area, weather, and cost. Direct count and mark-recapture methods require extensive road or trail systems that are not present throughout much of the archipelago. Additionally, mark-recapture studies require investigator expertise in animal handling and the use of cost-prohibitive tranquilizers. In light of these obstacles, the pellet count method was the most practical technique that could be designed into management guidelines for further monitoring by National Park Service staff.

It should be noted that pellet count surveys have limitations that can influence population estimates. Pellet groups may be missed, obscured by vegetation during the survey, or washed away by rainstorms, resulting in an underestimate of population density (Neff, 1968). Furthermore, the validity of estimating population density by pellet counts has been called into question by Fuller (1991), since these estimates rely on published defecation rates (e.g., Rogers, 1987; Neff, 1968) that may vary by age, sex, and diet. Early into our investigation we attempted to validate the pellet count method through the use of a noninvasive DNA-based tissue sampling procedure for individual identification of deer on Sand Island (Belant et al., 2007). Unfortunately funding for the procedures was declined. Recent advances in DNA markers and molecular techniques have enabled researchers to develop mark-recapture procedures for estimating populations of free-ranging ungulates using DNA from fecal pellets (Brinkman et al., 2011; Poole et al., 2011). Once available for white-tailed deer, this technique could be incorporated into a long-term monitoring and management plan for white-tailed deer on Apostle Islands. Although DNA sampling has been shown to provide a careful population estimates, it may not be amenable to repeated monitoring due to the costs associated with sampling and laboratory analysis.

Deer Browse Analysis

Food availability, water and cover are primary factors that determine the survival of animal populations. In places where water is relatively abundant, the availability of food and cover will strongly affect the number of animals occupying an area. This dynamic is exceeding evident on Apostle Islands National Lakeshore. Between 1998 and 2002, white-tailed deer are suspected to have migrated from the nearby Bayfield peninsula to Sand and York Islands. Neither island had a recorded history of over-wintering deer prior to this period. Research revealed that Sand and York Islands maintained 176-187% greater available forage when compared to Basswood and Oak islands (Figure 9).

Deer are choosy generalist herbivores that utilize many different types of plants for food, but do exhibit strong preferences within certain types. In many areas, buds and conifer leaves from trees and shrubs are an important dietary component for a deer, especially in fall and winter when herbaceous green vegetation is unavailable. A number of partial records documenting preferred deer foods in Wisconsin all agree that Canada yew, eastern hemlock and northern white cedar are highly preferred by deer during winter (Swift 1948; Curtis, 1959; Dahlberg & Guettinger 1956; Beals et al., 1960), and Canada yew is often sought out. From the 65 plots examined on Sand and York islands, 98% contained Canada yew and this species accounted for 95% of the available forage. Our examination into overall forage availability using a preference rating system also revealed that Sand and York islands were dominated by first choice foods. Basswood and Oak islands had a relatively even distribution of first, second and third choice forage, but significantly less overall abundance.

Theoretically, if a small population were to suddenly be confronted with an unoccupied environment with no predators and unlimited food, water and cover, it would expand exponentially until the availability of resources could no longer support the growing population. In 1947, Leopold et al. documented nearly 100 cases where white-tailed deer or mule deer populations grew to such numbers that food availability was jeopardized. Disaster was averted in notably half of these cases when humans altered the habitat or initiated hunting. In other cases over-browsing was followed by mass starvation and catastrophic effects on vegetation. There is no evidence that suggests the deer population is imperiled on Sand and York islands, but plant populations are showing levels of herbivory and damage by deer that warranty management action.

The browse preferences of deer have both direct and indirect effects on the growth, reproduction, and survival of plants through consumption of buds, leaves, stems, flowers and fruits. The current deer herd browsed 12-18% of available stems on Sand and York Islands (Figure 10). Once the browsing intensity was partitioned by species it revealed that Canada yew was highly preferred over eastern hemlock and northern white cedar (Figure 12). Although hemlock and cedar were not nearly as abundant as Canada yew, a number of sites across Sand and York Islands contained areas where a combination of these species existed (Figure 13). The relative absence of browse evidence on cedar and hemlock when Canada yew was present suggests that white-tailed deer were selecting yew over the latter two species. Calculated electivity values from Sand and York islands revealed strong selection for Canada yew and against cedar and hemlock (Table 6). The Basswood and Oak island deer herds showed strong selection for cedar and hemlock, which is no different from trends found elsewhere (Table 6).

Numerous studies have documented that cedar and hemlock regeneration is severely impacted by sustained deer browsing (Alverson et al., 1988; Frelich and Lorimer, 1985; Rooney et al., 2002; Stoeckeler et al., 1957). Northern white cedar shows evidence of impairment when less than 20 % of the new growth is removed (Aldous, 1952), and deer induced sapling mortality under high browse pressure (Rooney, 2001; Rooney et al., 2002). Frelich and Lorimer (1985) documented changes in the size-class distribution and eventual replacement of hemlock by hardwood species if deer populations remained high. To date there is limited information available on forest communities containing an abundance of Canada yew with white-tailed deer and populations of cedar and hemlock.

Early observations and documents of presettlement vegetation suggest that Canada yew was a dominant understory shrub that formed dense layers of vegetation in mature conifer hardwood forests of the Lake States (Curtis, 1959; Martell, 1974). Researchers have found that recruitment of conifer and hardwood seedlings under these conditions is low, signifying that Canada yew may inhibit seedling establishment or survival. Danz (1998) compared the density of seedlings and saplings of American beech and sugar maple both within and outside patches of Canada yew and found significantly fewer seedlings in yew patches, although yew density did not affect recruitment to saplings or trees. Tyrrell and Crow (1994) attributed the failed recruitment of hemlock seedlings in the deer-free Outer Island old-growth stand to dense Canada yew populations. Additionally, other authors have also noted reduced floristic diversity in yew stands found on select islands within Apostle Islands National Lakeshore (Judziewicz and Koch, 1993; Balgooyen and Waller, 1995). Contrary to these reports, one of the most remarkable observations documented during this study was the unexpected degree of cedar and hemlock regeneration on Sand and York Islands, where Canada yew is dense and deer populations exceed levels shown to be unfavorable. Although quantitative techniques to specifically measure this observation were not designed into this study, they are worthy of note for further conjecture.

A plot-by-plot comparison revealed that 23% and 29% of sites on Sand and York Islands contained measurable amounts of cedar and hemlock regeneration within Canada yew. Using three demographic categories based on height (Rooney et al., 2002), all the individuals recorded were within 30-300 cm tall. It should be noted that investigators in this study did not record individuals below 30 cm, though the presence of smaller categories was noted.

As a generalist herbivore, deer prefer edges containing abundant forage and reduce energy expenditures during winter by limiting activity to level habitat with less snow depth (Moen, 1976). These energy conservation adaptations are significant when considering deer foraging behavior within yew dominated communities. Canada yew was often found in two growth patterns: large dense patches or a mixed collection of stems that carpeted the forest floor. In both cases, Canada yew provides an abundant, highly preferred resource that is developmentally-limited to the foraging range of deer. With a large breadth in their diet, forage selection by deer may be the response of increased forage biomass (forage-abundance hypothesis) or nutrient quality of available forage (selective-quality hypothesis). Unfortunately, there is surprising little nutritional information available on Canada yew that could be compared with cedar and hemlock. There is however indirect evidence that suggests forage selection by white-tailed deer is related more to quality than abundance (Weckerly and Kennedy, 1992). The result of these observations suggests that both growth patterns of Canada yew may act as refugia for the regeneration of cedar and hemlock by providing not only an abundant resource, but also one of presumably higher nutrient quality.

While forage abundance and quality are arguable characteristics that are attributed to Canada yew preference, forage selection by deer and other herbivores may also be a result of the mechanical or chemical composition of the plant (Cote' et al., 2004). An examination of Canada yew revealed no thorns, spines, hairs or other physical mechanism to deter browsers. Many plants have also adapted sophisticated chemical strategies such as secondary metabolites and terpenoids for dealing with herbivores organisms. The *Taxus* genus has been implicated for its toxicity to animal populations for centuries (Wilson et al., 2001). With the exception of the fleshy aril fruit, all parts of the yew plant contain poisonous taxane alkaloids that have triggered death in domestic grazers such as horses, cattle and sheep (Wilson et al., 2001). Ruminants such as white-tailed deer and moose appear to be unaffected by the taxane alkaloids present in Canada yew (Risenhoover and Maass, 1987; Allison, 1990a-b; Allison, 1992; Stachowicz and Allison, 1995). Aside from possible difficulty for ungulates to maneuver through dense yew stands, there is no evidence to suggest this species is well adapted to a landscape with abundant herbivores. These results suggest that Canada yew will continue to suffer from high browsing pressure and increased mortality on Sand and York Islands unless management action is taken to reduce the deer population and implement a deer management and Canada yew monitoring program.

Dimensional Analysis and Resource Pressure on *Taxus canadensis*

The woody plants deer consume grow seasonally, sending out new growth from terminal or lateral stems in spring and summer. If animals eat too much of this tissue, the damaged plants cannot regenerate additional twigs. By examining an unbiased sample of diameter at point of browse (DPB) measurements taken from stems across Sand and York Islands, I was able to develop a diameter-biomass regression model that was used to more precisely determine the level of impact on Canada yew. The mean DPB for Sand and York Islands combined was 1.63 mm, although an examination of browse diameters revealed a slight bimodal distribution (Figure 14). King (1975) found similar results in Michigan and attributed this pattern to lateral stems being browsed at smaller diameters than terminal stems. Once the DPB measures were partitioned by island, two alternative distribution patterns emerged. The mean DPB was shown to be significantly higher on Sand Island than York Island. This may be a consequence of any number of factors, although there were two observational differences between these islands: deer history and Canada yew growth patterns.

The deer population began to show signs of expansion on Sand Island in 1998 and York Island in 2002. From observations, it appeared that deer on Sand Island were repeatedly browsing the same location on a yew stem. The buds or apical shoots of plants produce auxins that inhibit the growth of lateral buds (Cline, 1991). The removal of the apical shoot by deer results in the growth of more lateral shoots. The new lateral growth on Canada yew appeared to develop proximal to the point of browse. As forage availability becomes more limiting, deer may revisit the same plants to forage on new growth. This would produce higher DPB measures since deer likely browse the older stems in an attempt to consume new growth. Alternatively, differences in Canada yew structure could also account for the detectable variance in DPB measures between Sand and York Islands. The population structure of Canada yew on Sand Island appeared to grow as a mixed collection of stems that carpeted the forest floor rather than large discrete patches found on areas of York. This likely produces a higher density of terminal stems on Sand Island which would in turn be browsed by deer at a greater diameter (King, 1975).

Dimensional analyses on unbrowsed stems collected from Raspberry Island were used to develop an age-diameter relationship and regression model to determine the mean annual growth removed during browsing. The mean DPB estimates from Sand and York Islands indicate that greater than one year's growth was removed during a browsing event. Aside from the direct loss of new tissue, browsing by deer has been shown to skew sex ratios in yew populations and limit the availability of pollen to the point where sexual reproduction is impaired (Allison, 1990a,b,c; Allison, 1992). My analysis of yew stems revealed that 83% of pollen cones were located on age-1 shoots most susceptible to consumption, supporting the hypothesis that elevated deer browsing limits pollen production in Canada yew populations. Although Canada yew also reproduces asexually when arching branches are pressed to the soil surface and take root (Allison, 1990a), sexual reproduction is necessary to increase genetic diversity within and among metapopulations (Senneville et al., 2001). There has been very little published research done on the importance of seed dispersal and germination success in *Taxus canadensis*, yet this likely plays a vital role in recruitment and patch establishment.

Age-determined diameter and biomass measurements were fitted to $\log_{10}$-$\log_{10}$ regression. The allometric model was based on harvested stems that displayed no evidence of past deer browse and was shown to be an effective predictor of distal shoot biomass in Canada yew across the range of diameters used to develop the equation. High correlations have been observed between stem weight and diameter for a number of woody browse species (Shafer, 1963; Telfer, 1969, Lyon, 1970; King, 1975). Larger diameter values did exhibit greater error than smaller values, but such heteroscedasticity is common in biomass data (Parresol, 1993). Extrapolating beyond the data range used may cause bias in estimating biomass for larger diameters; however the maximum dpb measure from the field was within this range. A calculated correction factor (*CF*) of 1.069 was developed to compensate for the potential underestimation resulting from back-transforming logarithmic predictions to arithmetic units, as suggested by Baskerville (1972), Beauchamp and Olson (1973), and Sprugel (1983). The *CF* for Canada yew was similar to published values for other woody species in North America (Jenkins et al., 2004).

The density of large herbivores such as white-tailed deer is considered a major driver of forest ecosystem structure and function. Quantitative techniques for estimating the productivity of browse species and consumption by ungulates have proven to be effective in determining the relationship between animal populations and their habitat as well as projecting the changes that may occur within these habitats over time (Frelich and Lorimer, 1985; McInnes et al., 1992; Bilyeu et al., 2007). Allometric regression models exist for predicting aboveground biomass for many species (Jenkins et al., 2004) and may also be used to predict the biomass removed by ungulate populations. Research at Apostle Islands National Lakeshore determined that high-density deer populations were causing significant losses in Canada yew growth. To evaluate these losses, we applied the allometric model to DPB and utilization measures collected from Sand and York Islands to establish the proportion of biomass removed.

The mean mass of 642 age-1 shoots was used to determine grams of browsable tissue produced on an individual stem of Canada yew. We calculated biomass production by multiplying the number stems available for consumption by mean mass produced. The variation in biomass produced between Sand and York may be a consequence of age differences between populations. Although stem diameter has been shown to be a poor predictor of Canada yew age (Danz, 1998), the basal diameter and height of shoots on York Island was significantly greater than those found on Sand Island. Therefore, variation in production by island may be a function of size differences that are only partially explained by age.

The mean DPB measure from each plot was used in the allometric model to predict biomass consumed. This quantity was scaled up to the shoot level by multiplying the number of browsed stems by the mean mass consumed. These derived quantities revealed that approximately 74% and 53% of new growth on Sand and York Islands, respectively, were consumed by the current deer population. Research into elk browsing on two species of *Salix* suggests that these estimates may be conservative; Bilyeu et al. (2007) demonstrated that when greater than 45% of shoot biomass was removed, shoot-level estimates failed to accurately predict the actual removal at the stem level because some shoots were removed entirely. In this case, pre-browsed measurements may be necessary to account for completely consumed shoots. Field observations of Canada yew patches with this level of browsing intensity has resulted in reduced vigor and shoot mortality. Although there is no threshold to indicate the amount of browse Canada yew can experience before impairment, mortality and replacement ensues, it is obvious that the browse pressure endured on Sands and York Islands is detrimental to yew survival and reproduce. Even under low herbivore densities, exclosures have been shown to be the only line of defense for the recovery of a highly palatable species like Canada yew (Holmes et al., 2009).

The allometric model for predicting yew biomass in foliage and wood that deer consume relies on the DPB and utilization figures alone. The practicality of measuring a random sample of DPB in combination with shoot utilization makes this equation attractive and more likely to be used by natural resource managers and researchers. This species-specific model for quantifying browsable biomass on one of the most preferred forage species for white-tailed deer should significantly improve accuracy in estimating impact and losses. Quantifying browse utilization on shrubs at larger spatial scales is difficult because shrubs have complex and spatially variable growth forms, yet my model can be used to predict biomass removal at multiple spatial levels with fine-scale estimates of utilization at the stem level.

CONCLUSION

Studies throughout Michigan, Minnesota, and Wisconsin provide strong evidence of the persistent impact of deer on forest communities. In protected lands, deer populations are either controlled through some form of public hunting or they are left unmanaged. Throughout Apostle Islands National Lakeshore, deer population decisions should be driven by the protection and preservation of sensitive native vegetation. Estimates of winter deer densities provide natural resource managers with an important reference point; however deer should not be the only consideration in management decisions. In areas of known sensitive or threatened vegetation with high palatability, deer herbivory should be recognized, monitored and managed as a serious threat to the survival and reproduction of local flora.

On Apostle Islands there are clear and fundamental differences in forage availability, deer populations, and browsing intensities in communities dominated and not dominated by Canada yew. The development of deer management guidelines should reflect these structural differences in community composition. Although public hunting appears effective in managing populations on Basswood and Oak islands, deer densities on Sand and York Islands are at levels that warrant immediate implementation of an aggressive deer management program. The synergistic effect of an abundant highly preferred browse species and a lack of predators have caused deer populations to expand to levels that present significant losses in Canada yew growth and reproduction. While yew remains relatively abundant throughout the park, the results from this study demonstrate the dramatic effect recent colonization events can have on browse-sensitive vegetation. I strongly encourage park managers to routinely monitor islands with known deer as well as adjacent areas that may become populated.

Occam's razor would declare that as scientists we accept the simplest possible theoretical explanation for our data—white-tailed deer and Canada yew are incompatible.

Table 1: Characteristics of sampling sites at Apostle Islands National Lakeshore, Wisconsin.

Island	Island Area (km^2)	Distance from Mainland (km)	Number of Sites Sampled	Number of Covertypes Sampled
Sand	11.99	1.93	47	3
York	1.30	1.45	18	3
Raspberry	1.20	2.74	12	2
Oak	20.64	2.09	67	5
Basswood	7.79	1.93	47	3

Table 2: Winter forage species found on islands sampled at Apostle Islands National Lakeshore, Wisconsin.

Common Name	Latin Binomial	Abbreviation
Balsam Fir	*Abies balsamea*	ABIBAL
Red Maple	*Acer rubrum*	ACERUB
Sugar Maple	*Acer saccharum*	ACESAC
Mountain Maple	*Acer spicatum*	ACESPI
Speckled Alder	*Alnus rugosa*	ALNRUG
Serviceberry	*Amelanchier spp.*	AMESPP
Yellow Birch	*Betula alleghaniensis*	BETALL
White Birch	*Betula papyrifera*	BETPAP
Red Osier Dogwood	*Cornus stolonifera*	CORSTO
Beaked Hazel	*Corylus cornuta*	CORCOR
Black Ash	*Fraxinus nigra*	FRANIG
Green Ash	*Fraxinus pennsylvanica*	FRAPEN
Fly Honeysuckle	*Lonicera canadensis*	LONCAN
Ironwood	*Ostrya virginiana*	OSTVIR
White Pine	*Pinus strobus*	PINSTR
Big-Tooth Aspen	*Populus grandidentata*	POPGRA
Pin Cherry	*Prunus pensylvanica*	PRUPEN
Red Oak	*Quercus rubra*	QUERUB
Thimbleberry	*Rubus parviflorus*	RUBPAR
Mountain Ash	*Sorbus americana*	SORAME
Canada Yew	*Taxus canadensis*	TAXCAN
White Cedar	*Thuja occidentalis*	THUOCC
Basswood	*Tilia americana*	TILAME
Hemlock	*Tsuga canadensis*	TSUCAN

Table 3: Preference rating of winter forage species found on islands at Apostle Islands National Lakeshore, Wisconsin. Choices are according to Dahlberg and Guettinger (1956) and Beals et al. (1960).

1st Choice		**3rd Choice**	
Red Maple	*Acer rubrum*	Balsam Fir	*Abies balsamea*
Mountain Ash	*Sorbus americana*	Sugar Maple	*Acer saccharum*
Canada Yew	*Taxus canadensis*	White Birch	*Betula papyrifera*
White Cedar	*Thuja occidentalis*	Beaked Hazel	*Corylus cornuta*
Hemlock	*Tsuga canadensis*	Green Ash	*Fraxinus pennsylvanica*
		Black Ash	*Fraxinus nigra*
2nd Choice		Pin Cherry	*Prunus pensylvanica*
Mountain Maple	*Acer spicatum*	Big-Tooth Aspen	*Populus grandidentata*
Serviceberry	*Amelanchier spp.*	Red Oak	Quercus rubra
Yellow Birch	*Betula alleghaniensis*		
Red Osier Dogwood	*Cornus stolonifera*	**4th Choice**	
Fly Honeysuckle	*Lonicera canadensis*	Ironwood	*Ostrya virginiana*
Basswood	*Tilia americana*	Speckled Alder	*Alnus rugosa*
White Pine	*Pinus strobes*		
Thimbleberry	*Rubus parviflorus*		

Table 4: Mean pellet density and deer population estimates obtained by using the pellet count method from an 82 m^2 circular plot located on selected islands in Apostle Islands National Lakeshore, Wisconsin. Deer km^{-2} and deer population (total per island) estimates were determined using a deposition period of 195 days and defecation rates of 13 or 34 pellet groups $deer^{-1}$ day^{-1}.

Island	Mean Pellets Per Plot	SE Mean Pellets Per Plot	Deer km^{-2}		Deer Population	
			13	34	13	34
Sand	4.415	0.427	21.52	8.23	258	99
York	4.125	0.824	20.09	7.68	26	10
Basswood	0.979	0.300	4.77	1.82	37	14
Oak	0.836	0.196	4.07	1.56	84	32
Raspberry	0.000	0.000	0.00	0.00	0	0

Table 5: Species richness and relative density of preference ratings in winter forage on selected islands in Apostle Islands National Lakeshore, Wisconsin. See Table 3 for details on preference rating system.

Island	Species Richness	1st Choice	2nd Choice	3rd Choice	4th Choice
Sand	16	98.44	1.03	0.53	0.00
York	8	99.70	0.26	0.04	0.00
Basswood	19	29.49	30.91	39.54	0.06
Oak	13	56.46	6.63	31.13	5.75

Table 6: Electivities and tests for statistical significance on winter forage species utilized by white-tailed deer at sample locations within Apostle Islands National Lakeshore. Positive electivity values show selection for a species while negative values indicate selection against.

Species	Basswood		Oak		Sand		York	
	Electivity	χ^2	Electivity	χ^2	Electivity	χ^2	Electivity	χ^2
ACERUB	0.66	2.950	-0.29	2.395	0.26	1.232	-	-
ACESAC	0.79	1.810	-0.46	1.637	0.00	0.000	-	-
ACESPI	1.30	***27.959	-0.53	*5.894	0.35	***72.484	-0.23	3.652
AMESPP	-0.58	3.717	-0.42	*4.853	-1.09	***15.500	-	-
BETALL	-3.24	***20.844	0.00	0.000	0.04	0.038	1.12	***17.626
BETPAP	-0.90	**7.918	0.10	0.033	-0.69	***32.902	-	-
CORSTO	-	-	-	-	0.31	***19.157	-	-
CORCOR	-0.76	**8.772	-0.73	**8.454	-0.67	***63.792	-0.59	*4.247
FRAPEN	-0.17	0.559	-	-	-	-	-	-
LONCAN	-1.03	***18.804	-0.56	**8.577	-	-	-	-
OSTVIR	0.98	2.087	-0.30	1.801	-	-	-	-
POPGRA	1.16	***13.946	0.63	**10.034	-	-	-	-
PRUPEN	0.00	0.000	-	-	-	-	-	-
QUERUB	1.22	***16.957	0.44	2.755	-	-	-	-
RUBPAR	0.27	0.313	-	-	-	-	-	-
SORAME	-	-	-	-	-	-	-0.26	0.196
TAXCAN	-	-	-	-	1.34	***2682.295	2.90	***1109.707
THUOCC	1.71	***34.14	-	-	-3.66	***912.620	-5.93	***210.517
TILAME	0.99	***17.942	-	-	-	-	-	-
TSUCAN	-1.67	***47.216	0.71	*0.757	-6.44	***124.485	-	-

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 7: Canada yew (*Taxus canadensis*) age-diameter relationship determined from dimensional analysis of 48 unbrowsed stems collected from Raspberry Island. For comparison, the mean DPB for York Island was 1.44 mm (SE ± 0.03) and Sand Island was 1.71 mm (SE ± 0.02).

Stem	Mean Diameter (mm)	± SE (mm)
Age-1	1.06	0.01
Age-2	1.47	0.03
Age-3	1.99	0.08

Table 8: Mass-diameter regression model and analysis of variance for *Taxus canadensis* stems from Apostle Islands National Lakeshore, Wisconsin. Equation estimates biomass of twigs and leaves at a specified diameter.

Regression Equation: Log_{10} Biomass(g) = -1.09g + 3.03g/mm (Log_{10} mm diameter)					
Predictor	***Coef***	***SE Coef***	***T***	***P***	
Constant	-1.08506	0.00598	-181.36	0.000	
Log_{10} Diameter	3.03037	0.03327	91.08	0.000	
S = 0.170967	R-Sq = 0.888		R-Sq(adj)=0.888		
Analysis of Variance					
Source	***DF***	***SS***	***MS***	***F***	***P***
Regression	1	242.47	242.47	8295.24	0.000
Residual Error	1048	30.63	0.03		
Total	1049	273.10			

Table 9: Estimated mean biomass production (annual growth) and removal by white-tailed deer per individual shoot (ramet) of *Taxus canadensis* across all sampling locations on Sand and York Islands. Cumulative biomass removed represents the mean overall biomass consumed by deer irrespective of browse period. Biomass removal and production represent the mean biomass removed or produced during the previous year.

Cumulative Biomass Removed	**Mean (g)**	**±SE (g)**
Sand	23.18	2.65
York	27.67	10.42
Current Biomass Removed		
Sand	4.18	0.55
York	6.98	2.79
Biomass Production		
Sand	5.52	0.38
York	10.40	1.31
Biomass Removed vs Produced		
Sand	74.02 %	7.19
York	53.34 %	13.62

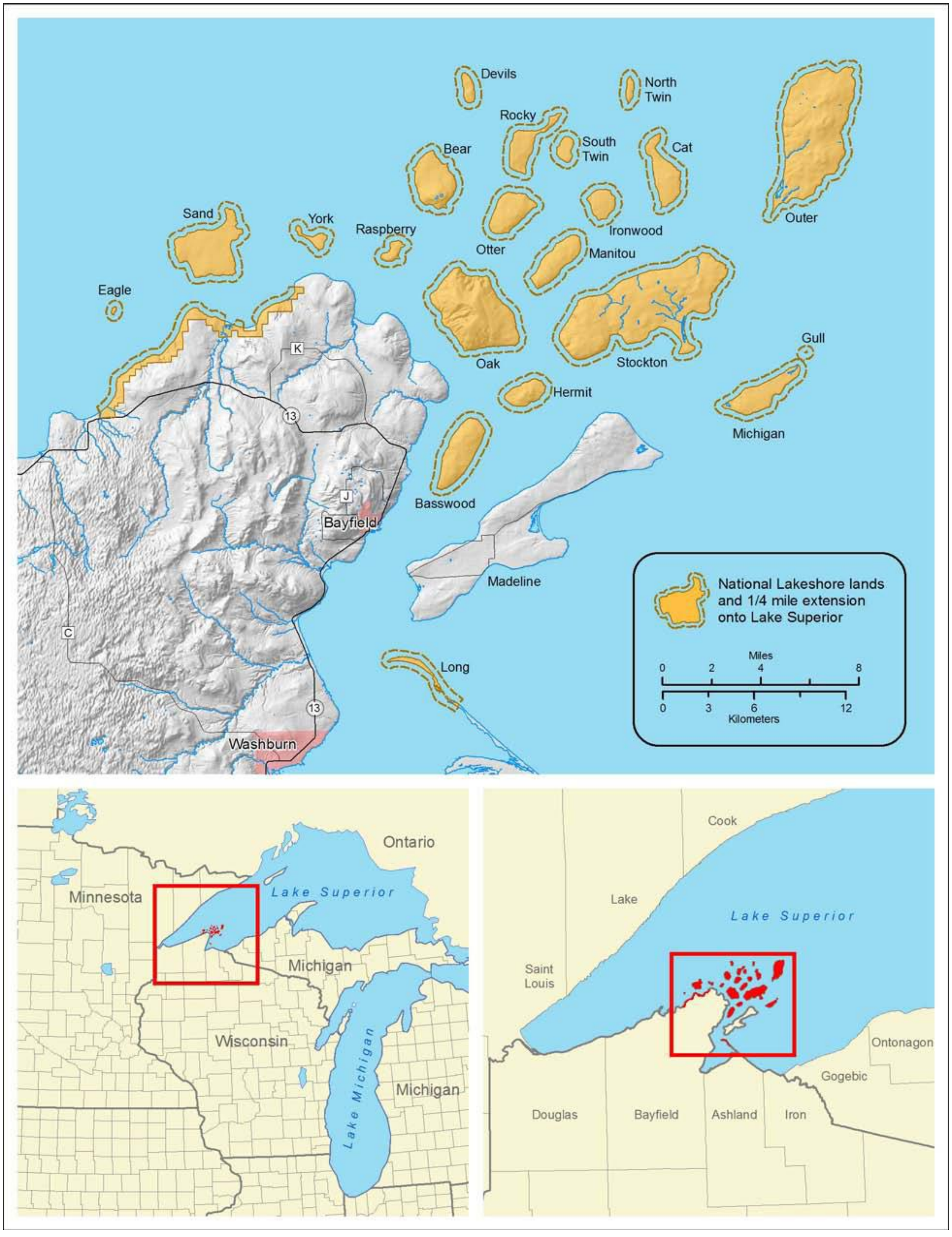


Figure 1: Location of Apostle Islands National Lakeshore and surrounding Great Lakes region, United States (Kraft et al. 2007).

Figure 2: Sampling locations across Basswood Island, Apostle Islands National Lakeshore.

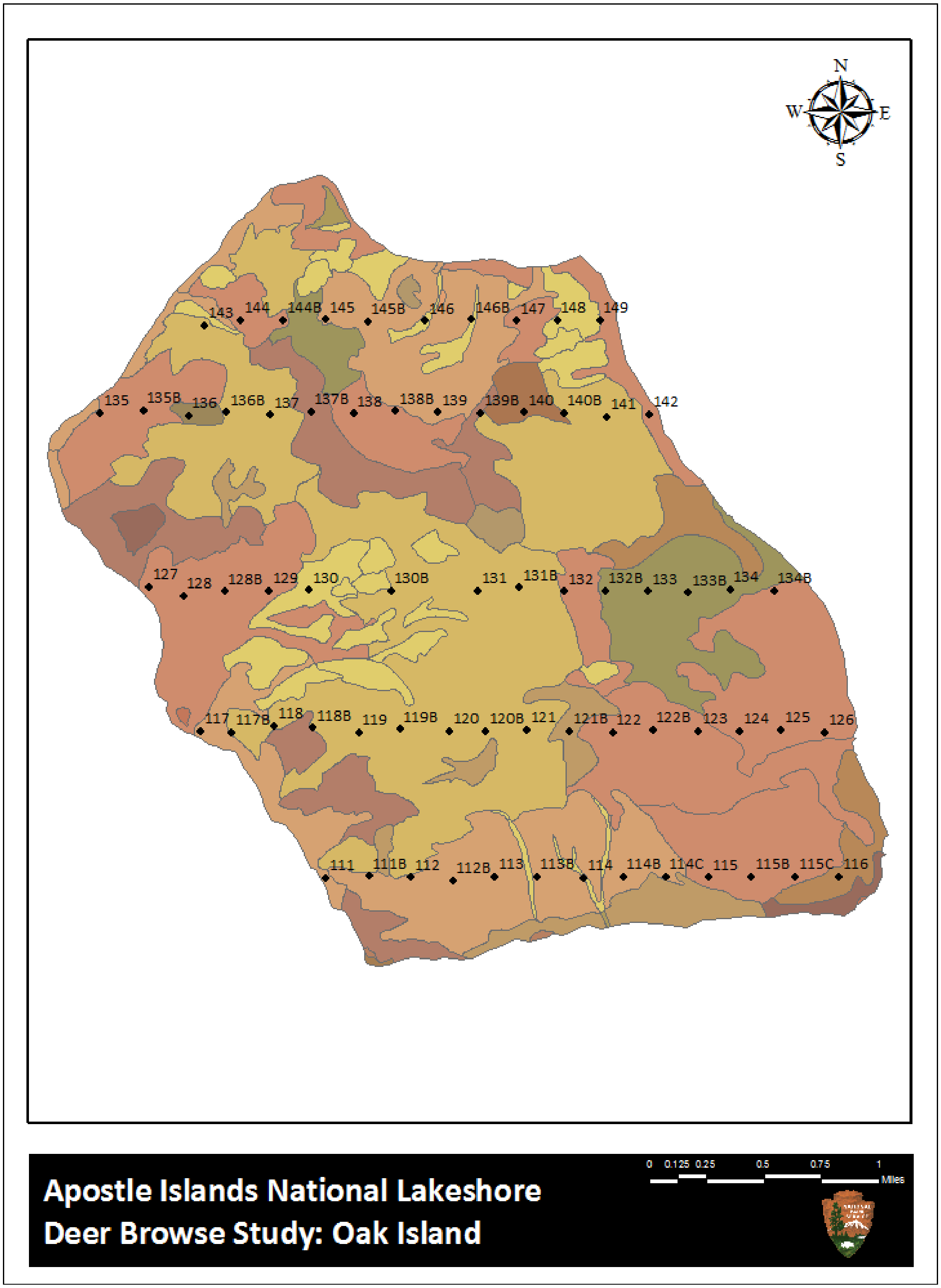


Figure 3: Sampling locations across Oak Island, Apostle Islands National Lakeshore.

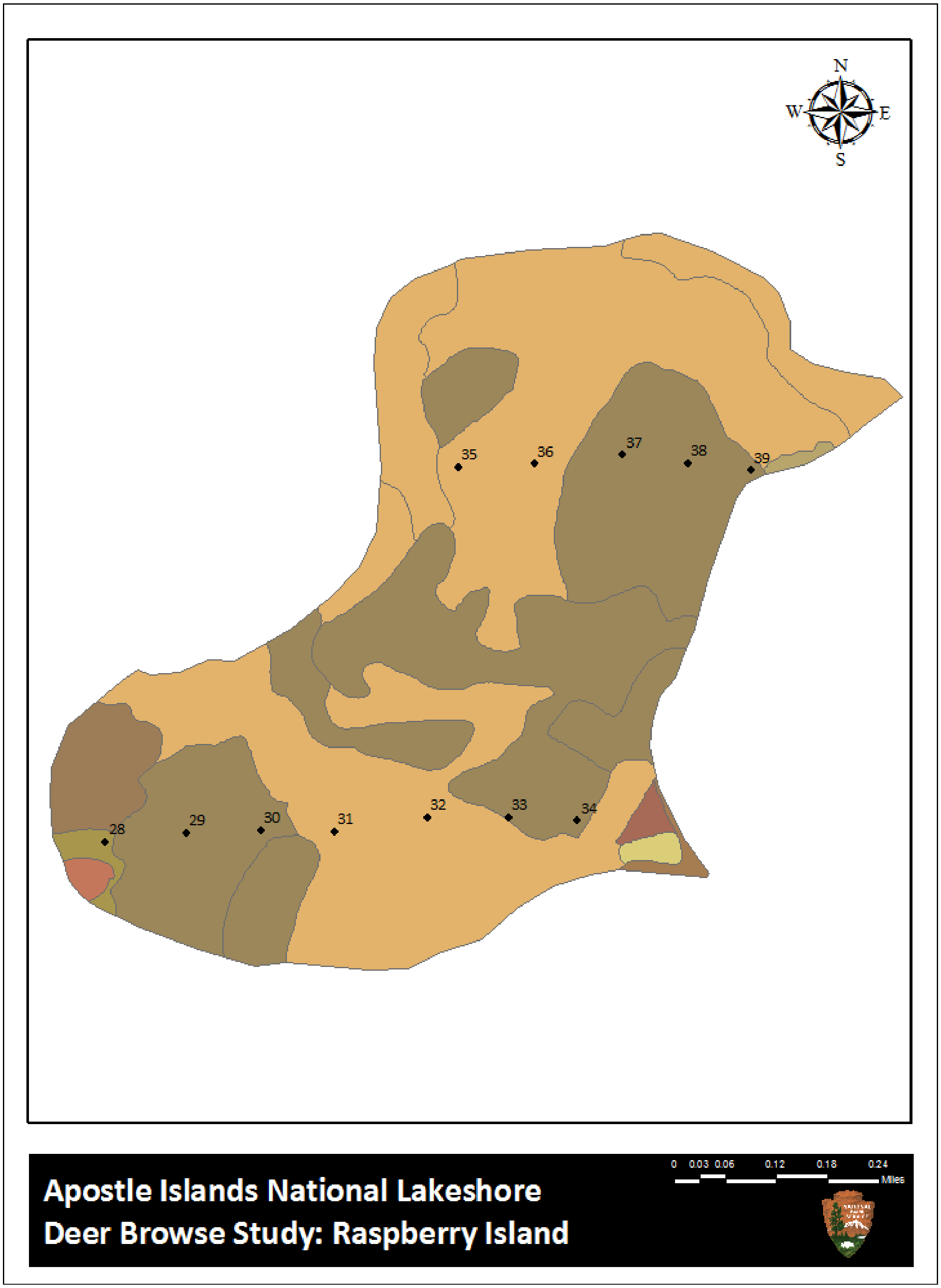


Figure 4: Sampling locations across Raspberry Island, Apostle Islands National Lakeshore.

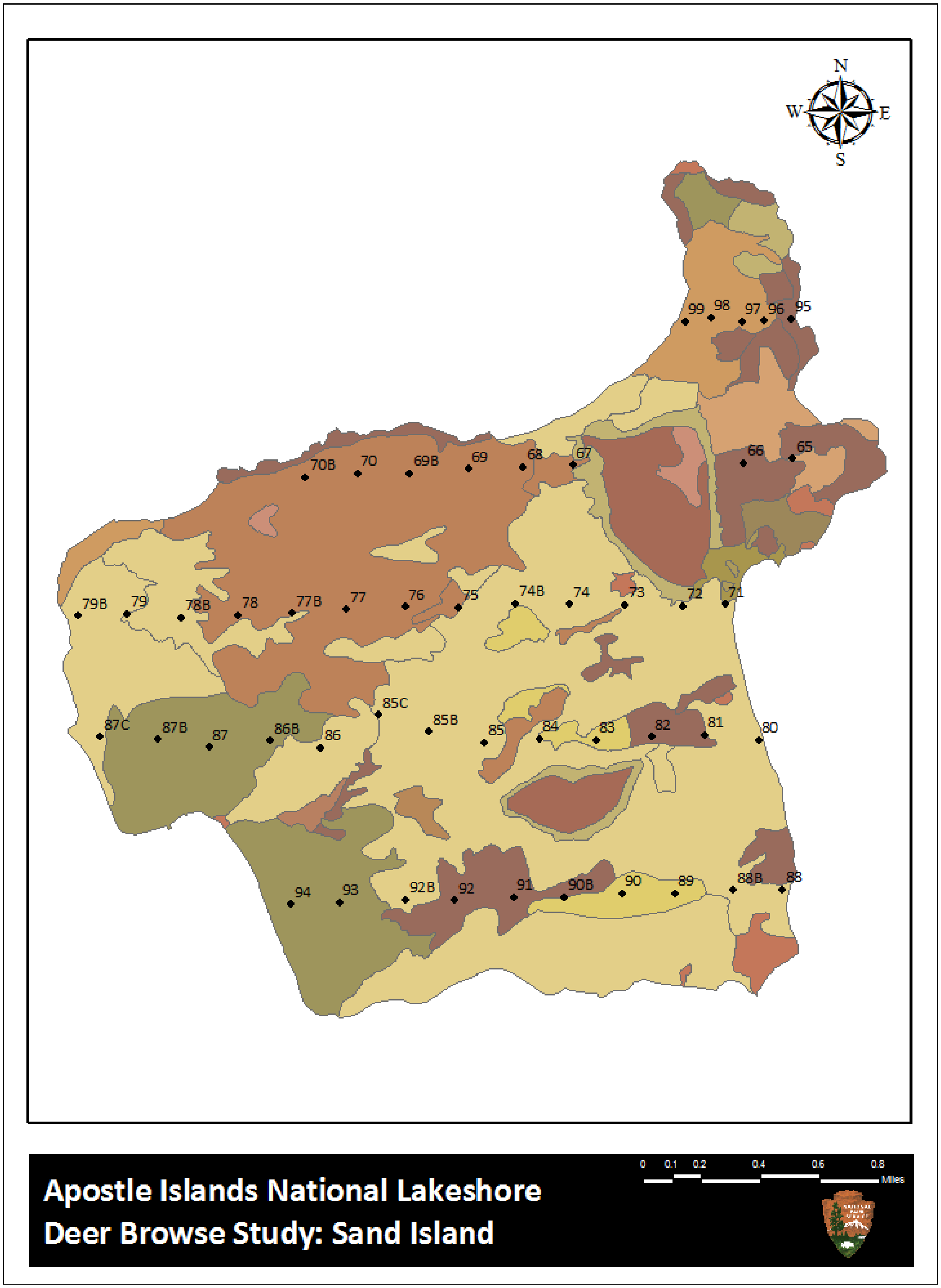


Figure 5: Sampling locations across Sand Island, Apostle Islands National Lakeshore.

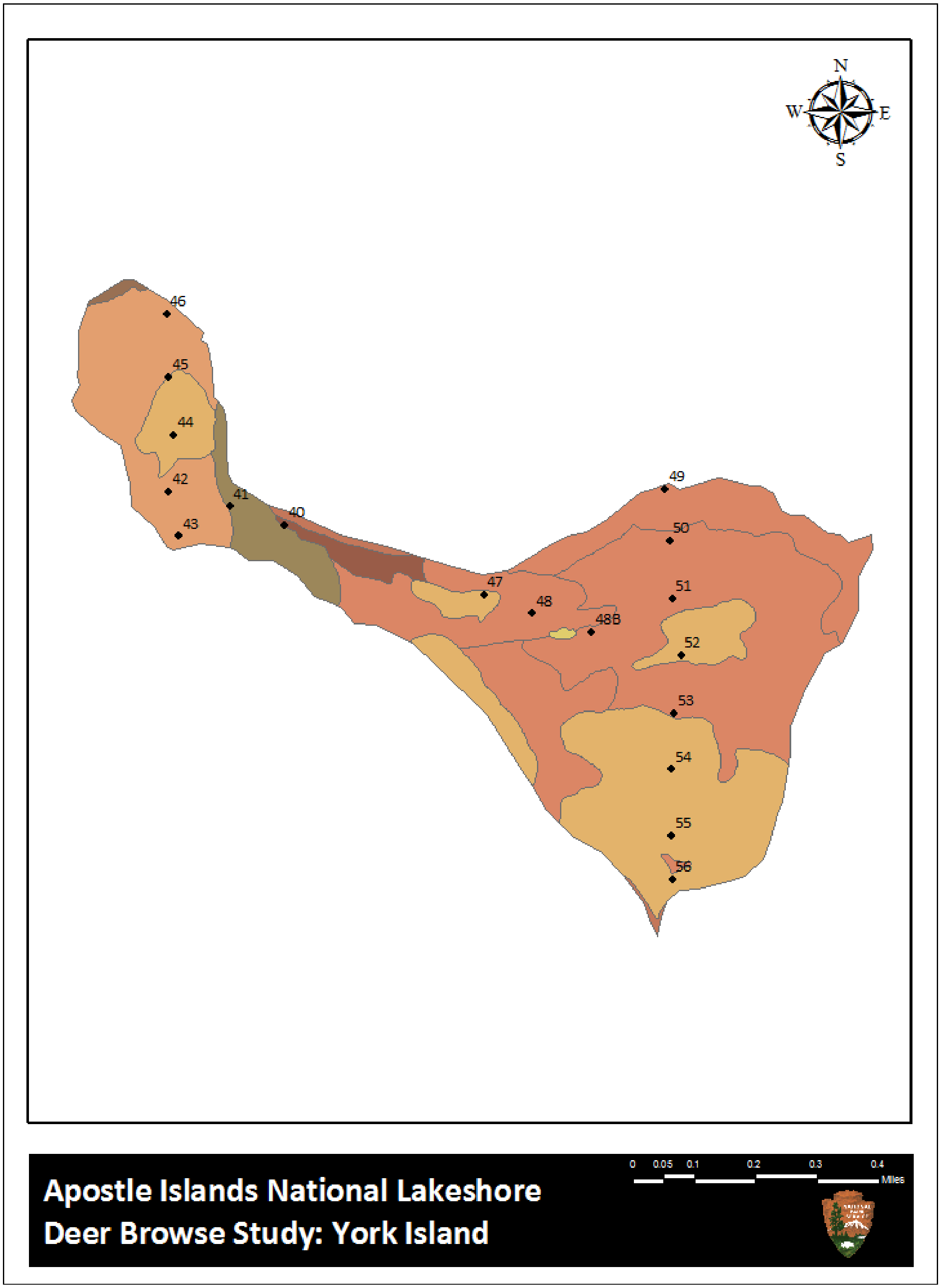


Figure 6: Sampling locations across York Island, Apostle Islands National Lakeshore.

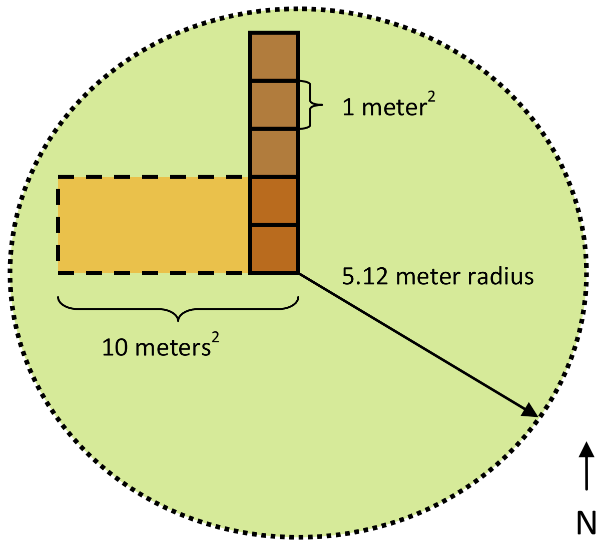


Figure 7: Layout for permanent plots sampled across selected islands within the Apostle Islands National Lakeshore, Wisconsin. White-tailed deer pellet density was recorded using the 5.12 meter radius plot. Available and browsed winter forage on all species except *Taxus canadensis* were recorded within the 10 m^2 rectangular plot. *Taxus* was examined within the five 1m^2 plots.

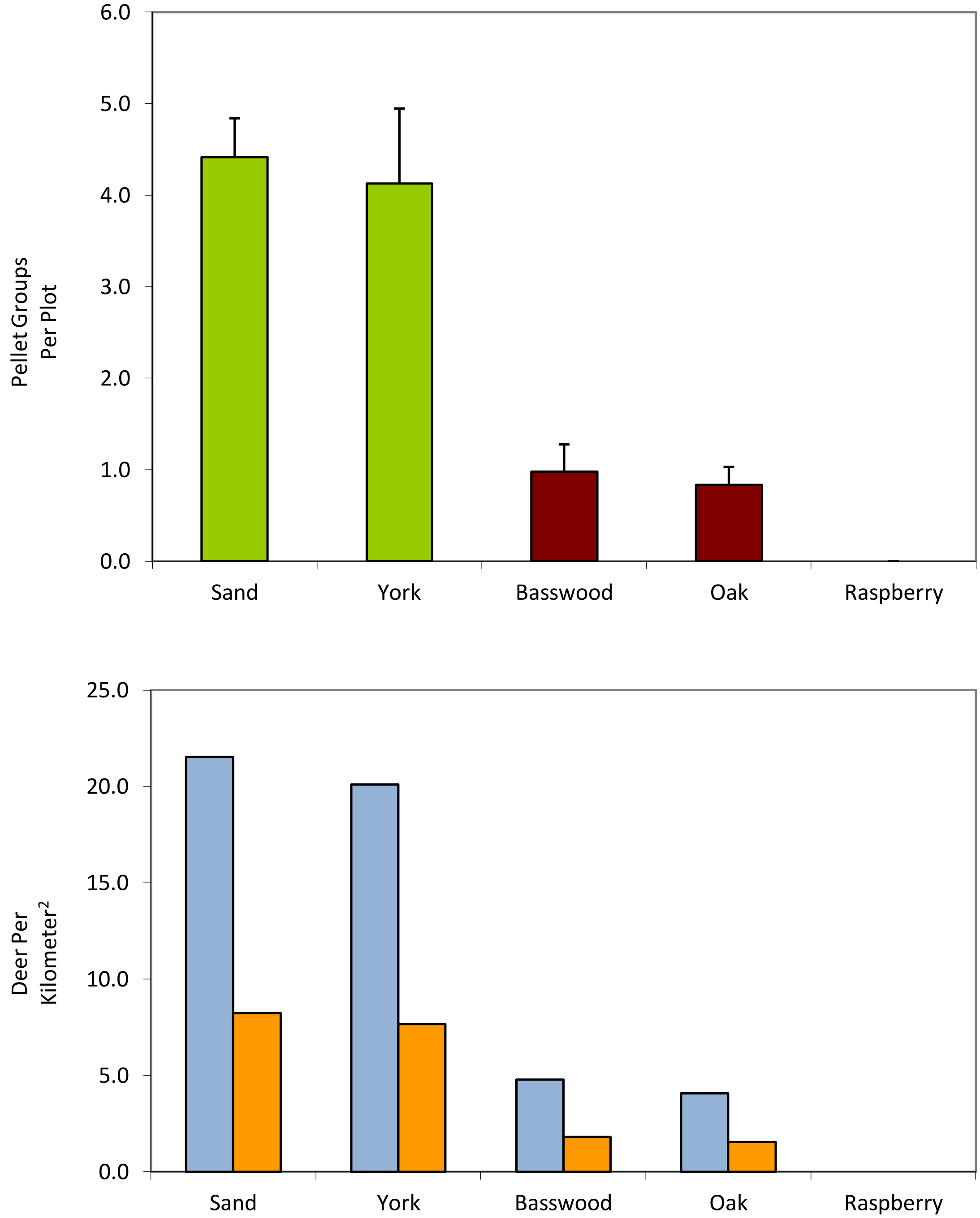


Figure 8: Mean pellet density and deer km^{-2} obtained using the pellet count method across all plots on selected islands in Apostle Islands National Lakeshore. Green bars denote islands dominated by TAXCAN and red bars signify islands without TAXCAN in the sampling plot. Deer km^{-2} were determined using a deposition period of 195 days and defecation rates of 13 (blue bars) and 34 (orange bars) pellet groups deer^{-1} days^{-1}.

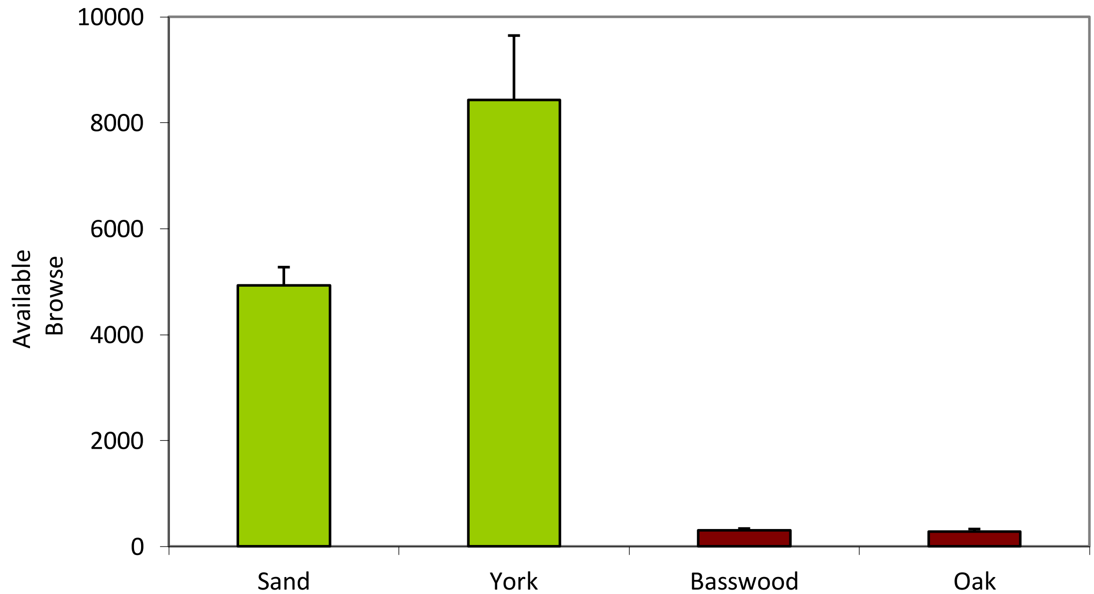


Figure 9: Cumulative number (mean + SE) of browse stems available for consumption across all 10 m^2 plots per island on selected islands at Apostle Islands National Lakeshore. Green bars denote islands dominated by TAXCAN and red bars signify islands without TAXCAN in the sampling plot.

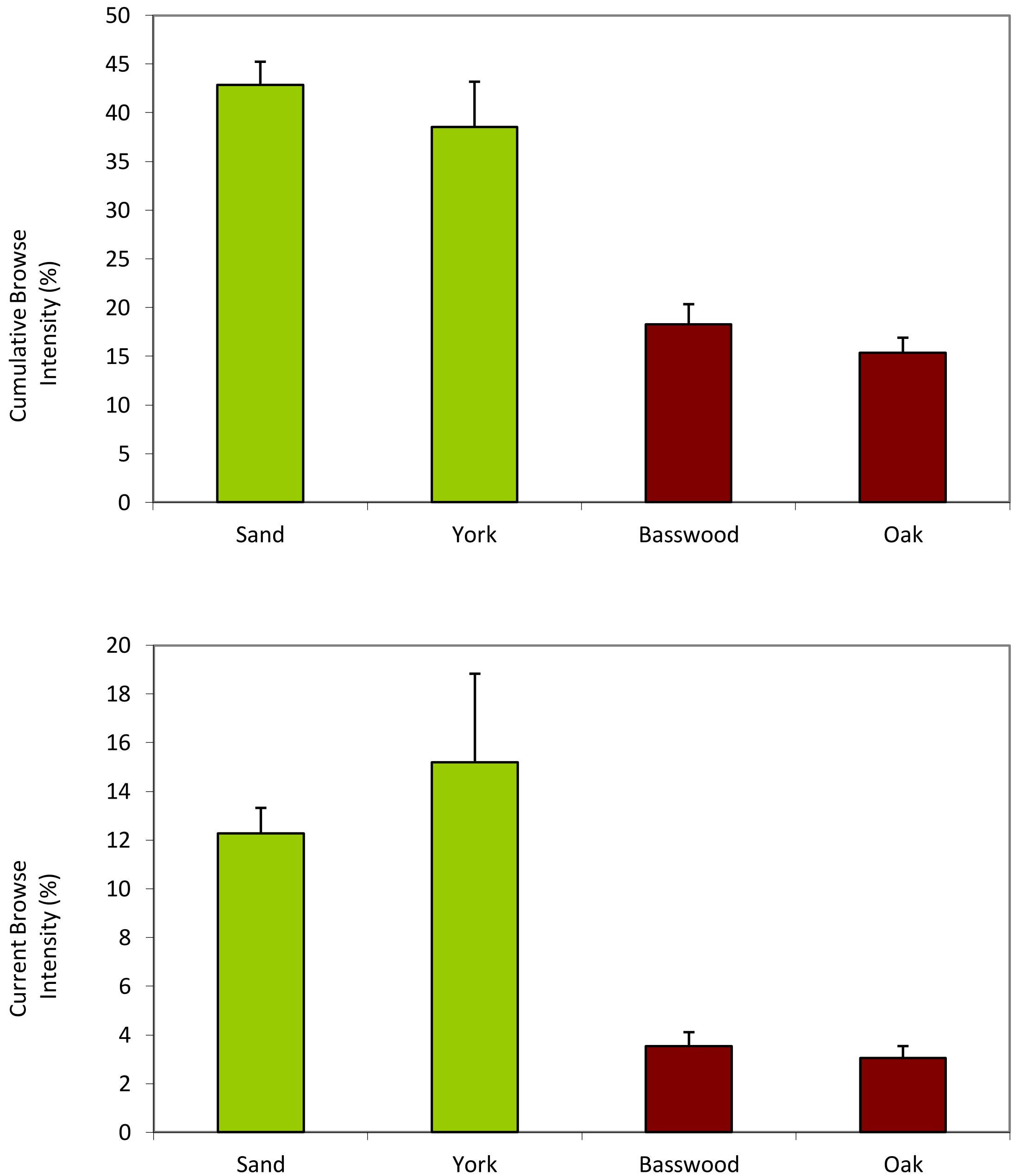
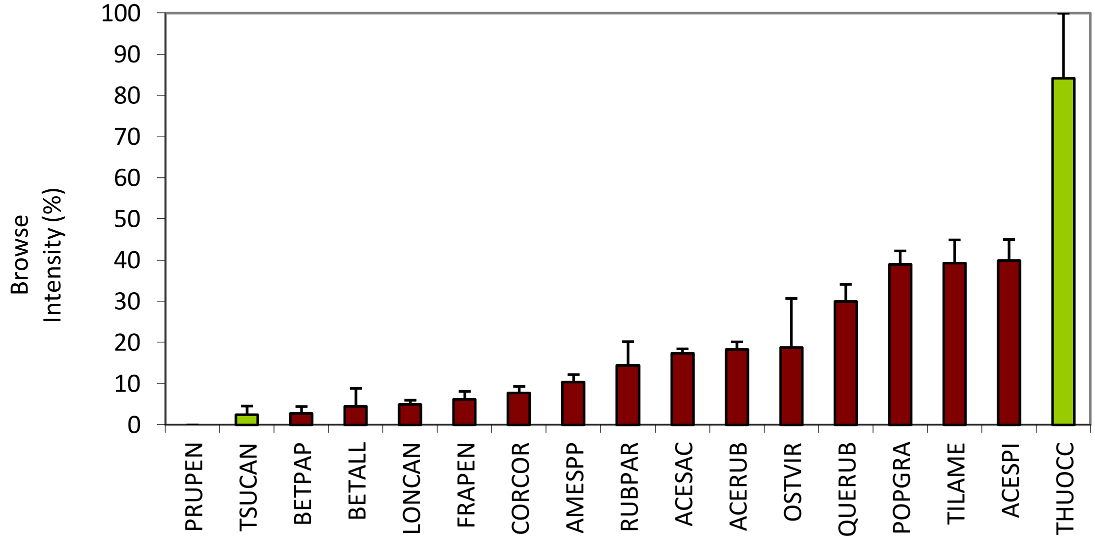


Figure 10: Cumulative and current browse intensity (mean + SE) across all 10 m^2 plots per island on selected islands at Apostle Islands National Lakeshore. Green bars denote islands dominated by TAXCAN and red bars signify islands without TAXCAN in the sampling plot.



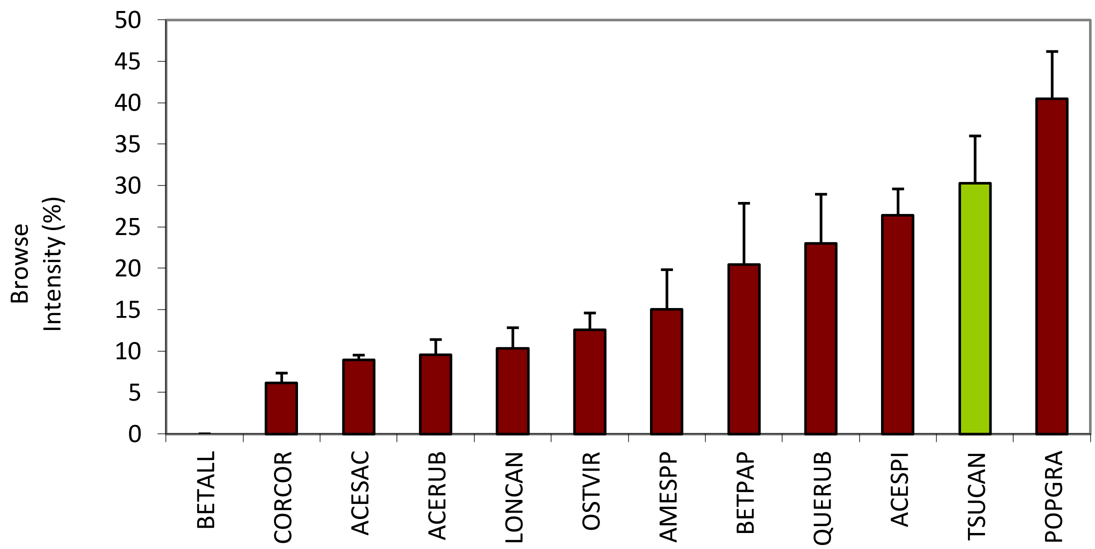


Figure 11: Browse intensity (mean + SE) by species arranged with increasing pressure on Basswood (top) and Oak (bottom) islands. Red bars denote deciduous browse species and green bars represent coniferous browse species.

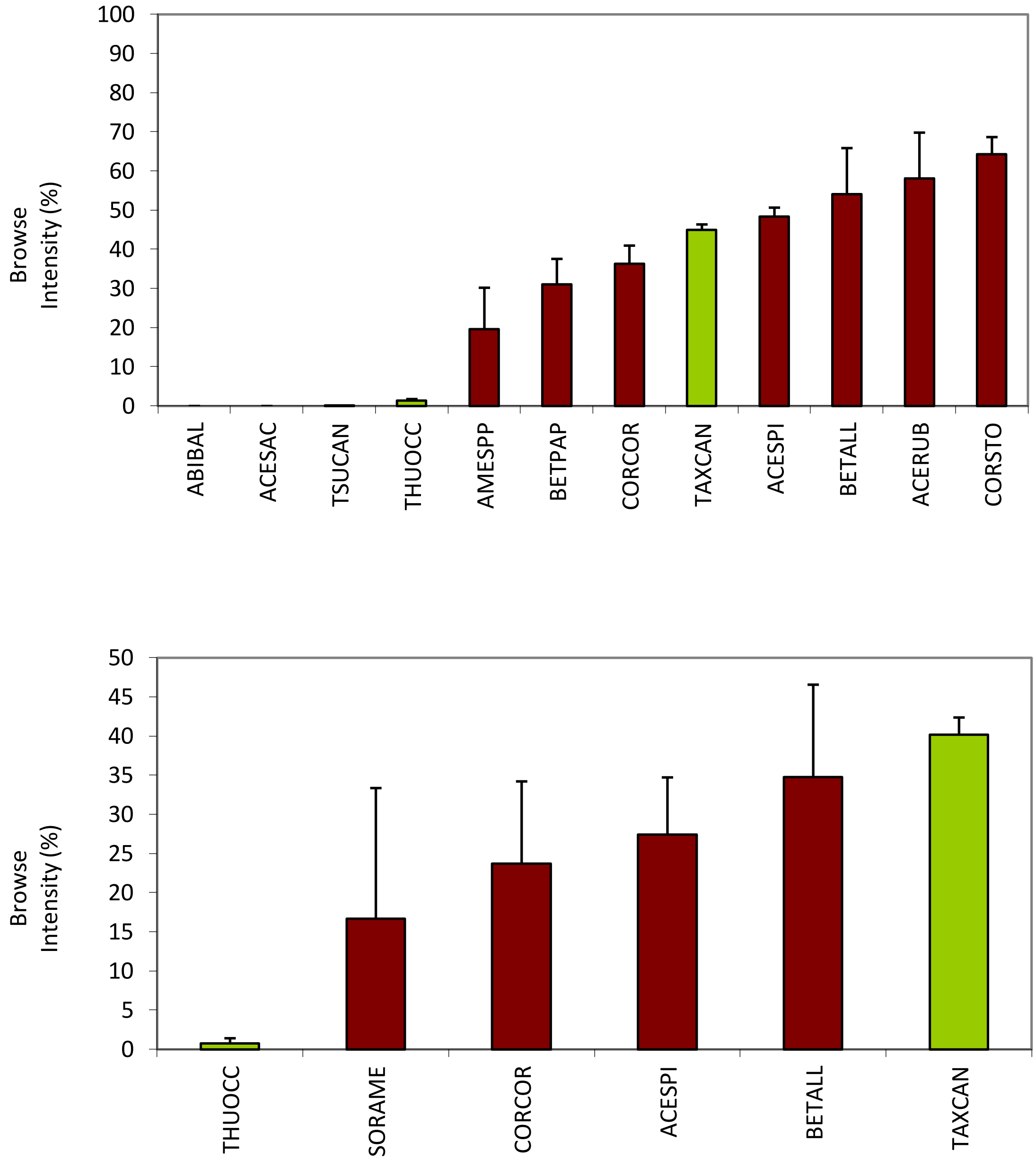


Figure 12: Browse intensity (mean + SE) by species arranged with increasing pressure on Sand (top) and York (bottom) islands. Red bars denote deciduous browse species and green bars represent coniferous browse species.

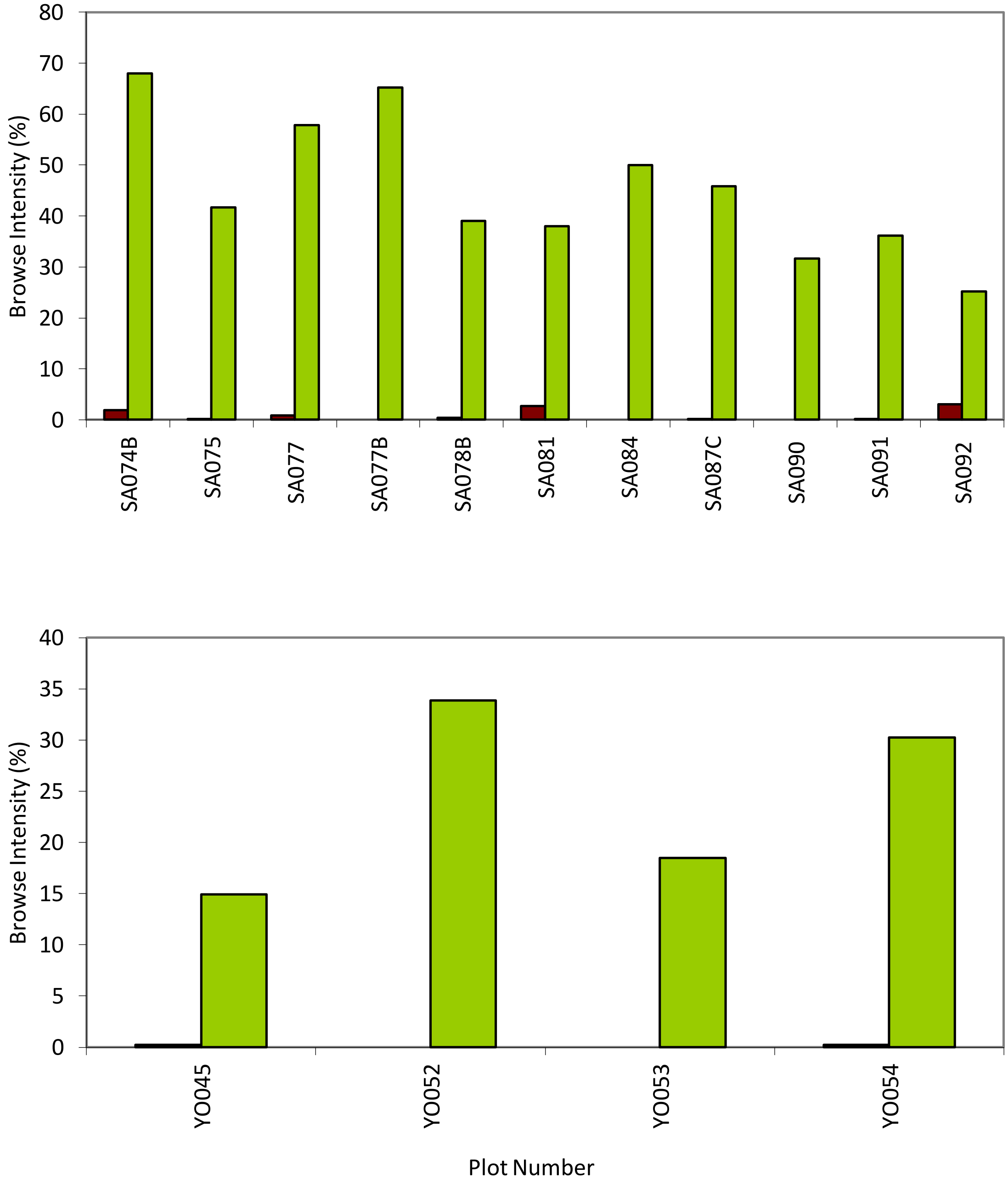
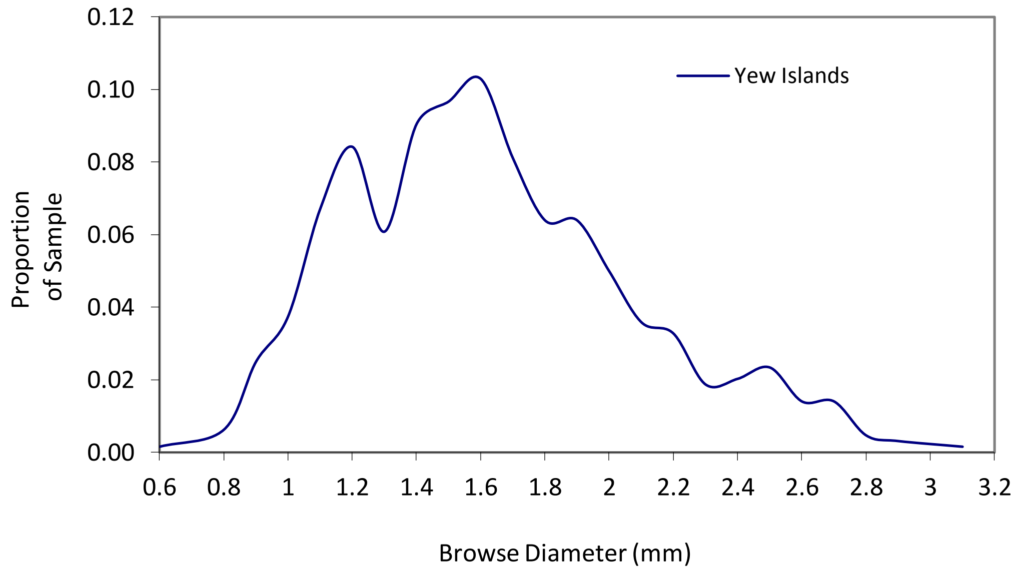


Figure 13: Conifer browse intensity comparison by plot for Sand (top) and York (bottom) island. Green bars represent TAXCAN and red bars signify all other conifer species at a plot.



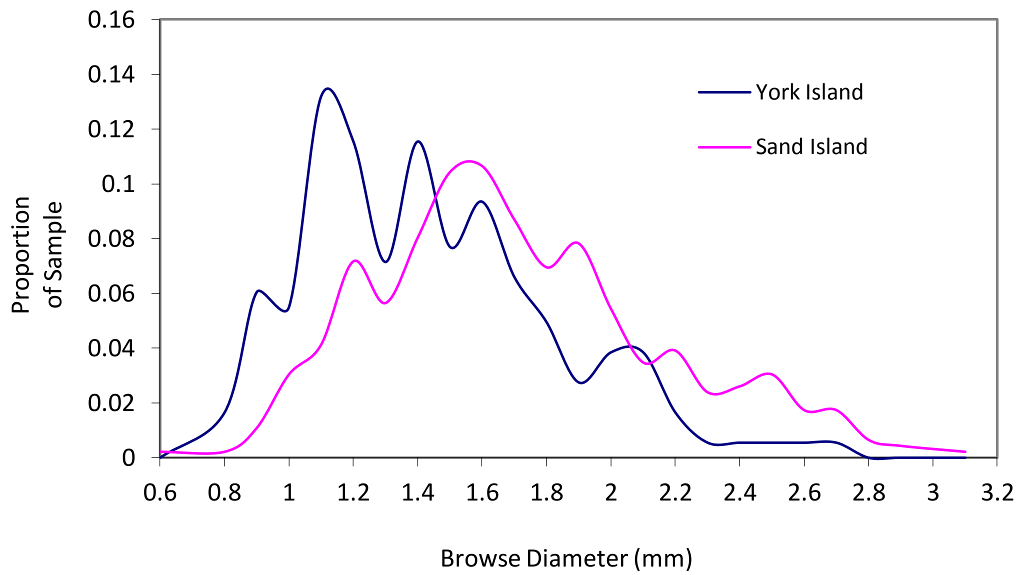


Figure 14: Proportion of *Taxus canadensis* diameter-point-browse (DPB) measures collected from the field on Sand and York Islands combined (top, mean = 1.63 mm ± 0.02 SE) and separated by island (bottom, York mean = 1.44 mm ± SE 0.03 mm and Sand mean = 1.71 mm ± SE 0.02 mm; $t = -7.05$, $p < 0.001$).

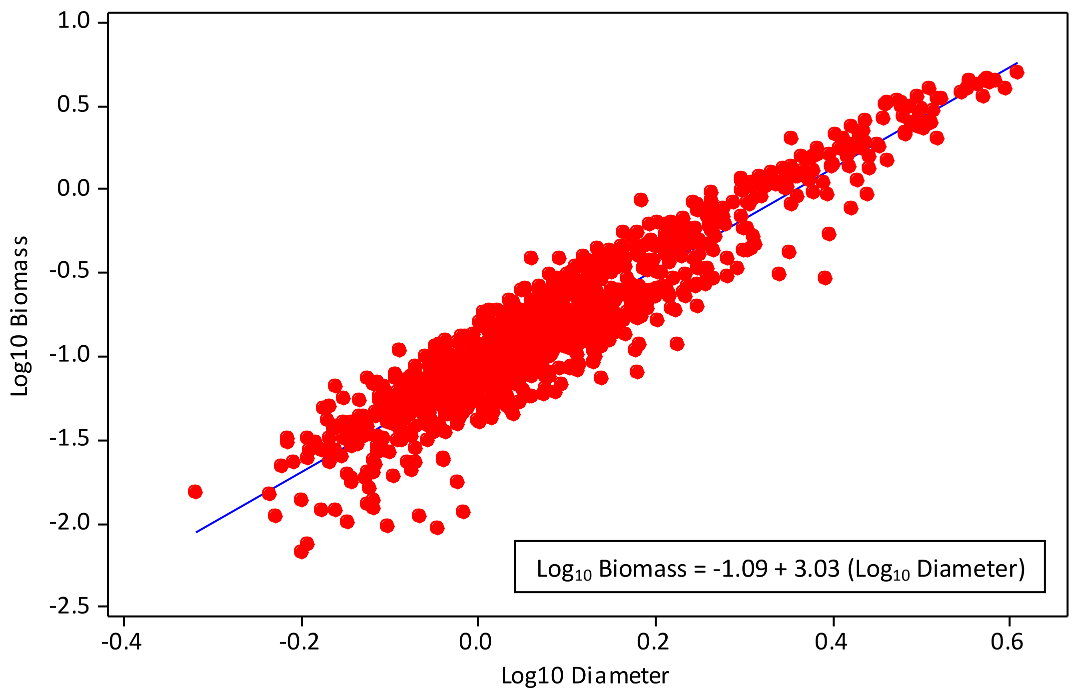


Figure 15: Allometric model for predicting stem biomass (g) from diameter (mm) in individuals of *Taxus canadensis* from Apostle Islands National Lakeshore, Wisconsin.

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APPENDIX A

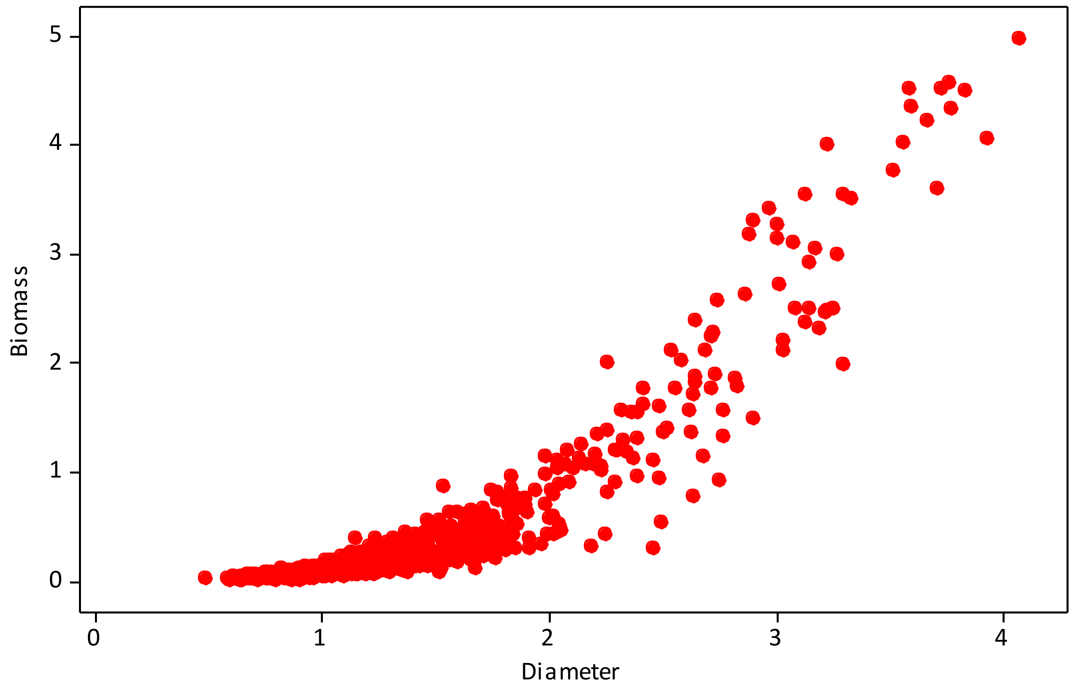

Figure A-1: Plot of diameter (mm) and biomass (g) values from *Taxus canadensis.*

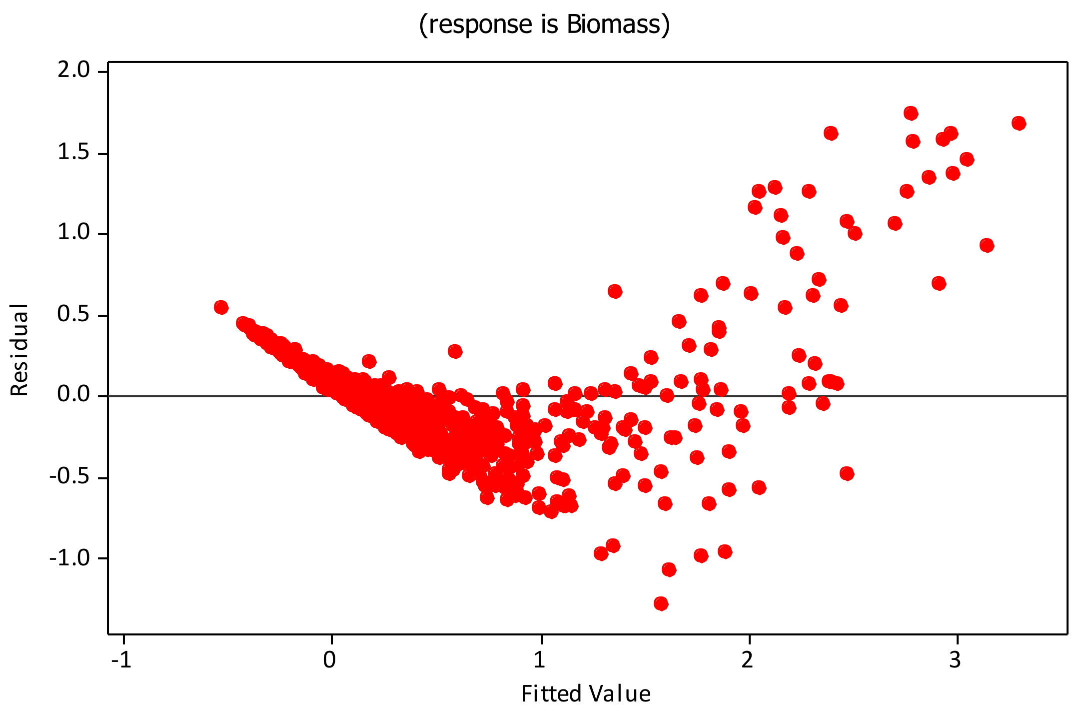

Figure A-2: Residuals vs fitted values of biomass from *Taxus canadensis*.

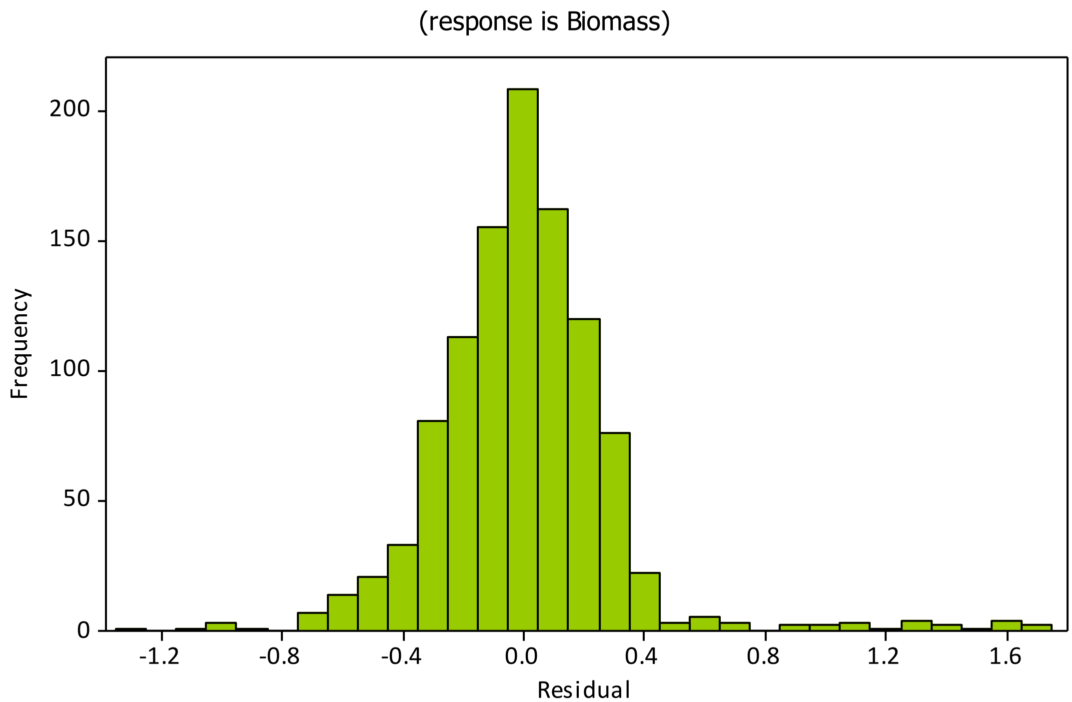

Figure A-3: Residual histogram of biomass values from *Taxus canadensis*.

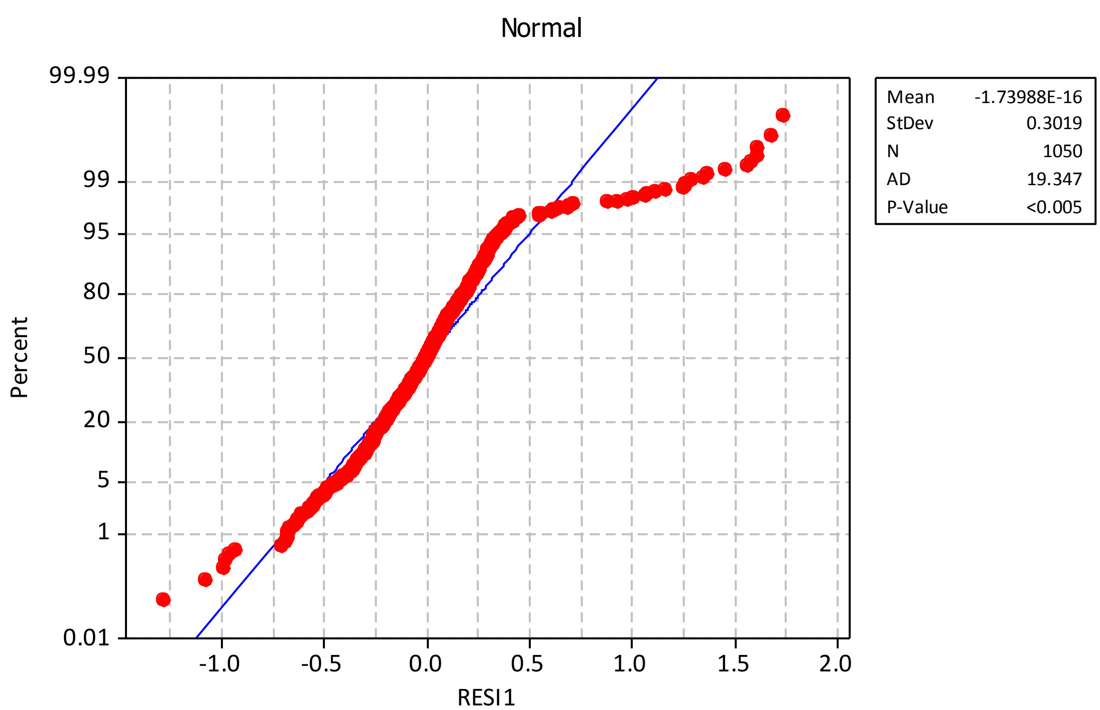

Figure A-4: Anderson-Darling probability plot of residual biomass values from *Taxus canadensis.*

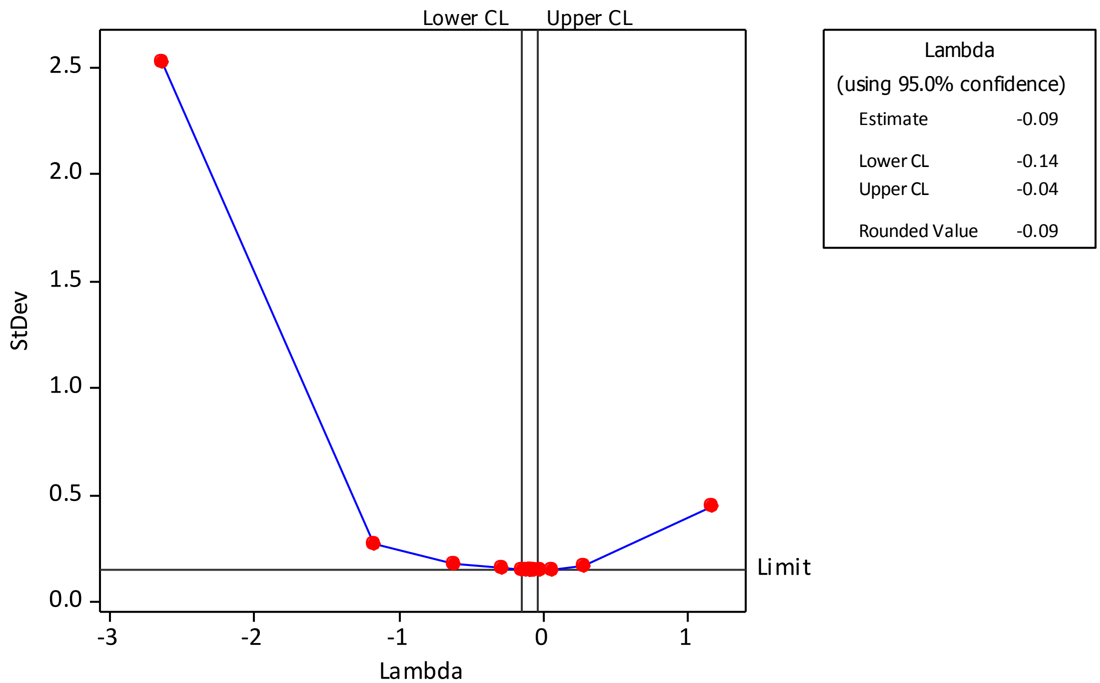

Figure A-5: Box-Cox transformation plot of biomass values from *Taxus canadensis*.

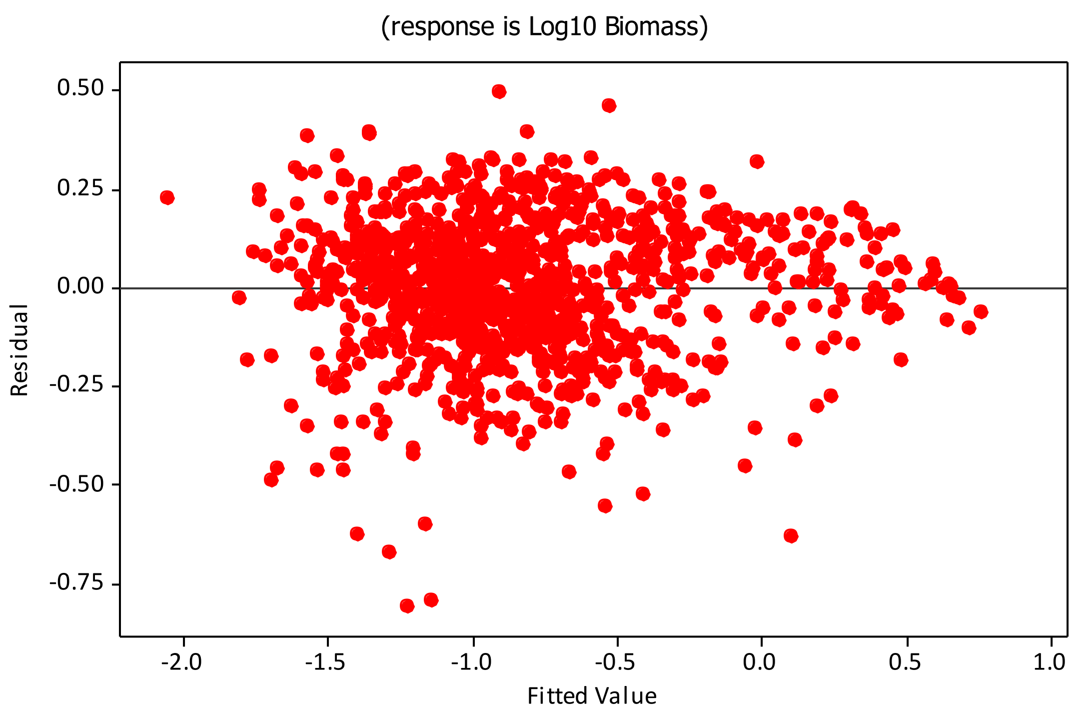

Figure A-6: Residuals vs fitted values of log10 biomass from *Taxus canadensis*.

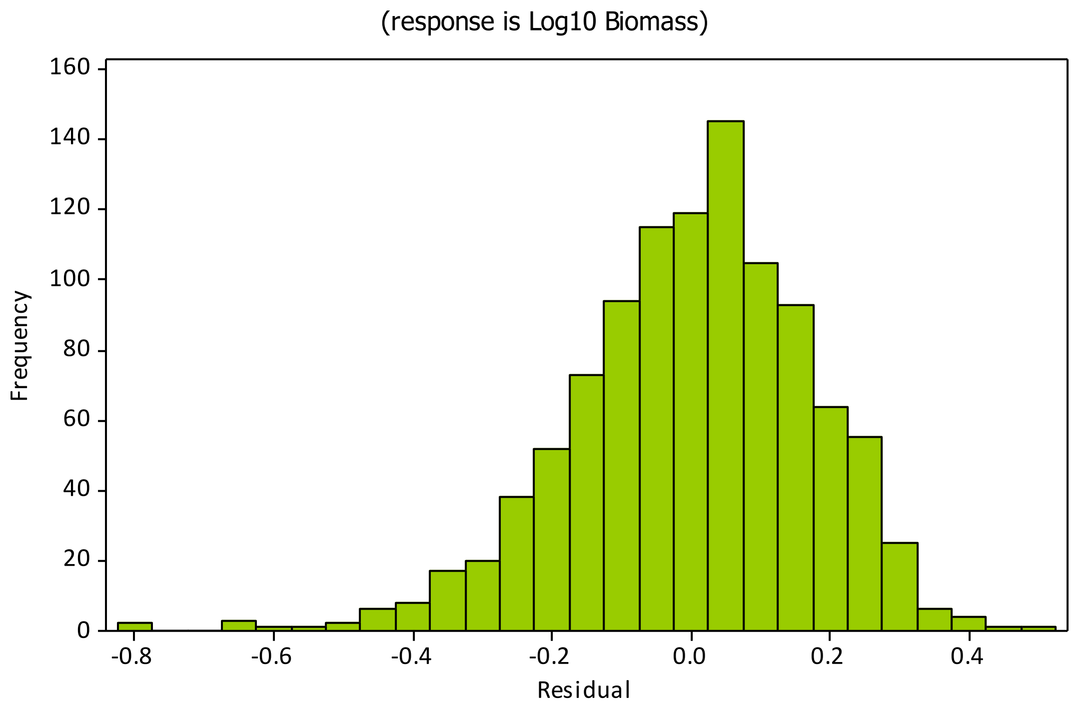

Figure A-7: Residual histogram of log10 biomass values from *Taxus canadensis*

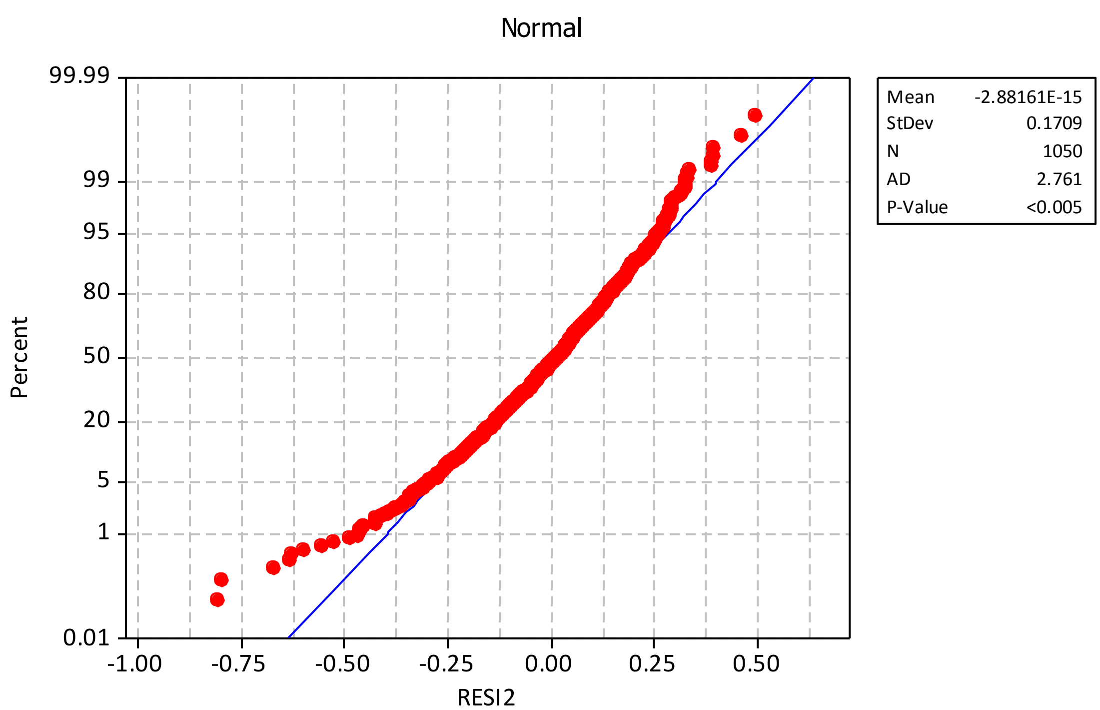

Figure A-8: Anderson-Darling probability plot of residual log10 biomass values from *Taxus canadensis..*

APPENDIX B

Apostle Islands Deer Pellet and Browse Survey					
Date:		Island:	Plot #:		
Browse Intensity Data					
Species	**DBH**	**Height**	**Available**	**Browse**	
			Total # of Stems	Total # of Stems	C/P

Commnts:

-

Browse Intensity Data					
Species	**DBH**	**Height**	**Available**	**Browse**	
			Total # of Stems	Total # of Stems	C/P

Dimensional Data for 10 individual stems per Species from w/in browse plot											
Species	Stem	1	2	3	4	5	6	7	8	9	10
	DPB										
	Length										
Species	Stem	1	2	3	4	5	6	7	8	9	10
	DPB										
	Length										
Species	Stem	1	2	3	4	5	6	7	8	9	10
	DPB										
	Length										
Species	Stem	1	2	3	4	5	6	7	8	9	10
	DPB										
	Length										
Species	Stem	1	2	3	4	5	6	7	8	9	10
	DPB										
	Length										
Species	Stem	1	2	3	4	5	6	7	8	9	10
	DPB										
	Length										
Species	Stem	1	2	3	4	5	6	7	8	9	10
	DPB										
	Length										
Species	Stem	1	2	3	4	5	6	7	8	9	10
	DPB										
	Length										

APPENDIX C

GPS Coordinates for Sampling Sites at Apostle Islands National Lakeshore, WI

Island	Site	Latitude	Longitude	Y-Projection	X-Projection	Altitude
Basswood	2	46.84053794	-90.75817063	5189883.968	670940.043	807
Basswood	3	46.84059058	-90.75635419	5189893.774	671078.3754	911
Basswood	3B	46.8404501	-90.75436324	5189882.504	671230.6272	821
Basswood	4	46.84082989	-90.75207917	5189929.69	671403.5744	846
Basswood	5	46.84080608	-90.75013013	5189931.301	671552.2593	812
Basswood	5B	46.84042144	-90.74873068	5189891.62	671660.1894	822
Basswood	5C	46.84030216	-90.74683327	5189882.516	671805.2433	750
Basswood	5D	46.84040903	-90.74474836	5189898.956	671963.8726	753
Basswood	5E	46.840246	-90.74298179	5189884.711	672099.0907	723
Basswood	5F	46.84018448	-90.74086091	5189882.527	672261.0006	626
Basswood	6	46.84961429	-90.75433315	5190900.876	671203.7907	720
Basswood	7	46.84975569	-90.75239693	5190920.813	671350.9483	715
Basswood	7B	46.85015492	-90.75073128	5190968.812	671476.6575	757
Basswood	8	46.85021477	-90.74912002	5190978.983	671599.2998	730
Basswood	8B	46.85031351	-90.74713293	5190994.301	671750.4688	768
Basswood	9	46.85016649	-90.74468373	5190983.326	671937.6502	784
Basswood	9B	46.8502778	-90.74269446	5191000.054	672088.9447	662
Basswood	10	46.85040311	-90.7405642	5191018.651	672250.942	795
Basswood	10B	46.85033161	-90.73892042	5191014.314	672376.4824	721
Basswood	11	46.85066043	-90.73662571	5191055.894	672550.3634	727
Basswood	11B	46.8505803	-90.7346257	5191051.388	672703.0878	726
Basswood	12	46.85085163	-90.73265713	5191085.871	672852.2879	474
Basswood	13	46.86702141	-90.72212418	5192905.873	673603.097	631
Basswood	14	46.86689459	-90.72394221	5192887.761	673464.9535	712
Basswood	14B	46.86661111	-90.72577768	5192852.206	673325.9846	608
Basswood	15	46.86668823	-90.72814741	5192855.544	673145.1376	749
Basswood	15B	46.8666443	-90.73011079	5192846.332	672995.6484	730
Basswood	16	46.86681504	-90.73217969	5192860.746	672837.4278	820
Basswood	16B	46.86663358	-90.73443141	5192835.625	672666.4053	792
Basswood	17	46.86659326	-90.73642412	5192826.762	672514.6687	764
Basswood	17B	46.86647206	-90.73868095	5192808.336	672343.0619	817
Basswood	18	46.86651371	-90.74054198	5192808.879	672201.0978	877
Basswood	18B	46.86658328	-90.74239539	5192812.544	672059.6253	746
Basswood	19	46.86653517	-90.74415718	5192803.337	671925.5115	635
Basswood	20	46.85784515	-90.74981413	5191825.339	671522.0772	806
Basswood	20B	46.85788706	-90.74795477	5191834.061	671663.67	809

GPS Coordinates for Sampling Sites at Apostle Islands National Lakeshore, WI

Island	Site	Latitude	Longitude	Y-Projection	X-Projection	Altitude
Basswood	21	46.85798077	-90.74580138	5191849.186	671827.5092	801
Basswood	21B	46.85804891	-90.7438442	5191861.045	671976.4737	872
Basswood	22	46.85807783	-90.74192475	5191868.466	672122.6873	812
Basswood	22B	46.85797239	-90.74021224	5191860.506	672253.5571	775
Basswood	23	46.85807993	-90.73822305	5191876.824	672404.8348	832
Basswood	24	46.85810566	-90.73640199	5191883.685	672543.5588	837
Basswood	24B	46.8580184	-90.73446049	5191878.259	672691.8253	749
Basswood	25	46.85831755	-90.73223166	5191916.406	672860.7527	759
Basswood	26	46.85851947	-90.73001616	5191943.725	673028.9747	744
Basswood	27	46.85849701	-90.72774651	5191946.235	673202.0447	721
Basswood	27B	46.8583189	-90.7256372	5191931.101	673363.3946	720
Raspberry	28	46.9709166	-90.80450001	5204271.708	667001.9436	656
Raspberry	29	46.97102926	-90.80249288	5204288.508	667154.2608	694
Raspberry	30	46.97103471	-90.80062732	5204293.095	667296.1437	664
Raspberry	31	46.97097234	-90.79880618	5204290.055	667434.8595	740
Raspberry	32	46.9711689	-90.79648524	5204316.86	667610.7827	758
Raspberry	33	46.97113822	-90.79447282	5204317.758	667763.9487	695
Raspberry	34	46.97104904	-90.79276853	5204311.5	667893.8608	691
Raspberry	35	46.9771234	-90.79548008	5204980.677	667668.6174	671
Raspberry	36	46.97713925	-90.7935825	5204986.502	667812.8867	708
Raspberry	37	46.97724762	-90.79138468	5205003.254	667979.7005	647
Raspberry	38	46.97707755	-90.78977125	5204987.817	668102.9416	642
Raspberry	39	46.97692207	-90.78821238	5204973.887	668221.9881	600
York	40	46.98585617	-90.87135223	5205791.469	661871.841	604
York	41	46.98633595	-90.87321586	5205840.933	661728.6791	609
York	42	46.98673133	-90.8753058	5205880.555	661568.5653	625
York	43	46.98566825	-90.87499375	5205763.068	661595.4989	630
York	44	46.98805709	-90.87507907	5206028.342	661581.8092	634
York	45	46.98943307	-90.87520153	5206180.99	661568.3493	632
York	46	46.99090476	-90.87520128	5206344.526	661563.9316	625
York	47	46.98410151	-90.86456096	5205610.547	662393.579	645
York	48	46.98362575	-90.86291249	5205561.1	662520.3785	645
York	48B	46.98314245	-90.8608901	5205511.593	662675.6383	698
York	49	46.98645741	-90.8582208	5205885.501	662868.5547	630
York	50	46.98524237	-90.85812894	5205750.676	662879.2321	665
York	51	46.98387193	-90.85807823	5205598.497	662887.2527	668
York	52	46.98253761	-90.85783909	5205450.724	662909.4931	661

GPS Coordinates for Sampling Sites at Apostle Islands National Lakeshore, WI

Island	Site	Latitude	Longitude	Y-Projection	X-Projection	Altitude
York	53	46.98117337	-90.85813866	5205298.505	662890.8571	657
York	54	46.97985884	-90.85827193	5205152.157	662884.716	659
York	55	46.97830349	-90.85833027	5204979.204	662885.0046	658
York	56	46.97726456	-90.85834033	5204863.736	662887.3958	721
Sand	65	46.98873008	-90.9303278	5205990.63	657378.7727	607
Sand	66	46.98857811	-90.93383697	5205966.698	657112.3873	645
Sand	67	46.98870401	-90.94611822	5205956.127	656178.1736	621
Sand	68	46.98865556	-90.94968899	5205943.629	655906.7993	636
Sand	69	46.98863897	-90.95363217	5205933.944	655607.0146	652
Sand	69B	46.9884917	-90.9578481	5205909.212	655286.8688	667
Sand	70	46.98856336	-90.961584	5205909.775	655002.5889	693
Sand	70B	46.98841928	-90.96532937	5205886.36	654718.2124	663
Sand	71	46.98165064	-90.93547722	5205193.621	657007.9552	634
Sand	72	46.98163354	-90.93845305	5205185.76	656781.6985	644
Sand	73	46.98176052	-90.9426321	5205191.515	656463.5184	647
Sand	74	46.98185164	-90.94660043	5205193.722	656161.4689	679
Sand	74B	46.9819725	-90.95056423	5205199.257	655859.6785	697
Sand	75	46.98183051	-90.95456827	5205175.52	655555.5919	675
Sand	76	46.98193579	-90.95839284	5205179.631	655264.4358	632
Sand	77	46.98189975	-90.96261875	5205167.259	654943.1683	652
Sand	77B	46.98177821	-90.96653896	5205146.007	654645.3949	675
Sand	78	46.98176363	-90.97042934	5205136.714	654349.5806	675
Sand	78B	46.98169649	-90.97450722	5205121.226	654039.6581	660
Sand	79	46.98193453	-90.97839022	5205140.049	653743.6798	702
Sand	79B	46.98190947	-90.98192872	5205130.326	653474.6558	640
Sand	80	46.9749307	-90.93333028	5204451.2	657190.9265	657
Sand	81	46.97525466	-90.93718621	5204479.469	656896.7051	663
Sand	82	46.97522943	-90.94098598	5204469.062	656607.7784	654
Sand	83	46.97513865	-90.94495255	5204451.053	656306.3561	659
Sand	84	46.97527436	-90.94906026	5204457.946	655993.5391	679
Sand	85	46.97514737	-90.95299071	5204436.016	655694.9682	674
Sand	85B	46.97576168	-90.95692635	5204496.465	655393.8529	663
Sand	85C	46.9766624	-90.96055336	5204589.366	655115.3888	666
Sand	86	46.97510026	-90.96473878	5204407.5	654801.5748	682
Sand	86B	46.97552213	-90.96838986	5204447.171	654522.6665	711
Sand	87	46.9752876	-90.97274333	5204412.532	654192.2288	643
Sand	87B	46.97574181	-90.97640689	5204455.801	653912.2842	670

GPS Coordinates for Sampling Sites at Apostle Islands National Lakeshore, WI

Island	Site	Latitude	Longitude	Y-Projection	X-Projection	Altitude
Sand	87C	46.97594114	-90.98060455	5204469.712	653592.4528	667
Sand	88	46.96757575	-90.93188809	5203636.806	657322.1908	667
Sand	88B	46.96758329	-90.93544437	5203630.509	657051.6488	789
Sand	89	46.96750299	-90.93961529	5203613.234	656734.609	671
Sand	90	46.9675765	-90.94341028	5203613.818	656445.716	675
Sand	90B	46.96745815	-90.94752336	5203592.462	656133.1857	700
Sand	91	46.96753778	-90.95117829	5203594.034	655854.9295	718
Sand	92	46.96743644	-90.95539405	5203574.396	655534.5375	716
Sand	92B	46.96752654	-90.95893297	5203577.389	655265.0764	685
Sand	93	46.96749939	-90.96366271	5203565.011	654905.3712	653
Sand	94	46.96745689	-90.96716266	5203553.374	654639.258	703
Sand	95	46.99561279	-90.93016293	5206755.777	657371.0961	621
Sand	96	46.99553367	-90.9320854	5206743.124	657225.1659	643
Sand	97	46.99552252	-90.93370319	5206738.638	657102.2004	698
Sand	98	46.99577364	-90.93594845	5206762.042	656930.7611	712
Sand	99	46.99560827	-90.93779909	5206739.959	656790.5442	621
Oak	111	46.91943764	-90.74015541	5198690.564	672061.1284	748
Oak	111B	46.9194715	-90.7361808	5198703.056	672363.6301	749
Oak	112	46.91932348	-90.73232445	5198695.093	672657.7122	898
Oak	112B	46.91905861	-90.7284386	5198674.225	672954.418	857
Oak	113	46.91922206	-90.72466222	5198700.725	673241.4107	887
Oak	113B	46.91911108	-90.72074996	5198697.044	673539.6335	769
Oak	114	46.91898979	-90.71638148	5198693.245	673872.6258	784
Oak	114B	46.91897437	-90.71276318	5198699.562	674148.1602	797
Oak	114C	46.91892332	-90.70887121	5198702.541	674444.6467	768
Oak	115	46.91877119	-90.70491789	5198694.44	674746.1334	701
Oak	115B	46.91876541	-90.70097697	5198702.588	675046.2008	727
Oak	115C	46.91867514	-90.69691988	5198701.623	675355.3888	693
Oak	116	46.91859509	-90.69288659	5198701.756	675662.7324	702
Oak	117	46.92896686	-90.75132187	5199725	671180.5885	646
Oak	117B	46.92880525	-90.74843145	5199713.357	671401.1299	746
Oak	118	46.92915612	-90.74456102	5199760.815	671694.6354	1029
Oak	118B	46.92893819	-90.74093744	5199744.541	671971.1678	943
Oak	119	46.92859956	-90.73676158	5199716.082	672290.1306	990
Oak	119B	46.92870517	-90.7329437	5199736.215	672580.4191	1093
Oak	120	46.92847283	-90.72836618	5199720.485	672929.6204	1073
Oak	120B	46.92844441	-90.7250555	5199724.635	673181.731	769

GPS Coordinates for Sampling Sites at Apostle Islands National Lakeshore, WI

Island	Site	Latitude	Longitude	Y-Projection	X-Projection	Altitude
Oak	121	46.9284103	-90.72121382	5199729.339	673474.2815	992
Oak	121B	46.92824836	-90.71729519	5199720.023	673773.1036	1004
Oak	122	46.92813428	-90.71335075	5199716.097	674073.7371	1019
Oak	122B	46.92820008	-90.70963372	5199731.669	674356.4766	886
Oak	123	46.92805231	-90.70543027	5199724.606	674676.9378	864
Oak	124	46.92794695	-90.70166923	5199721.286	674963.5847	804
Oak	125	46.92799087	-90.69785236	5199734.692	675253.9955	778
Oak	126	46.92772868	-90.69385462	5199714.503	675559.1749	715
Oak	127	46.93817471	-90.75571574	5200738.586	670816.8222	710
Oak	128	46.93750969	-90.75256851	5200671.552	671058.4746	724
Oak	128B	46.93774363	-90.74871576	5200705.963	671350.9618	806
Oak	129	46.93768487	-90.74465029	5200708.329	671660.5723	957
Oak	130	46.93766124	-90.74094146	5200713.832	671942.927	792
Oak	130B	46.93746803	-90.73338635	5200708.963	672518.5674	1042
Oak	131	46.93731221	-90.72534962	5200709.369	673130.7474	1113
Oak	131B	46.93745303	-90.72154633	5200733.424	673419.7627	1052
Oak	132	46.9371227	-90.7174661	5200705.753	673731.3789	963
Oak	132B	46.93706302	-90.71368176	5200707.517	674019.6011	976
Oak	133	46.93696713	-90.70966951	5200705.777	674325.2878	814
Oak	133B	46.93680041	-90.70600159	5200695.415	674604.9987	827
Oak	134	46.9369269	-90.70216485	5200718.024	674896.6052	764
Oak	134B	46.9367777	-90.69808329	5200710.561	675207.7434	769
Oak	135	46.94922633	-90.75972606	5201957.906	670476.4961	685
Oak	135B	46.94928886	-90.75572781	5201973.559	670780.5387	746
Oak	136	46.94892283	-90.75160081	5201941.888	671095.7437	844
Oak	136B	46.94903422	-90.7480484	5201962.027	671365.7054	931
Oak	137	46.94879567	-90.74410421	5201944.152	671666.5972	992
Oak	137B	46.94891662	-90.74025457	5201966.031	671959.1451	1029
Oak	138	46.94872761	-90.73639571	5201953.503	672253.388	934
Oak	138B	46.94881671	-90.73250022	5201971.973	672549.5261	888
Oak	139	46.94865092	-90.72855662	5201962.241	672850.1449	876
Oak	139B	46.94854924	-90.72466968	5201959.523	673146.2472	937
Oak	140	46.9485044	-90.7206612	5201963.404	673451.4155	922
Oak	140B	46.94841254	-90.71698548	5201961.339	673731.4151	847
Oak	141	46.94808841	-90.71302151	5201934.117	674034.1032	829
Oak	142	46.94815471	-90.70914019	5201950.11	674329.2373	675
Oak	143	46.95454993	-90.74987465	5202570.939	671209.1399	869

GPS Coordinates for Sampling Sites at Apostle Islands National Lakeshore, WI

Island	Site	Latitude	Longitude	Y-Projection	X-Projection	Altitude
Oak	144	46.95485453	-90.74652985	5202612.1	671462.6593	902
Oak	144B	46.95476585	-90.74261458	5202610.82	671760.8389	924
Oak	145	46.95471757	-90.73869704	5202614.049	672059.0627	910
Oak	145B	46.95454633	-90.7348158	5202603.551	672354.92	884
Oak	146	46.95444575	-90.72951886	5202604.038	672758.267	735
Oak	146B	46.9544444	-90.72524996	5202613.309	673083.0755	769
Oak	147	46.95428398	-90.72109764	5202604.663	673399.5279	865
Oak	148	46.95424525	-90.71736753	5202608.62	673683.4637	765
Oak	149	46.95416587	-90.71344228	5202608.507	673982.3793	729