CAN SHORT-ROTATION HARVESTS INCREASE MANAGEMENT OPTIONS FOR THE ENDANGERED KIRTLAND'S WARBLER?

By

Daphna Gadoth-Goodman

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ABSTRACT

CAN SHORT-ROTATION HARVESTS INCREASE MANAGEMENT OPTIONS FOR THE ENDANGERED KIRTLAND'S WARBLER?

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Since the early 1980's, 1550 ha of high-density jack pine (*Pinus banksiana*) plantations have been established annually in Northern Lower Michigan to serve as habitat for the federally-endangered Kirtland's warbler (*Setophaga kirtlandii*). Because these plantations do not produce merchantable sawlogs by their planned 50-year harvest age, I investigated the potential to implement reduced rotation lengths in these stands to produce alternative wood products, namely biomass and pulpwood. I used space-for-time substitution to assess biomass and volume accrual over time, sampling a total of 37 warbler plantations ranging from 7 to 52 years of age. I also destructively sampled 26 living and 8 dead stems to develop allometric equations specific to jack pine grown in these plantations. Potential maximum biomass was estimated to be ~71 Mg ha^{-1} and potential maximum volume was estimated to be ~71 m^3 ha^{-1}. The predicted optimal rotation age for biomass was 20 years and the predicted optimal rotation age for volume was 28 years. I calculated and compared the total land area required for management under these rotation scenarios to continue establishing 1550 ha of habitat annually. Management on the current 50-year cycle requires ~77,500 ha. Management for volume would reduce this to ~43,400 ha and management for biomass would require ~31,000 ha. My results suggest that rotation lengths in these plantations could be significantly reduced, allowing for reductions in the total land area dedicated to warbler habitat, allowing for management diversification at the landscape level.

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1. Introduction

Anthropogenic alterations of land use have been the dominant driver of biodiversity loss in terrestrial ecosystems over the last 50 years, and are projected to continue to be major drivers of global biodiversity change over the coming decades (MEA 2005). Rapidly-increasing demands for food, water, timber, fiber and fuel have led to mass land use conversion, largely from natural systems to agriculture or other forms of production management. In forest systems, demands for wood-based commodities and biofuels are addressed in the form of maximization of harvest yields via the implementation of production-based management strategies (Roberge et al. 2016). In the face of global climate change, priorities for forest management have expanded beyond traditional provisioning services to include regulating services related to climate change mitigation and conservation of biological diversity.

Simultaneous management for multiple ecosystem services has proven to be a major challenge in forest management, as strong trade-offs exist between strategies for optimization of production, climate change mitigation, and biodiversity (Triviño et al. 2017). A primary silvicultural strategy used to meet these objectives involves the extension or reduction of rotation length, defined as the time elapsed between successive final harvests (Felton et al. 2017). Extending rotation lengths is widely considered to be compatible with promotion of biodiversity conservation (Lindenmayer et al. 2006). Long rotations are associated with increased habitat availability, as they provide structural complexity and microhabitats in the form of large diameter trees, snags, and coarse woody debris in addition to compositional heterogeneity (Lindenmayer et al. 2006; Roberge et al. 2016). Extending rotations can also prove to be a beneficial strategy for climate change mitigation by increasing carbon sequestration (Sohngen and Brown 2008).

Alternatively, reducing rotation lengths, a common strategy of commodity-oriented forestry, is typically associated with negative impacts on ecosystem biodiversity (Felton et al. 2015). Strategies that prioritize maximizing economic returns often call for harvesting well before structural and compositional complexity can develop (Franklin et al. 2007). Furthermore, large-scale implementation of commercial forest management can cause a shift to younger landscape-level stand age distributions which favor pioneer shade-intolerant species, and is widely viewed to be inconsistent with aims to emulate historically heterogeneous natural disturbance regimes (Roberge et al. 2016).

However, there is a gap in the current literature regarding the potential benefits of reducing rotations in landscapes where biodiversity is limited by a lack of young stands dominated by shade-intolerant species. Jack pine (*Pinus banksiana*) forests in the northeastern region of Michigan's Lower Peninsula were historically dominated by frequent, stand-replacing wildfires on a return interval of *ca.* 60 years (Cleland et al. 2004). Fire suppression efforts in the 20th century led to widespread habitat loss for a diversity of early-successional species adapted to these frequent disturbances, driving one species, the Kirtland's warbler (*Setophaga kirtlandii*) to near extinction (MDNR 2014). These birds, which depend on continuous, even-aged jack pine stands of at least 32 ha for breeding habitat, cease to nest in these stands approximately 23 years after establishment (Meyer 2010).

In an effort to recover this species, public land agencies have been planting new jack pine stands on an annual basis since 1981 to provide a continuous supply of early-successional habitat on the landscape (MDNR 2014). This strategy has had enormous benefits for the warbler, restoring their population to a size more than double the original recovery goal. These habitat plantations, which currently encompass approximately 77,000 ha, were intended to be managed on a 50-year rotation, a typical rotation length for production of jack pine sawtimber (Byelich et al. 1985). However, it is becoming apparent that these stands will not reach merchantable sawlog size by their planned 50-year rotation, and management agencies are becoming concerned over the long-term economic sustainability of continuing management into the future. Furthermore, implementation of this plan has drastically altered the distribution of mature forest stands on the landscape, resulting in a shift to a younger, more homogenized stand age distribution, which may be detrimental to species dependent on later-successional habitat (Tucker et al. 2016). This study aims to analyze the potential economic and ecological benefits of reducing rotation lengths in a portion of habitat plantations, and reducing the total area under Kirtland's warbler management, to simultaneously manage for increased wood production, biodiversity, and climate change mitigation services at the landscape level.

CHAPTER 2: Can Short-Rotation Harvests Increase Management Options for the Endangered Kirtland's Warbler?

1. Introduction

In the face of global climate change, there is much interest in shifting from traditional forest silvicultural practices to alternative management strategies that utilize forest resources to enhance climate change mitigation services (Chum et al. 2011). Production forests provide climate benefits in the form of carbon storage and sequestration (Zanchi et al. 2014). Implementation of production management for bioenergy can broaden these benefits to include reductions in greenhouse gas emissions via co-generation and provisioning of a sustainable, renewable energy source (Vass 2017). The implementation of climate change adaptation and mitigation strategies (CCAMS) in production forests can directly and indirectly impact the provisioning of other ecosystem services and may involve alterations in rotation length, species composition, and harvest removals (Felton et al. 2015; Immerzeel et al. 2014). Of specific concern is the potential impacts these CCAMS may have on other ecosystem services, such as biodiversity, at both the stand and landscape levels. The extent and nature of these impacts vary system to system and are highly dependent on the climate, natural disturbance dynamics, tree species composition, and historical and current land-use of the ecosystem at hand (Felton et al. 2015).

Several studies have identified a direct link between altering rotation lengths and impacts on biodiversity (Felton et al. 2017; Lindenmayer et al. 2006). Extending rotation lengths to increase carbon storage and sequestration is one of the few CCAMS commonly viewed to be compatible with biodiversity goals (Felton et al. 2015). Shifting to longer rotations can increase habitat availability through the provisioning of key habitat structural features such as coarse woody debris and old, large diameter trees (Felton et al. 2017; Chum et al. 2011; Lindenmayer et al. 2006). Alternatively, reducing rotations to produce wood-based bioenergy and mitigate climate associated risks is a strategy commonly considered to be incompatible with biodiversity goals (Felton et al. 2015; Lindenmayer et al. 2006). Forests under short-rotation management are characterized by simplified structural and compositional features, and therefore, widespread implementation of this strategy can lead to increased landscape homogeneity (Spaulding and Rothstein 2009; Berch et al. 2011).

However, there is a lack of scientific literature that directly addresses the potential impacts of reducing rotations on biodiversity in landscapes where species of conservational concern are disturbance-adapted and whose populations are limited by a lack of available early-successional habitat. The key to minimizing negative impacts associated with shortened rotation lengths lies in adherence to the principles of ecological forestry, which emphasize the implementation of management strategies that emulate natural disturbance regimes and stand development processes (Franklin et al. 2007). Thus, reducing rotation lengths in forest ecosystems naturally adapted to frequent, stand-replacing disturbances could, in some cases, prove to be both ecologically and economically beneficial (Tarr et al. 2017).

In the Lake States region, jack pine (*Pinus banksiana*) forest systems are adapted to such a disturbance regime. This fast-growing species occurs in even-aged stands historically perpetuated by frequent stand-replacing fires on an average return interval of *ca.* 60 years (Cleland et al. 2004). The stands provide critical habitat to a variety of species of conservation concern, including the federally endangered Kirtland's warbler (*Setophaga kirtlandii*), hereafter referred to as KW (MDNR 2014). This migratory bird is endemic to the region during the summer months and occupies young jack pine stands between the ages of 5 and 23 years that are a minimum 32 ha in size (Meyer 2010). Fire suppression efforts during the early- to mid- 1900's greatly reduced the amount of early-successional habitat available to KW, and drove its population to near-extinction by the mid-1970's, with record low population levels of 167 singling males recorded in 1974 and 1987 (MDNR 2014).

Efforts to create habitat for KW began as early as 1957 on state lands and 1962 on federal lands (Mayfield 1963; Radtke and Byelich 1963). In 1981, public agencies including the Michigan Department of Natural Resources (MDNR), the United States Forest Service (USFS), and the United States Fish and Wildlife Service (USFWS), established an expanded habitat management program to ensure sufficient breeding habitat for KW population recovery (Kepler et al. 1996). Under this plan, approximately 77,000 ha have been designated as KW management areas, with agencies establishing more than 1500 ha annually to provide a continuous supply of early-successional habitat (MDNR 2014). To mimic the historical structure of jack pine stands maintained by wildfire, which are characterized by a mosaic of dense thickets and scattered openings, managed habitat plantations are planted at high stocking densities (~1.5 m x 1.8 m spacing) in an 'opposing wave' pattern that incorporates unplanted gaps to provide structural diversity and foraging opportunities for the bird. These gaps account for approximately 1/5 of total habitat land area. The conservation efforts of this program have been overwhelmingly successful, with the KW population reaching an all-time high in 2015, representing more than a 10-fold increase in population size since its record low levels (MDNR 2014). The current population size is more than double the original goal set out by the recovery plan of 1,000 mating pairs.

Under the guidelines of the KW recovery program, these stands are managed on a 45- to 50-year commercial harvest rotation based on the notion that they would provide habitat during earlier stages of stand development, and be of merchantable size for commercial cutting at harvest age (Byelich et al. 1985). However, as those stands established at the onset of recovery efforts begin to reach their 50-year rotation mark, land managers are becoming increasingly concerned over the marketability of stems produced in these habitat plantations. It appears that the extremely dense stocking of these stands is causing growth suppression of individual stems, and in the absence of pre-commercial thinnings they are highly unlikely to produce marketable sawlogs by age 50. Therefore, management for nontraditional wood products, such as pulpwood or biomass, on reduced rotations could contribute to increased financial returns and climate change mitigation benefits, while providing critical endangered species habitat and supporting biodiversity conservation.

This system represents a unique opportunity to simultaneously manage for forest products and biodiversity, while imposing minimal negative impacts on conservation efforts that typically coincide with maximizing production yields. For one, implementation of short-rotation production management in this system would not require any land use conversion, a primary driver of global declines in biodiversity (Chum et al. 2011), and would continue to provide breeding habitat for the endangered KW. It is commonly assumed that biomass plantations are established on surplus agricultural land with favorable production conditions (Chum et al. 2011). However, jack pine stands of Northern Lower Michigan occur on acidic, sandy outwash soils of low fertility (Werlein 1998) and thus, KW management for biomass would not conflict with alternative land use interests, such as food production. Additionally, at the stand level, the harvesting methods and planting structure of these habitat plantations largely adhere to the principles of ecological forestry in that they are designed to emulate the disturbance patterns and growth structure of wildfire-originated stands in the region (Franklin et al. 2007; MDNR 2014).

The implementation of short-rotation management requires the ability to quantify the amount of aboveground biomass and pulpwood that is produced in these stands over time, such that optimal rotation lengths for maximum yields can be identified.

1.1 Objectives

My overall objective was to characterize growth of jack pine in KW plantations in the northeastern region of the Lower Peninsula of Michigan, USA to better predict rates of production over time and to provide agencies with vital information that can be integrated into management decisions, as adaptive management is a primary goal of the KW Breeding Range Conservation Plan (MDNR 2014). My specific objectives were:

1) To estimate harvestable biomass and pulpwood volumes at different stages of stand development following whole-tree harvesting.

2) To determine optimal rotation lengths for biomass and pulpwood production yields and compare them to the current 50-year rotation.

3) To assess the potential impacts of alternate rotation lengths in KW plantations on biomass, volume, and KW habitat provisioning over the coming decades.

2. Methods

2.1 Study area description

All study sites were located within the KW management areas of northeastern Lower Michigan, USA. The historical disturbance regime of this region was dominated by stand-replacing wildfires on a return interval of *ca.* 60 years, a result of the landscape's exceedingly dry conditions, relatively level topography, and flammable vegetation (Cleland et al. 2004). KW plantations in the area consist of even-aged, monoculture jack pine plantings interspersed with a minimal component of volunteer hardwood species, primarily *Quercus ellipsoidalis* and *Prunus serotina.*

Within this area, I designated three geographic regions of study to analyze whether variations in production could be attributed to variations in soils and climate. The regions I selected represent three distinct subsections defined in the Ecosystem Classification of the State of Michigan by Albert (1995), and were labeled accordingly. The Highplains region is characterized by excessively drained sandy soils and a predominantly flat topography, with an extreme frost danger persisting throughout its short growing season (80-120 days). The Arenac region has a growing season ranging from 120-140 days and a flat to gently sloping topography. The third region, Presque Isle, is characterized by drumlins separated by areas of outwash sands and gravels. The growing season for this region ranges from 100-130 days (Albert 1995).

In 2015, I established a single chronosequence within each of the three regions to determine whether they were characterized by differences in productivity. Because new KW plantations are established annually, I was able to sample from several plantations (hereafter referred to as 'stands') across a spectrum of ages within each region to assess changes in productivity over time. The lack of variation in climate, topography, soil characteristics, species composition, and planting density among stands within a given region provided for an ideal scenario with which to compare differences in growth characteristics across various stages of stand development.

The number of stands I selected for each chronosequence was dependent on the overall prevalence of KW plantations existing within the respective region. I selected a total of nine stands from the Highplains region, eight stands from Presque Isle, and seven stands from Arenac. Stands selected from Highplains were aged 8, 11, 15, 18, 22, 28, 35, 41, and 52 years. Stands selected from Presque Isle were aged 7, 10, 13, 16, 20, 23, 30, and 32 years, while those selected from Arenac were aged 10, 13, 19, 22, 28, 32, and 35 years. These initial chronosequences were unreplicated, with the primary intent being to understand the dynamics of stand development over time. In 2016, I sampled an additional 13 stands from the Highplains region to better understand variability in production within two age classes, 17-24 and 31-34 years, and across the two major soil series supporting jack pine forests in this region, Graycalm and Grayling sands (Werlein 1998).

2.2 Allometric equation development

To estimate biomass as a function of stand age, I first developed my own local allometric equations predicting biomass of individual stems as a function of diameter at breast height (DBH). Because the geography, climate, and silvicultural practices of the KW management system are distinct from traditional jack pine systems, I opted to develop my own allometric equations, as opposed to adopting pre-existing equations from the literature. For one, these studies were largely conducted in areas geographically distinct from Lower Michigan, such as

Canada and Minnesota. Since the Lower Peninsula of Michigan marks the southern limit of jack pine's natural growth range (Rudolph 1985), I hypothesized that the extreme climate and suboptimal growth conditions of this region would negatively impact the species' production rates. This, coupled with the fact that KW plantations are planted at a higher density than is practiced in traditional plantations managed for timber, 1.5 x 1.8 m vs. 1.8 x 2.4 m (MDNR 2014; Benzie 1977), could contribute to suppressed growth of individual stems. Therefore, it was imperative that I develop my own allometric equations specific to jack pine grown in this system to achieve reliable growth estimates.

To develop an initial equation predicting biomass from stem diameter, in 2015 I destructively sampled a total of 26 living stems from 14 stands within two of the selected regions, Highplains and Presque Isle (7 stands and 13 stems each). The 13 trees sampled from the Highplains region ranged in DBH from 0.7 to 22.9 cm (0.7, 2.5, 2.7, 5.0, 6.5, 7.6, 8.5, 9.5, 10.7, 12.2, 12.8, 17.7, 22.9), whereas the 13 stems harvested from Presque Isle ranged in DBH from 2.0 to 21.5 cm (2.0, 3.3, 4.5, 5.0, 5.8, 7.6, 8.2, 10.1, 11.4, 12.3, 16.5, 17.5, 21.5). Initially, I did not collect destructive samples from the Arenac region because stands in this region fall under USFS jurisdiction, and attaining permission to harvest there was more difficult. Once I observed no significant differences between the Highplains and Presque Isle regions, I decided not to harvest from the Arenac region altogether (see Section 3.1 for details). Within each stand selected for destructive sampling, I harvested a large stem and an average-sized stem. In 2016, I destructively sampled 8 dead stems from 3 stands within the Highplains region, aged 20, 28, and 41 years, to develop an allometric equation specific to standing dead trees, predicting biomass from diameter. The DBH's for harvested dead stems ranged from 2.4 to 18.4 cm (2.4, 4.3, 5.9, 7.2, 8.1, 11.3, 13.2, 18.4).

Each tree was felled and harvested stems were cut into 1.22 m vertical sections, aside from the lowest section, which measured the length between the height of the stump and breast height (1.37 m from the ground). I then separated the branches from each vertical bole section and determined the fresh mass of bole and branches from each section using a portable field scale. I then collected a subsample of representative branches and a 3-6 cm thick stem disc from the bole of each vertical section and recorded their fresh weights in the field. All bole and branch subsamples were returned to the lab and dried in a forced-air oven at 65°C before recording their dry weights. I determined the dry mass proportions of each subsample and applied them to the total branch and bole fresh weights of each respective section to achieve dry mass estimates. I summed the dry mass estimates of the boles and branches of each section to obtain an estimate of total aboveground biomass of each individual stem.

Log-transformations were performed on the recorded dry weight and DBH data of the destructively sampled stems and I ran separate linear regressions on the transformed live and dead stem data to determine the parameters of each respective allometric equation. Additionally, ANCOVA was performed on live stem data to test for statistical differences in the biomass-diameter relationship across the two regions sampled (Highplains and Presque Isle). The alpha level of significance set for all statistical analyses was $P < 0.05$. Log-biomass estimates for live and dead stems were obtained using the following common linear function (Picard et al. 2012):

$$\ln B = a + (b * \ln D) \qquad \textbf{(1)}$$

where $\ln(B)$ is the natural log of biomass (kg), a is the y-intercept of the regression line, b is the slope and $\ln(D)$ is the natural log of DBH (cm). I later compared biomass estimates produced by my live stem model to those produced by six other allometric equations for jack pine derived from studies conducted throughout the northeastern USA and Canada (reported in Ter-Mikaelian and Korzukhin 1997).

2.3 Stand inventory

Within each stand, I established between three and five 6 x 12 m (0.0072 ha) plots for inventory sampling. Each plot was oriented with the long axis running parallel to the planting rows, and each plot contained three rows. For each standing tree within the plot, I recorded species, DBH, and status (live or dead).

I estimated the individual log-biomass of each living and dead stem recorded in the inventory data with their respective allometric equation. I then back-transformed these estimates of log-biomass to reflect actual estimates of biomass in kilograms for each tree. Individual stem biomass estimates were then summed for each plot and utilized to estimate total standing biomass in Mg ha^{-1} for the plot using the following equation:

$$B = \Sigma(b_1 : b_n)/A/1000 \qquad \textbf{(2)}$$

where B is the biomass estimate for the plot (Mg ha^{-1}), b is the biomass estimate for an individual stem (kg), n is the number of individual stems within a given plot and A is the plot area (ha). Dividing by 1000 converts mass units from kg to Mg. Plot-level estimates were then averaged for each stand to produce mean stand-level biomass estimates in Mg ha^{-1}. It should be noted that these estimates of biomass per unit area only apply to planted zones within KW plantations, and do not account for the unplanted foraging gaps that comprise approximately 20% of the total habitat land area (MDNR 2014).

2.4 Volume estimation

To estimate volume production over time, I first calculated the individual volumes of live stems from inventory data using equations and procedures outlined by Hahn (1984). I excluded all dead stems from volume estimates, as they are not considered a source of merchantable timber and thus, their contribution to stand-level volume is of little relevance to land manager decision-making processes. Additionally, volume was estimated only for stems that met the 1-stick minimum size requirement for pulpwood production (2.44 m pulp stick below a 10.16 cm top). Sawlog volumes in these stands ranged from negligible to nonexistent and therefore, for the purposes of this study, I only reported estimates of pulpwood volume production.

I applied input parameters of field-measured DBH and stand basal area from inventory data to Hahn's (1984) equations to estimate the merchantable pulpwood volume of each stem. I assumed a species-specific site index of 50 for all stands in the study based on available stand inventory data from the USFS and MDNR. All other equation parameters were derived from Hahn (1984). I then summed the volumes of each stem within a given plot to estimate plot-level volume in cords ac^{-1}. I converted these estimates to metric units and averaged the plot-level estimates within each stand to achieve mean stand-level volume estimates in m^3 ha^{-1}. These volume estimates per unit area only apply to planted areas of KW habitat, and do not account for the approximate 1/5 total land area left unplanted as foraging gaps.

2.5 Production over time

For the purposes of this study, stand age refers to the number of years since plantation establishment, which I acquired from MDNR and USFS year of origin data. To estimate biomass as a function of stand age, a nonlinear relationship was described using a modification of the Richards logistic function (Richards 1959):

$$B_t = a\,(1\text{-e}^{(-b*t)})^c \qquad \textbf{(3)}$$

where B_t represents aboveground biomass (Mg ha^{-1}) for planted areas at time t, a represents the potential maximum biomass (Mg ha^{-1}), e is the base of a natural logarithm, t is stand age in years, b is a parameter controlling the rate of biomass accumulation, and c is a parameter controlling the inflection point of the curve.

Similarly, I described a volume-age relationship using the same modified version of the Richards logistic function (Richards 1959):

$$V_t = a\,(1\text{-e}^{(-b*t)})^c \qquad \textbf{(4)}$$

where V_t represents aboveground volume (m^3 ha^{-1}) for planted areas at time t, a represents the potential maximum volume (m^3 ha^{-1}), e is the base of a natural logarithm, t is stand age in years, b is a parameter controlling the rate of volume accumulation, and c is a parameter controlling the inflection point of the curve.

Differences in biomass and volume production across regions were estimated by analyzing differences of least squares means. I obtained parameters for the functional forms of each growth curve from iterations produced by the nonlinear regression procedure for Chapman-Richards equations in SAS, using code outlined by Sit and Poulin-Costello (1994). These analyses were performed on stand-level biomass and volume data.

2.6 Covariate analyses

To better understand variations in estimated biomass and volume across stands of equal and similar ages, I tested three covariates for statistical significance in the modified Richards models. Covariates I tested included stand density, natural soil drainage index (DI) (Schaetzl et al. 2009), and soil productivity index (PI) (Schaetzl et al. 2012). The Natural Soil Drainage Index (DI) is a general reflection of the amount of water that a soil supplies to plants under natural conditions over long timescales, and is primarily derived from a soil's taxonomic classification. The DI ranges from 0 for the driest soils (bedrock in a desert) to 99 (open water) (Schaetzl et al. 2009). The soil Productivity Index (PI) ranks soils from 0 (least productive) to 19 (most productive) using interpretations of features or properties of a soil's family-level taxonomic classification (Schaetzl et al. 2012).

I calculated stand-level density estimates from stand inventory data as the mean plot-level density value for all plots within the stand. Stand densities ranged from ~1,917 to ~4,861 trees ha^{-1}. I obtained the DI and PI of each plot from MDNR and USFS GIS data layers. DI and PI values were generally consistent across plots within a given stand. For stands in which index values varied across plots, the mode index value was selected for analyses. DI values ranged from 14 to 35 and PI values ranged from 4 to 9. I regressed each covariate against the residuals of the biomass and volume curves to test for statistical significance and whether there was a need to include any in the final growth models.

2.7 MAI and optimal rotation ages

To identify an optimal rotation length for biomass production, I analyzed Mean Annual Increment (MAI) values for biomass estimates produced by the growth model. Cooper (1984) states that maximum sustained yield is attained when a forest is harvested at the age it reaches culmination of MAI. For an S-shaped growth curve, this age can be determined mathematically, and is defined as the age at which MAI equals the derivative of the growth function (Cooper, 1984). I first calculated MAI values for biomass estimates at each year from 0 to 60 years. I then determined the derivative of the growth function for biomass, and calculated estimates for this derivative function at each year from 0 to 60 years. Finally, I plotted the MAI curve against the derivative growth function curve and identified the age at which their response values were equal. This age was then rounded to the nearest whole year, and reported that as the optimal rotation length for biomass production. The same procedure was applied to my volume curve data to identify an optimal rotation age for pulpwood production in KW stands.

2.8 Regional impact assessment

Following determination of the optimal rotation ages for biomass and volume production in KW stands, I performed a regional impact assessment to compare 3 rotation lengths: the estimated optimal rotation age for biomass, the estimated optimal rotation age for pulpwood volume, and the current business-as-usual (BAU) rotation age of 50 years. I assessed the potential ecosystem service outputs of each rotation length for a 1550 ha area over the course of 100 years. I selected a land area of 1550 ha for this analysis based on the reported average total land area that is harvested and planted into KW breeding habitat annually (MDNR 2014). For each rotation length, I calculated the number of full rotations that would occur over a 100-year period (assuming establishment at year 0), the potential biomass output per rotation (Gg 1550 ha^{-1}), the cumulative potential biomass output over a 100-year period (Gg 1550 ha^{-1} 100 yrs^{-1}), the potential volume output per rotation (m^3 1550 ha^{-1}), and the cumulative potential volume output over a 100-year period (m^3 1550 ha^{-1} 100 yrs^{-1}). For this analysis, all potential biomass and volume yield outputs were calculated to account for the unplanted foraging gaps that are included in KW plantations, assuming these make up 1/5 of the total land area (MDNR 2014).

Additionally, I calculated the cumulative number of years that the land would provide suitable breeding habitat for KW over a 100-year period. KW plantations only provide suitable breeding habitat between the ages of 5 and 23 years (Meyer 2010), so I calculated this figure based on the total number of years plantations under each rotation scenario would spend within this age range over a 100-year period, assuming establishment at year 0. Finally, I calculated the total land area that would need to be designated as KW habitat for each rotation scenario to continue to meet the annual habitat development objective of 1550 ha, as outlined in the KW Breeding Range Conservation Plan (MDNR 2014) by multiplying the rotation length (years) by 1550 ha.

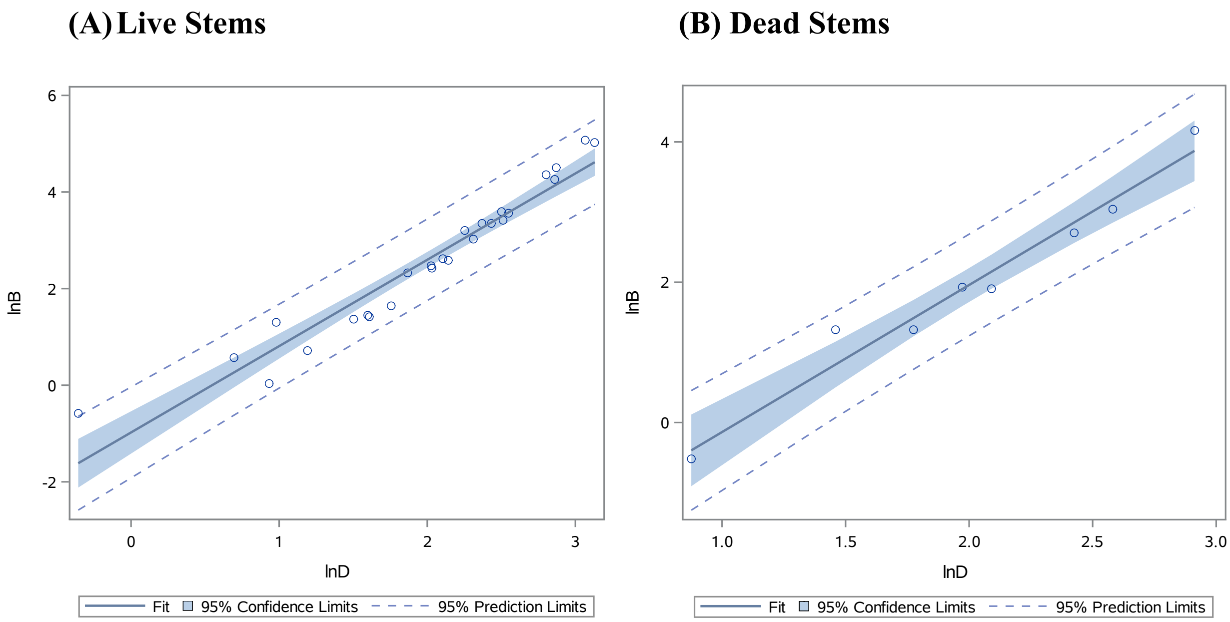
3. Results

3.1 Biomass allometrics

To most accurately estimate tree biomass from stand inventory, I first determined whether it was necessary to utilize separate allometric equations for stems of each region. ANCOVA of the log-transformed biomass-to-diameter relationships of live stems in the Highplains and Presque Isle regions showed an insignificant difference between the two regions ($P = 0.097$), suggesting the use of one model with a common slope parameter. Although the effect of region was close to statistically significant, parameter differences between the regions were quite small. For example, applying separate, region-specific allometric equations to inventory data resulted in a less than 5% difference from combined equation estimates in stands older than 20 years (Table 1). Therefore, I proceeded with a single generalized model to predict biomass of live stems for all regions in the study. The final combined allometric biomass equation was: $\ln B$ (kg) = -0.978 + (1.787 x $\ln D$ (cm)); adjusted $R^2 = 0.929$; $P < 0.001$ (Figure 1A). A comparison of estimates produced by this equation to six other pre-existing allometric equations for jack pine derived from areas throughout the northeastern USA and Canada (reported in Ter-Mikaelian and Korzukhin 1997) resulted in significant differences in stand-level biomass estimates. For example, applying these equations to inventory data from a 20-year old stand resulted in overestimations as high as 25%, or approximately 13 Mg ha^{-1}. Application of these equations to inventory data from a 52-year old stand resulted in overestimations as high as 40%, or approximately 40 Mg ha^{-1}.

Stand Age	Highplains Eq. Estimate (Mg ha^{-1})	Presque Isle Eq. Estimate (Mg ha^{-1})	Combined Eq. Estimate (Mg ha^{-1})	% diff. Highplains Eq.	% diff. Presque Isle Eq.
23	63.51	58.10	60.59	4.60	4.28
32	63.79	60.55	61.62	3.40	1.77
41	66.07	65.70	64.81	1.91	1.36

Table 1. Comparison of plot-level biomass estimate outputs from the Highplains-specific equation, Presque Isle-specific equation, and the combined allometric equation that does not account for effect of region. Differences between region-specific equation outputs and the combined equation outputs are expressed as percentages.


(A) Live Stems

(B) Dead Stems

Figure 1. Fit plots of ln*Biomass* (kg) against ln*DBH* (cm) produced by linear regression analyses of (A) live stem data and (B) standing dead stem data. Log-transformed biomass and diameter data show strong positive linear relationships between the two variables. Solid lines represent the linear regression lines described in the text. Shaded areas around these lines represent the 95% confidence limits, and dashed lines represent 95% prediction limits.

To further strengthen the accuracy of my plot-, stand-, and landscape-level biomass estimates, I developed a separate allometric equation to estimate biomass of dead stems in KW plantations. Dead stems are typically harvested in short-rotation bioenergy management systems, and I anticipated that these stems would contain lower levels of biomass than their live-stem counterparts of equal diameter due to mortality-induced damage and decay. The linear regression I performed on log-transformed diameter data confirmed this prediction, and resulted in the following local allometric equation estimating log-biomass of dead stems as a function of log-diameter: $\ln B$ (kg) = -2.232 + (2.096 x $\ln D$ (cm)); adjusted $R^2 = 0.960$; $P < 0.001$ (Figure 1B).

3.2 Production over time

Analysis of differences of least squares means showed no significant effect of region on biomass and volume production in relation to stand age. P-values for regional contrasts of biomass production ranged from 0.164 (Arenac vs Presque Isle) to 0.455 (Highplains vs Presque Isle). P-values for regional contrasts of volume production ranged from 0.742 (Highplains vs Presque Isle) to 0.972 (Highplains vs Arenac). Therefore, I proceeded with a single growth model for biomass and a single growth model for volume for all regions in the study.

Stand-level biomass accumulation followed a classic sigmoidal pattern across the chronosequence. This pattern was characterized by a period of rapid accumulation between *ca.* 10 and 30 years, followed by a decline in the rate of production approaching an asymptote of 71 Mg ha^{-1} (Figure 2). The pattern of biomass accrual over time conformed well to the modified Richards function for logistic growth (Richards 1959): B_t (Mg ha^{-1}) = $70.856(1-e^{(-0.118*t)})^{4.201}$; $P < 0.001$. These estimates represent biomass production per hectare of planted area and do not account for unplanted areas within KW stands designated as foraging gaps.

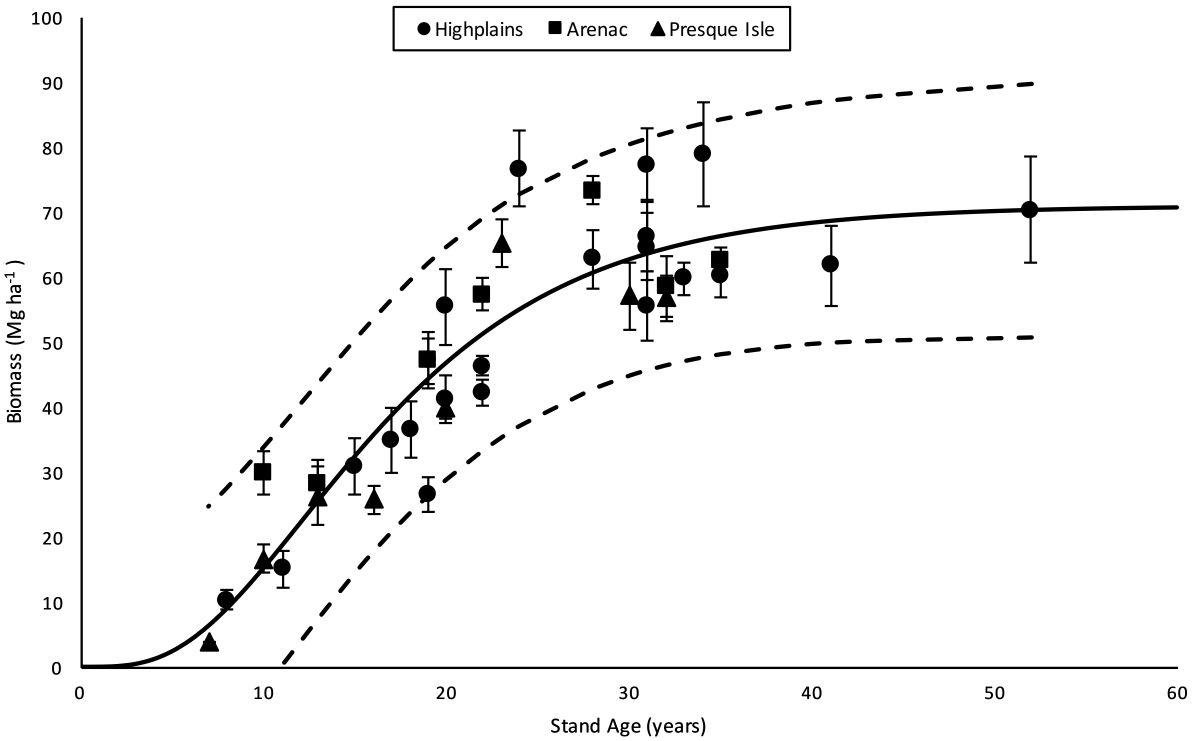


Figure 2. Aboveground biomass content as a function of stand age. Biomass accounts for both living and standing dead trees. Symbols represent stand means (±1 SE), and the solid curve represents the nonlinear regression line described in the text. Dashed lines represent the upper and lower 95% confidence limits across the age range of the dataset.

To compare the optimal rotation lengths for biomass and pulpwood production in KW stands, I developed a similar growth curve to map volume accumulation over time (Figure 3). The shape of the curve for stand-level volume growth differed greatly from that of biomass production, showing no accumulation until *ca.* 20 years after planting. The minimum size requirements for pulpwood production limit volume accumulation until stems reach a threshold minimum merchantable size (2.44 m pulp stick below a 10.16 cm top), which occurs at approximately 20 years. This lag period is followed by a sharp uptick in the growth curve, reflecting rapid volume accrual between *ca.* 20 and 30 years, after which there is a decline in the rate of accumulation approaching an asymptote of 71 m^3 ha^{-1} (Figure 3). Stand-level pulpwood volume data was described using a modified Richards function for logistic growth (Richards 1959): V_t (m^3 ha^{-1}) = $71.118(1\text{-}e^{(-0.355*t)})^{1932.7}$; $P < 0.001$. I found that the upper and lower 95% confidence limits for the volume function did not fit as tightly to the regression curve as those observed in the biomass regression, indicating lower estimate precision (Figs. 2 and 3).

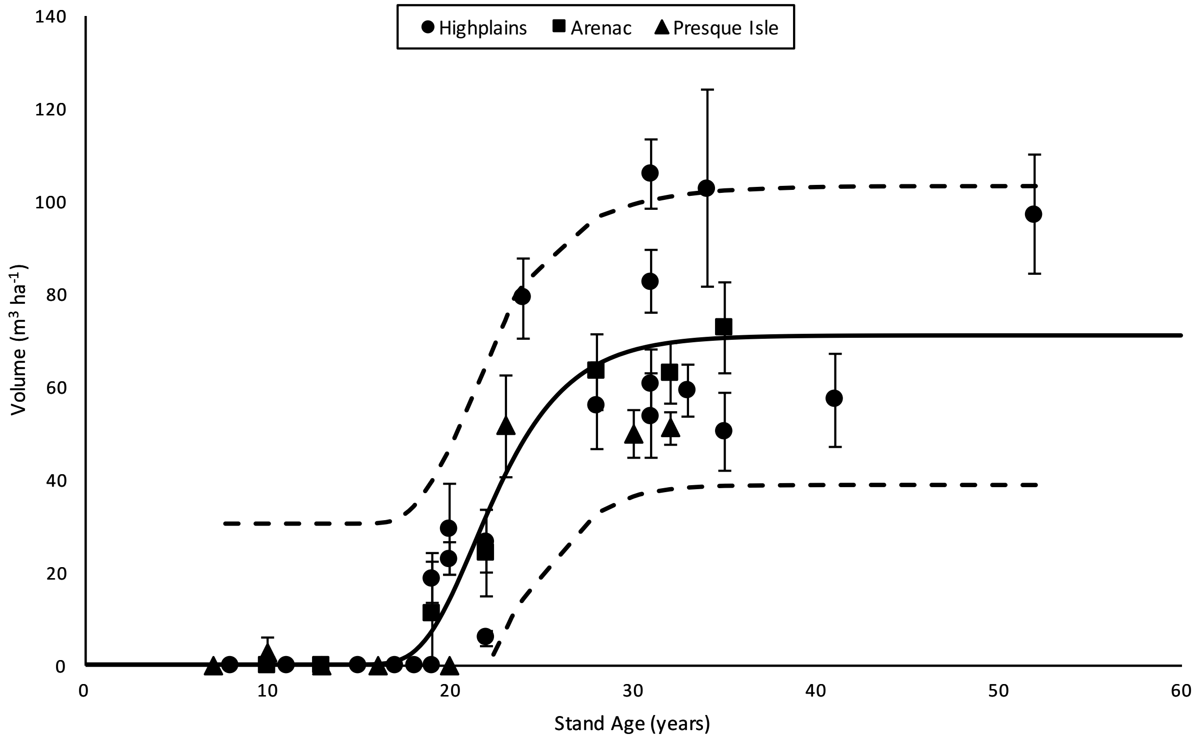


Figure 3. Volume content as a function of stand age. Volume is estimated for all living stems with a minimum 2.44 m length to a 10.16 cm top. Symbols represent stand means (±1 SE), and the solid curve represents the nonlinear regression line described in the text. Dashed lines represent the upper and lower 95% confidence limits across the age range of the dataset.

3.3 Covariate analyses

I regressed three covariates of potential significance against the residuals of both the biomass and volume growth curves. However, none of these regressions yielded statistically significant results for either biomass or volume growth (Tables 2 and 3). Contrary to my initial predictions, stand density and available soil drainage and productivity data did not explain observed variations across stands of equal and similar ages. Therefore, these covariates were not included in the final growth models.

Statistical Variable	**Stand Density**	**Drainage Index**	**Productivity Index**
R^2	0.0005	0.0003	0.0127
P-value	0.8933	0.9184	0.5059

Table 2. Statistical outputs of covariate regressions plotted against biomass curve residuals.

Statistical Variable	**Stand Density**	**Drainage Index**	**Productivity Index**
R^2	0.0337	0.0000	0.0313
P-value	0.2770	0.9910	0.2945

Table 3. Statistical outputs of covariate regressions plotted against volume curve residuals.

3.4 Optimal rotation ages

I determined the optimal rotation age for maximum biomass yields to be 20 years after stand establishment. At this age, MAI was equivalent to the derivative of the biomass growth function, a point also known as the culmination of MAI (Figure 4A). Stands at this age contained an estimated 47 Mg ha^{-1} of aboveground biomass in planted zones of KW habitat. Additionally, I observed the culmination of MAI for the volume curve to occur at 28 years after establishment, and determined this to be the optimal rotation length to maximize pulpwood yields (Figure 4B). At this age, stands are expected to yield approximately 65 m^3 ha^{-1} of pulpwood volume in planted areas of KW habitat.

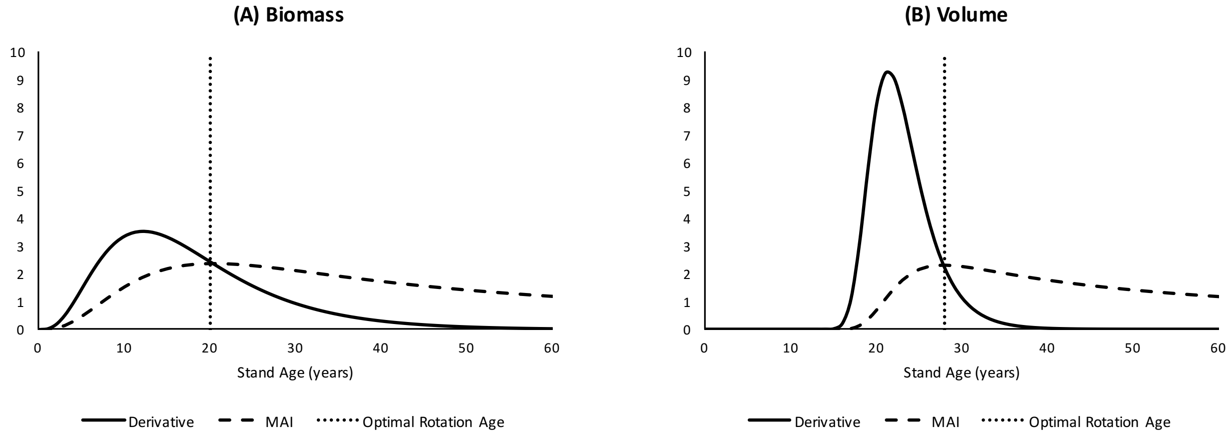


Figure 4. Derivatives of (A) biomass and (B) volume growth curves plotted against their respective MAI curves over time. Solid curves represent the growth curve derivatives and dashed curves represent MAI over time. Vertical dotted lines represent the stand age at which culmination of MAI occurs, where MAI equals the derivative of the growth function.

3.5 Regional impact assessment

I compared the potential ecosystem service outputs that would be provided from 1550 ha of KW habitat managed under 3 different rotation scenarios over a 100-year period (Table 4). The three rotation lengths of interest were 20 years (estimated optimal rotation age for maximum biomass yields), 28 years (estimated optimal rotation age for maximum volume yields), and 50 years (current BAU rotation length for KW plantations; MDNR 2014). I selected a land area of 1550 ha to reflect the annual harvest and planting area objective outlined in the Kirtland's Warbler Breeding Range Conservation Plan (MDNR 2014). All biomass and volume outputs reported in Table 4 reflect forest production on 4/5 of a 1550 ha area (the approximate ratio of planted to unplanted patches within KW stands), equating to a total planted land area of 1240 ha.

Rotation Length	# Rotations 100 years^{-1}	Biomass Rotation^{-1} (Gg)	Cumulative Biomass (Gg 100 yrs^{-1})	Volume Rotation^{-1} (10^3 m^3)	Cumulative Volume (10^3 m^3 100 yrs^{-1})	Suitable Habitat (yrs 100 yrs^{-1})	Total Required Habitat Area (ha)
20	5	58	290	18	88	80	31,000
28	3	75	225	80	241	69	43,400
50	2	87	174	88	176	38	77,500

Table 4. Potential ecosystem service outputs from 1550 ha of managed KW habitat over 100 years.

Assuming establishment at year zero, management for biomass on a 20-year harvest cycle would undergo 5 full rotations within a 100-year period, followed by management for pulpwood, which would produce 3 harvests in this time, whereas management under the BAU rotation of 50 years would only be harvested twice. A 20-year rotation would yield the most cumulative biomass over 100 years (approximately 290 Gg) and a 28-year rotation would yield the most cumulative pulpwood over this period (approximately 241,000 m^3). Although management on a 50-year rotation produces the highest biomass and volume outputs per harvest cycle, cumulative yields over a 100-year period are predicted to be significantly lower than those produced by stands managed on reduced rotations.

For each rotation scenario, I calculated the cumulative years that stands would provide early-successional habitat suitable for KW breeding. Lands managed on the current 50-year rotation only fall within the age range of suitability for a total of 38 years per every 100 years of management. Managing for pulpwood production on a 28-year rotation would increase this to a total of 69 years spent as suitable habitat, and managing for biomass on a 20-year rotation would further increase this value to a total of 80 years, more than double that of the BAU 50-year rotation. Additionally, I determined the total land area that would be required under each management scheme to continue harvesting and re-establishing 1550 ha of KW habitat on an annual basis. The 50-year rotation requires a total of 77,500 ha to be dedicated as KW habitat at any given time, whereas a 28-year rotation would reduce this to 43,400 ha. A 20-year rotation would require the lowest total land area to be under KW management at a given time, with a minimum 31,000 ha of designated habitat required to continue to meet current annual development objectives.

4. Discussion

4.1 Overview

The results of my study indicate that a shift to short-rotation management could maximize pulpwood and biomass outputs in KW stands without affecting their ability to support endangered species conservation. Limiting implementation of this strategy to a portion of current KW stands would also allow for increased management options and ecosystem diversification at the landscape level. Because KW habitat-specificity is restricted to young stands between the ages of 5 and 23 years (Meyer 2010), stands managed under the current plan only provide suitable habitat for a fraction of their 50-year rotation, suggesting that rotation lengths could be substantially reduced without impacting the duration of time spent within the age range of suitability per rotation. Furthermore, reducing rotation lengths would increase the habitat turnover rate, in turn decreasing the total land area required to be under KW management at any given time to maintain adequate levels of available habitat on the landscape. Under this scenario, land managers would gain the opportunity to implement alternative silvicultural strategies in surplus KW stands to simultaneously manage for multiple objectives at the landscape level and increase the long-term economic and ecological sustainability of the system at large.

Several studies have reported that optimization of forest multifunctionality cannot be achieved under a single management regime due to strong trade-offs that exist between maximization of provisioning services, regulating services, and biodiversity conservation, recommending management diversification at the landscape level as the only viable method to minimize these trade-offs and simultaneously meet multiple objectives (Triviño et al. 2017; Felton et al. 2015). However, the results of this study indicate that in jack pine stands of

Northern Lower Michigan, these often-conflicting goals have the potential to instead complement one another under a short-rotation management regime. At the stand level alone, reducing rotations could simultaneously increase timber revenues through the production of nontraditional wood products, maximize climate regulation benefits through carbon offsets via co-generation of biomass, and contribute to biodiversity conservation efforts by providing critical early-successional habitat, upon which an array of species of conservation concern are dependent (Corace et al. 2010). Supplemental implementation of diversified management at the landscape level would expand both the quantity and variety of benefits and services that may be rendered, allowing for true optimization of ecosystem multifunctionality. The following sections detail the potential ecological, economic, and climate-related implications associated with implementation of limited short-rotation management in KW habitat plantations.

4.2 Ecological implications

To effectively maintain the current KW population on fewer lands, it is crucial that land managers be highly selective in determining which stands should remain under KW management, as the birds are not evenly distributed across their breeding range and tend to concentrate in specific geographical areas. Census data recorded since 2000 has shown that more than 86% of all singing males reside within 5 counties in Northern Lower Michigan, 33% in just one of these counties, and 15% in a single township alone (MDNR 2014). Therefore, discontinuing KW management in stands outside these locales should have minimal to no impact on the current bird population. Implementing reduced rotations in core nesting zones may in fact benefit KW population growth as more stands within these zones would be within the age range of suitability at any given time, and distances between suitable habitats would be reduced.

Additionally, this strategy could have enormous ecological benefits at the landscape level. In a study conducted by Tucker et al. (2016), current jack pine age distributions in Northern Lower Michigan were compared to estimated historical distributions from pre-European settlement surveys. The authors compared the distributions of three age classes (<20, 20-50, and >50 years) and found that conversion of older jack pine stands to early-successional KW plantations has caused significant landscape homogenization over time, with a pronounced reduction in the prevalence of mature stands. On the current landscape, they found 31% of jack pine stands fell within the youngest age class (<20 years), 39% in the intermediate class (20-50 years), and 30% in the mature age class of >50 years. In contrast, estimates of pre-European distributions showed much higher levels of landscape variability with a mere 5% of stands belonging to the youngest class, 19% in the intermediate, and 76% in the mature age class. Over time, KW recovery efforts have converted most of these mature stands into habitat plantations, resulting in a major deviation from historical landscape distributions. Furthermore, the study found that KW management has displaced certain major cover types in the region in favor of jack pine, resulting in an estimated 29% decrease in red pine (*Pinus resinosa*) cover and a 67% reduction in barrens from their pre-European distributions (Tucker et al. 2016). Although the KW recovery plan has proven successful at restoring endangered KW populations in the region, its widespread implementation has come at the expense of landscape diversity, displacing valuable habitat ecosystems once prevalent on the landscape.

Reducing the total habitat land area with the implementation of short-rotation management would allow for the restoration of landscape age distributions and cover types that better emulate historical patterns and distributions. A couple viable silvicultural strategies that may be implemented on surplus KW stands include extending rotations to restore historical age class distributions and variability, and replanting harvested stands with cover species that are currently under-represented on the landscape. This ecosystem-based approach, which promotes structural and compositional heterogeneity, would increase biodiversity at the landscape level through provisioning of diverse habitat types, including later-successional forests which are characterized by key habitat features absent in younger stands (Lindenmayer et al. 2006; Franklin et al. 2007).

4.3 Economic implications

4.3.1 Overview of economic implications

From an economic standpoint, short-rotation management of KW stands is expected to increase timber revenues at both the stand and landscape levels. At the stand level, this strategy would likely improve land-use efficiency of habitat plantations and boost financial returns via increased harvest frequencies and production of marketable wood products such as biomass and pulpwood. Shifting timber management goals to these nontraditional products should not interfere with current revenues from habitat harvests, as it has become apparent that these high-density stands do not produce merchantable sawlogs by their planned harvest age. Thus, management for alternative wood products could in fact increase returns from harvest yields.

At the landscape level, agencies could manage surplus habitat stands to produce more profitable timber products (such as sawlogs) and further increase financial returns from this system. Managers could extend rotations in surplus KW stands and conduct pre-commercial thinnings to manage for jack pine sawlogs, and replant these stands with under-represented high-value timber species such as red pine to increase future financial gains. Diversification of timber production on the landscape could help subsidize the high costs of annual habitat harvests and re-establishment to ensure long-term economic sustainability of KW management.

4.3.2 Local economic opportunity

IPCC (2014) reports that emissions reduction strategies with low lifecycle emissions, such as fast growing tree species and sustainable use of biomass residues, can be effective in reducing greenhouse gas emissions, but rely on efficient integrated “biomass-to-bioenergy systems.” There are currently five wood-based electric power plants in the northeastern region of Michigan’s Lower Peninsula, which coincide with the core area of KW’s breeding range (Leefers 2011; MDNR 2014). In 2011, managers of these power plants reported that almost 80 percent of the wood fuel they use was sourced from a distance of 97 km or less from the facility, with several managers reporting 100 percent of their wood fuel as being sourced within this distance (Leefers 2011). Nearly all MDNR and USFS KW plantations in this region exist within a 50 km radius of at least one of these plants, and those that do not lie just outside this boundary (Figure 5). Short transport distances, coupled with high processing capacities, gives rise to the potential for an efficient integrated “biomass-to-bioenergy system” with low lifecycle emissions that would simultaneously provide multiple benefits in the form of climate change mitigation, increased options for land managers, biodiversity conservation, and support of the local economy. It should be noted, however, that the viability of implementing bioenergy production management in this system is highly dependent on renewable energy policies and market demand.

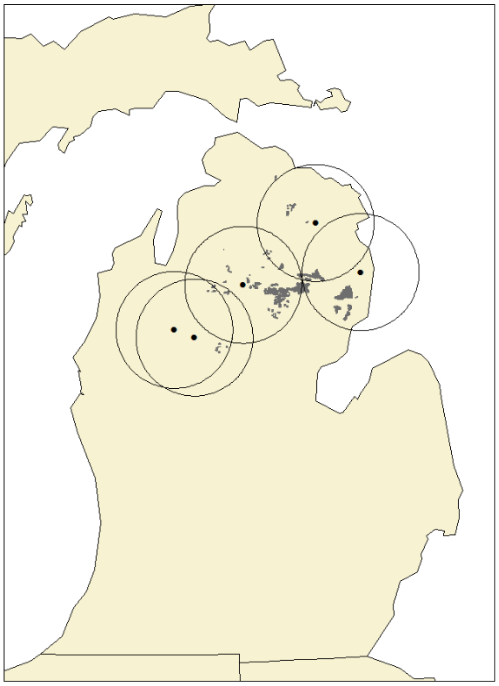


Figure 5. Locations of existing wood-based electric power plants and publicly-owned KW plantations in the northern region of Michigan's Lower Peninsula. Black dots represent power plant locations and shaded gray areas represent areas under KW management. The circles represent 50 km radii around each power plant.

Additionally, production of conifer pulpwood may soon gain significance and value in this region. The world's second-largest producer of wood products, ARAUCO, is currently building a state-of-the-art particleboard plant in Grayling, Michigan, situated in the heart of the KW management area, and is expected to begin operation in late 2018. The plant will be North

America’s largest single continuous particleboard press with an annual processing capacity of approximately 800,000 m^3 (ARAUCO 2017). This presents an outstanding opportunity for land managers to sell low-quality wood produced in KW stands to a high-capacity local manufacturing plant. In addition to the benefits of low transportation costs and distances, and indirect support of the local economy, selling KW harvests to ARAUCO could provide a more stable source of income for land agencies for decades to come, and resolve many of the marketability issues currently experienced with KW jack pine.

4.4 Climate-related implications

Limited short-rotation management of KW habitat plantations would diversify and improve climate change mitigation benefits at both the stand and landscape levels. Sohngen and Brown (2008) report that extending rotation lengths, even by just a few years, is the quickest way to increase carbon stock on a landscape. Therefore, extending rotations in surplus KW stands would diversify climate change mitigation services at the landscape level to include enhanced carbon sequestration benefits alongside potential fossil-fuel reductions rendered from KW biomass harvests for bioenergy production. Furthermore, this mixed-management strategy could have significant benefits for the ecosystem in terms of risk mitigation. At the stand level, short-rotation KW habitats reduce risks associated with natural disturbances such as wind storms, as well as insect pests and diseases that target mature jack pine (Felton et al. 2015; Carey 1993). Whereas, at the landscape level, heterogeneity of species compositions, age distributions, and cover types increase landscape resilience and mitigate risks associated with species-specific pests and diseases, which can be devastating in regions with widespread monoculture plantings (Felton et al. 2015; Ennos 2014).

4.5 Uncertainty and implications for future research

Although this study identified optimal rotation lengths for biomass and volume production (20 and 28 years, respectively), these conclusions are highly dependent on the accuracy of my growth curves. There are a few key limitations that should be considered before these rotations are implemented on a large scale. The primary source of uncertainty related to my recommended harvest ages pertains to the lack of data I had for older KW stands. Because large-scale KW habitat establishment began in 1981, few mature plantations were available for sampling. Therefore, I was only able to collect data in two stands >35 years, aged 41 and 52. It is possible that parameter values for the biomass and volume growth curves could change as more data from mature KW stands becomes available. Alterations to model parameters would affect predictions of optimal rotation lengths for biomass and pulpwood production. In the absence of sufficient data from older KW plantations, a comparison of my estimates of biomass and volume production to those from the literature will be used to determine whether reported rotation ages from this study seem plausible, or whether they appear to be skewed by the limited age range of the dataset.

To address uncertainties related to biomass production over time, I compared my results to two studies conducted on jack pine grown in the northern region of Michigan’s Lower Peninsula, the same geographic location in which this study is based. Rothstein et al. (2004) studied the loss and recovery of carbon pools following stand-replacing fire in jack pine stands in this region. They estimated overstory biomass in a chronosequence ranging in age from 1-72 years and found that growth over time in this system followed an S-shaped pattern with biomass production peaking at 16 years and approaching an asymptotic value of 106 Mg ha^{-1} by age 40. In a separate study, Spaulding and Rothstein (2009) evaluated stand structural differences between fire-origin jack pine stands and jack pine plantations. In this study, they collected data from two jack pine plantations aged 65 and 69 which averaged 100 and 105 Mg ha^{-1} of biomass, respectively. Although both studies' estimates of maximal biomass were higher than my estimate of 71 Mg ha^{-1}, both studies utilized Perala and Alban's (1994) allometric equation to estimate jack pine biomass, which I found could lead to a nearly 40% overestimation of stand-level biomass in older KW stands. Overall, results from these two studies support the conclusions of this study on both the timing and magnitude of biomass production for jack pine in this area.

To my knowledge, no studies examining volume accumulation by jack pine in Northern Lower Michigan exist in the current literature. However, studies of jack pine and closely related species from other regions are available for comparison. Hébert et al. (2016) compared volume increment rates of individual stems in jack pine plantations of varying densities (1111 trees ha^{-1} to 4444 trees ha^{-1}) in Quebec, Canada. Although values for volume increment varied by stand density, all stem increment rates followed the same general pattern across the 25-year study period, peaking at an age of approximately 15 years. Long and Smith (1992) measured stem volume increment as a function of age and relative density for the closely-related lodgepole pine (*Pinus contorta*) in south-central Wyoming, between the ages of 10 and 117 years. They found that at a stand density of 1200 trees ha^{-1} volume increment peaked approximately 40 years after establishment. Considering the high density and harsh environmental conditions under which jack pine grow in KW plantations, these results suggest that a culmination of MAI for volume occurring at 28 years appears to be a valid assessment.

I also compared my results for volume production to two studies which compared growth and development of jack pine grown in extremely dense fire-originated stands to less dense plantations. Morris et al. (2014) found that 5-year periodic increments for stand-level volume peaked at 20 years following establishment in both planted and naturally-regenerated stands in Ontario, Canada. The authors associated the age of peak volume increment to the age at which crown closure occurs, and photosynthetic capacity is reduced in the stand. In another study in Ontario, Canada, Janas and Brand (1988) found that volume increment for high-density natural jack pine stands peaked at 18 years, and plantations of 2.13 m spacing peaked at 15 years. They concluded that an optimal biological rotation for volume production would be shortest for the densest stands and longer for stands of lower density, unless those stands were to be managed for sawlog production, in which case the reverse would be true. Overall, these studies provide strong support for my conclusion that rotation lengths in high-density KW plantations could be substantially reduced to maximize volume yields prior to growth stagnation.

Despite supportive data from other studies of jack pine and related species, it is important that we continue to monitor trends in biomass and volume accrual as younger KW habitats mature and enter older age classes. Future research should focus on KW stands grown beyond 50 years to determine if and when they reach merchantable sawlog size. Due to the high planting density of these stands, it may be necessary to conduct one or more pre-harvest thinnings to release residual stems and allow them to grow to merchantable size (Morris et al. 2014; Janas and Brand 1988). Continued monitoring and experimentation is needed to adequately assess which management strategies, or combination of management strategies, prove to be the most feasible and beneficial to the system.

It is also important to note that my 100-year regional impact assessment is based on current growth patterns, which are likely to change over the next century as the effects of global climate change continue to intensify (Chum et al. 2011). Increased levels of atmospheric carbon dioxide could contribute to increased production rates, whereas rapidly warming temperatures and drought could have the opposite effect on jack pine growth in KW stands. Geographically, KW plantations exist at the southern limit of jack pine's current natural growth range (Rudolph 1985). However, it has been projected that in the northern hemisphere, tree species will begin to migrate northward as changes in temperature and precipitation patterns at the southern margins of their current distributions become unsuitable for growth (Case and Lawler 2017). Furthermore, it is predicted that over the next 100 years, the frequency and severity of natural disturbances will increase, raising concerns that a suite of threats could impact growth patterns over the coming decades (MEA 2005; Felton et al. 2015). Because KW plantations are a monoculture system, they are prone to species-specific pest outbreaks (Thompson et al. 2009; Ennos 2014). Additionally, pathogen pressures tend to be consistently high in stands with high host densities (Ennos 2014). Implementing short rotations could potentially mitigate these risks by harvesting stems before they reach the peak age of susceptibility (Roberge et al. 2016).

Another important caveat to consider is the potential long-term consequences of repeated whole-tree harvests on site productivity and nutrient availability in forest ecosystems. Several studies have shown that low-fertility sites, such as those utilized in KW management, are most likely to be negatively impacted by repeated intensive management practices, such as whole-tree harvests, and associated nutrient removals over the long-term (Blanco et al. 2005; Kaarakka et al.

2014). There is also evidence that pioneer shade-intolerant tree species such as jack pine, which exhibit rapid rates of resource acquisition, are most strongly impacted by changes in soil nutrient status associated with increased harvest intensities (Thiffault et al. 2006). Therefore, it is important to monitor for changes in soil quality and productivity over time in intensively-managed KW stands and adjust management accordingly; this may involve alternating harvesting methods and rotation lengths on a given site to balance production with long-term soil sustainability.

5. Conclusions

Implementation of short-rotation management in jack pine habitat plantations in Michigan's Lower Peninsula has the potential to benefit the system on multiple levels. Reducing rotation lengths in a portion of these stands would expand the quantity of ecosystem services that can be rendered to include provisioning of forest products and climate change mitigation benefits, without negatively impacting their ability to provide critical early-successional habitat to endangered species and species of conservation concern. Additionally, shifting to shorter rotations would reduce the total land area required to be under KW management at any given time, allowing for significant ecological and economic benefits while continuing to meet annual habitat development objectives. For one, land agencies would gain the opportunity to diversify management goals at the landscape level and produce more valuable timber species on extended rotations to subsidize costs associated with annual KW habitat harvests and development projects. Diversification would also increase habitat variation and availability, improving the landscape's ability to support a variety of species adapted to various disturbance regimes and forest cover types. Limiting KW management to a portion of its current domain would improve landscape resilience to disturbance events, while better emulating the region's historical forest distributions.

APPENDIX

Table 5. Plot-level data

Stand ID	Age	Region	Ownership	Plot	Latitude	Longitude	Planted Area Density (stems ha^{-1})	Total Area Density (stems ha^{-1})	Planted Area Biomass (Mg ha^{-1})	Total Area Biomass (Mg ha^{-1})	Planted Area Live Stem Density (stems ha^{-1})	Total Area Live Stem Density (stems ha^{-1})	Planted Area Volume (m^3 ha^{-1})	Total Area Volume (m^3 ha^{-1})
1	52	Highplains	MDNR	1	44.8422	-84.4624	2917	2333	83	66	1667	1333	107	85
1	52	Highplains	MDNR	2	44.8453	-84.4654	1389	1111	55	44	833	667	72	57
1	52	Highplains	MDNR	3	44.8427	-84.4700	1944	1556	73	59	1250	1000	113	90
2	41	Highplains	MDNR	1	44.4403	-84.2972	3611	2889	61	49	1806	1444	55	44
2	41	Highplains	MDNR	2	44.4383	-84.2973	2778	2222	45	36	1944	1556	21	17
2	41	Highplains	MDNR	3	44.4356	-84.3016	3194	2556	75	60	2222	1778	65	52
2	41	Highplains	MDNR	4	44.4393	-84.2943	3194	2556	76	61	2361	1889	81	65
2	41	Highplains	MDNR	5	44.4389	-84.2930	1806	1444	52	42	1389	1111	63	50
3	35	Highplains	MDNR	1	44.4325	-84.2673	3194	2556	56	45	2222	1778	42	34
3	35	Highplains	MDNR	2	44.4347	-84.2602	2917	2333	50	40	1250	1000	25	20
3	35	Highplains	MDNR	3	44.4343	-84.2505	2500	2000	64	51	1250	1000	73	59
3	35	Highplains	MDNR	4	44.4338	-84.2557	4167	3333	69	55	2222	1778	46	37
3	35	Highplains	MDNR	5	44.4340	-84.2613	3194	2556	62	49	1250	1000	65	52
4	35	Arenac	USFS	1	44.5130	-83.6298	2500	2000	61	49	1528	1222	70	56
4	35	Arenac	USFS	2	44.5120	-83.6328	4167	3333	60	48	2361	1889	57	45
4	35	Arenac	USFS	3	44.5113	-83.6426	2361	1889	67	53	1667	1333	90	72
5	34	Highplains	MDNR	1	44.5363	-84.8270	2639	2111	75	60	1806	1444	84	67
5	34	Highplains	MDNR	2	44.5360	-84.8273	2778	2222	104	83	1944	1556	156	125
5	34	Highplains	MDNR	3	44.5358	-84.8269	1806	1444	60	48	1389	1111	87	69
5	34	Highplains	MDNR	4	44.5352	-84.8267	3611	2889	66	52	2222	1778	41	33
5	34	Highplains	MDNR	5	44.5361	-84.8278	1944	1556	90	72	1806	1444	145	116
6	33	Highplains	MDNR	1	44.5966	-84.6245	3333	2667	62	49	1250	1000	43	34
6	33	Highplains	MDNR	2	44.5962	-84.6236	2222	1778	52	42	1389	1111	54	44
6	33	Highplains	MDNR	3	44.5964	-84.6223	2639	2111	67	54	1528	1222	66	53
6	33	Highplains	MDNR	4	44.5965	-84.6213	2222	1778	60	48	1111	889	75	60
6	33	Highplains	MDNR	5	44.5964	-84.6248	2917	2333	58	46	1667	1333	56	45
7	32	Arenac	USFS	1	44.4844	-83.5455	2222	1778	55	44	1806	1444	76	61
7	32	Arenac	USFS	2	44.4838	-83.5457	4167	3333	67	54	2778	2222	57	46
7	32	Arenac	USFS	3	44.4839	-83.5445	2500	2000	53	42	1806	1444	55	44
8	32	Presque Isle	MDNR	1	45.1962	-84.1577	3194	2556	63	50	2778	2222	40	32
8	32	Presque Isle	MDNR	2	45.1953	-84.1566	3472	2778	66	53	2500	2000	57	46
8	32	Presque Isle	MDNR	3	45.1964	-84.1514	2639	2111	53	42	1944	1556	48	38
8	32	Presque Isle	MDNR	4	45.1971	-84.1527	2361	1889	49	39	1528	1222	52	41
8	32	Presque Isle	MDNR	5	45.1971	-84.1506	2500	2000	53	42	1667	1333	58	47
9	31	Highplains	MDNR	1	44.4323	-84.2475	2361	1889	69	55	1806	1444	82	65
9	31	Highplains	MDNR	2	44.4332	-84.2482	2500	2000	59	47	1111	889	41	33
9	31	Highplains	MDNR	3	44.4317	-84.2480	1944	1556	59	47	1250	1000	64	51
9	31	Highplains	MDNR	4	44.4331	-84.2480	1667	1333	53	42	1250	1000	70	56
9	31	Highplains	MDNR	5	44.4312	-84.2481	1111	889	37	30	972	778	46	37
10	31	Highplains	MDNR	1	44.7470	-84.4324	2639	2111	74	59	2083	1667	91	72
10	31	Highplains	MDNR	2	44.7461	-84.4320	2639	2111	76	61	1944	1556	92	74
10	31	Highplains	MDNR	3	44.7456	-84.4312	1806	1444	62	50	1528	1222	82	66
10	31	Highplains	MDNR	4	44.7459	-84.4300	2500	2000	72	57	2083	1667	91	73
10	31	Highplains	MDNR	5	44.7461	-84.4314	1667	1333	47	38	1250	1000	56	45
11	31	Highplains	MDNR	1	44.5733	-84.5569	2778	2222	69	55	1806	1444	84	67
11	31	Highplains	MDNR	2	44.5729	-84.5571	3472	2778	69	55	3194	2556	32	26
11	31	Highplains	MDNR	3	44.5737	-84.5571	3333	2667	75	60	2639	2111	61	49
11	31	Highplains	MDNR	4	44.5737	-84.5579	2639	2111	45	36	1806	1444	38	30
11	31	Highplains	MDNR	5	44.5725	-84.5579	3472	2778	64	52	2083	1667	52	42
12	31	Highplains	MDNR	1	44.8379	-84.4901	1806	1444	66	53	1528	1222	96	77
12	31	Highplains	MDNR	2	44.8384	-84.4900	2500	2000	91	72	2222	1778	122	98
12	31	Highplains	MDNR	3	44.8389	-84.4896	1944	1556	66	53	1528	1222	92	73
12	31	Highplains	MDNR	4	44.8397	-84.4896	2222	1778	72	57	2083	1667	93	74
12	31	Highplains	MDNR	5	44.8377	-84.4903	2917	2333	91	73	2083	1667	127	101
13	30	Presque Isle	MDNR	1	45.1956	-84.1440	2778	2222	62	50	2361	1889	49	39
13	30	Presque Isle	MDNR	2	45.1949	-84.1439	2778	2222	54	43	2361	1889	48	38
13	30	Presque Isle	MDNR	3	45.1955	-84.1419	2917	2333	68	55	1944	1556	58	46
13	30	Presque Isle	MDNR	4	45.1956	-84.1430	2361	1889	38	31	1111	889	32	25
13	30	Presque Isle	MDNR	5	45.1954	-84.1428	2917	2333	63	50	1806	1444	63	50
14	28	Highplains	MDNR	1	44.4776	-84.3174	2778	2222	48	39	2083	1667	21	16
14	28	Highplains	MDNR	2	44.4771	-84.3123	3611	2889	62	49	2083	1667	55	44
14	28	Highplains	MDNR	3	44.4771	-84.3080	2778	2222	71	57	2361	1889	72	58
14	28	Highplains	MDNR	4	44.4771	-84.3140	2917	2333	74	59	2083	1667	69	55
14	28	Highplains	MDNR	5	44.4772	-84.3133	2361	1889	59	47	1806	1444	62	50
15	28	Arenac	USFS	1	44.5363	-83.6261	3056	2444	69	55	3056	2444	48	38
15	28	Arenac	USFS	2	44.5345	-83.6273	2778	2222	74	59	2778	2222	75	60
15	28	Arenac	USFS	3	44.5401	-83.6206	3611	2889	76	61	3472	2778	66	53
16	24	Highplains	MDNR	1	44.5434	-84.8321	3194	2556	74	59	2500	2000	72	57
16	24	Highplains	MDNR	2	44.5438	-84.8333	3611	2889	81	65	2917	2333	93	74
16	24	Highplains	MDNR	3	44.5433	-84.8338	4028	3222	62	50	2500	2000	49	39
16	24	Highplains	MDNR	4	44.5438	-84.8338	2639	2111	70	56	2222	1778	83	66
16	24	Highplains	MDNR	5	44.5431	-84.8325	4028	3222	96	77	3472	2778	98	78
17	23	Presque Isle	MDNR	1	45.1269	-84.1947	4028	3222	61	48	4028	3222	34	27
17	23	Presque Isle	MDNR	2	45.1253	-84.1947	2639	2111	71	57	2222	1778	93	75
17	23	Presque Isle	MDNR	3	45.1271	-84.1919	3056	2444	55	44	2917	2333	32	26
17	23	Presque Isle	MDNR	4	45.1270	-84.1924	2639	2111	65	52	2639	2111	52	42
17	23	Presque Isle	MDNR	5	45.1267	-84.1916	3611	2889	75	60	2917	2333	45	36
18	22	Highplains	MDNR	1	44.4329	-84.2732	3333	2667	43	34	2500	2000	22	18
18	22	Highplains	MDNR	2	44.4341	-84.2741	2639	2111	49	39	2500	2000	16	13
18	22	Highplains	MDNR	3	44.4336	-84.2745	2500	2000	44	35	2222	1778	28	23
18	22	Highplains	MDNR	4	44.4334	-84.2754	2083	1667	51	40	2083	1667	51	41
18	22	Highplains	MDNR	5	44.4338	-84.2722	3611	2889	46	36	3333	2667	14	11

Table 5 (cont’d)

Stand ID	Age	Region	Ownership	Plot	Latitude	Longitude	Planted Area Density (stems ha^{-1})	Total Area Density (stems ha^{-1})	Planted Area Biomass (Mg ha^{-1})	Total Area Biomass (Mg ha^{-1})	Planted Area Live Stem Density (stems ha^{-1})	Total Area Live Stem Density (stems ha^{-1})	Planted Area Volume (m^3 ha^{-1})	Total Area Volume (m^3 ha^{-1})
19	22	Highplains	MDNR	1	44.4625	-84.2931	3594	2875	47	38	3047	2438	10	8
19	22	Highplains	MDNR	2	44.4559	-84.2913	2778	2222	40	32	2778	2222	6	5
19	22	Highplains	MDNR	3	44.4510	-84.2935	3056	2444	36	29	2778	2222	0	0
19	22	Highplains	MDNR	4	44.4546	-84.2916	3194	2556	42	34	2639	2111	6	5
19	22	Highplains	MDNR	5	44.4551	-84.2921	3194	2556	45	36	2639	2111	6	5
20	22	Arenac	USFS	1	44.5175	-83.6221	3472	2778	61	49	2917	2333	29	23
20	22	Arenac	USFS	2	44.5210	-83.6233	3056	2444	53	42	3056	2444	6	5
20	22	Arenac	USFS	3	44.5172	-83.6216	3333	2667	58	46	3056	2444	37	30
21	20	Highplains	MDNR	1	44.4685	-84.3514	3056	2444	48	38	2917	2333	20	16
21	20	Highplains	MDNR	2	44.4707	-84.3517	3056	2444	42	34	2500	2000	15	12
21	20	Highplains	MDNR	3	44.4714	-84.3516	2361	1889	42	34	2222	1778	36	29
21	20	Highplains	MDNR	4	44.4723	-84.3520	1389	1111	27	22	1389	1111	21	17
21	20	Highplains	MDNR	5	44.4679	-84.3515	2500	2000	47	37	2361	1889	21	17
22	20	Highplains	MDNR	1	44.6247	-84.6266	3333	2667	43	34	2639	2111	0	0
22	20	Highplains	MDNR	2	44.6252	-84.6263	3056	2444	53	42	2639	2111	37	29
22	20	Highplains	MDNR	3	44.6257	-84.6272	4028	3222	73	58	2361	1889	51	41
22	20	Highplains	MDNR	4	44.6255	-84.6280	3472	2778	44	35	2222	1778	12	10
22	20	Highplains	MDNR	5	44.6248	-84.6269	3194	2556	65	52	2778	2222	45	36
23	20	Presque Isle	MDNR	1	45.1458	-84.1741	3472	2778	42	34	3333	2667	0	0
23	20	Presque Isle	MDNR	2	45.1459	-84.1708	3056	2444	36	29	2917	2333	0	0
23	20	Presque Isle	MDNR	3	45.1486	-84.1736	3750	3000	37	30	3611	2889	0	0
23	20	Presque Isle	MDNR	4	45.1468	-84.1736	3333	2667	40	32	3194	2556	0	0
23	20	Presque Isle	MDNR	5	45.1469	-84.1742	3472	2778	44	35	3472	2778	0	0
24	19	Highplains	MDNR	1	44.5981	-84.5836	3194	2556	23	18	3194	2556	0	0
24	19	Highplains	MDNR	2	44.5981	-84.5827	3750	3000	22	18	3750	3000	0	0
24	19	Highplains	MDNR	3	44.5979	-84.5820	3611	2889	30	24	3611	2889	0	0
24	19	Highplains	MDNR	4	44.5979	-84.5815	3056	2444	23	18	3056	2444	0	0
24	19	Highplains	MDNR	5	44.5980	-84.5835	4583	3667	35	28	4583	3667	0	0
25	19	Highplains	MDNR	1	44.7579	-84.3545	2778	2222	51	41	2778	2222	15	12
25	19	Highplains	MDNR	2	44.7580	-84.3542	2639	2111	45	36	2639	2111	30	24
25	19	Highplains	MDNR	3	44.7617	-84.3541	3194	2556	58	47	3194	2556	29	23
25	19	Highplains	MDNR	4	44.7626	-84.3542	2083	1667	37	29	2083	1667	19	15
25	19	Highplains	MDNR	5	44.7608	-84.3546	3611	2889	45	36	3472	2778	0	0
26	19	Arenac	USFS	1	44.5262	-83.6114	3333	2667	55	44	3333	2667	33	26
26	19	Arenac	USFS	2	44.5262	-83.6029	3333	2667	46	37	3333	2667	0	0
26	19	Arenac	USFS	3	44.5301	-83.6031	2500	2000	40	32	2361	1889	0	0
27	18	Highplains	MDNR	1	44.4731	-84.2791	2639	2111	32	26	2639	2111	0	0
27	18	Highplains	MDNR	2	44.4756	-84.2786	4861	3889	40	32	4583	3667	0	0
27	18	Highplains	MDNR	3	44.4734	-84.2751	2222	1778	21	17	2222	1778	0	0
27	18	Highplains	MDNR	4	44.4766	-84.2619	4306	3444	42	34	4028	3222	0	0
27	18	Highplains	MDNR	5	44.4765	-84.2616	4167	3333	47	38	3750	3000	0	0
28	17	Highplains	MDNR	1	44.5838	-84.6198	4861	3889	46	37	4722	3778	0	0
28	17	Highplains	MDNR	2	44.5834	-84.6193	4444	3556	41	33	4444	3556	0	0
28	17	Highplains	MDNR	3	44.5837	-84.6201	2917	2333	36	28	2917	2333	0	0
28	17	Highplains	MDNR	4	44.5833	-84.6203	2500	2000	34	27	2500	2000	0	0
28	17	Highplains	MDNR	5	44.5835	-84.6199	1667	1333	17	13	1667	1333	0	0
29	16	Presque Isle	MDNR	1	45.2018	-84.1653	3889	3111	20	16	3750	3000	0	0
29	16	Presque Isle	MDNR	2	45.2034	-84.1642	3472	2778	26	21	3333	2667	0	0
29	16	Presque Isle	MDNR	3	45.2057	-84.1610	3750	3000	30	24	3611	2889	0	0
29	16	Presque Isle	MDNR	4	45.2069	-84.1627	3472	2778	21	17	3472	2778	0	0
29	16	Presque Isle	MDNR	5	45.2039	-84.1627	4583	3667	31	25	4583	3667	0	0
30	15	Highplains	MDNR	1	44.4796	-84.3463	6944	5556	29	23	6944	5556	0	0
30	15	Highplains	MDNR	2	44.4829	-84.3451	5139	4111	26	21	5139	4111	0	0
30	15	Highplains	MDNR	3	44.4790	-84.3416	3333	2667	20	16	3056	2444	0	0
30	15	Highplains	MDNR	4	44.4789	-84.3451	4444	3556	34	27	4444	3556	0	0
30	15	Highplains	MDNR	5	44.4799	-84.3443	4444	3556	45	36	4444	3556	0	0
31	13	Arenac	USFS	1	44.5210	-83.5290	3333	2667	30	24	3333	2667	0	0
31	13	Arenac	USFS	2	44.5253	-83.5603	3750	3000	34	27	3750	3000	0	0
31	13	Arenac	USFS	3	44.5253	-83.5581	2778	2222	22	17	2778	2222	0	0
32	13	Presque Isle	MDNR	1	45.1487	-84.1980	6528	5222	28	22	6528	5222	0	0
32	13	Presque Isle	MDNR	2	45.1487	-84.1957	2500	2000	9	7	2361	1889	0	0
32	13	Presque Isle	MDNR	3	45.1457	-84.1968	3611	2889	26	20	3611	2889	0	0
32	13	Presque Isle	MDNR	4	45.1425	-84.1909	4444	3556	36	29	4444	3556	0	0
32	13	Presque Isle	MDNR	5	45.1435	-84.1933	4861	3889	32	26	4861	3889	0	0
33	11	Highplains	MDNR	1	44.4051	-84.3876	2778	2222	8	6	2778	2222	0	0
33	11	Highplains	MDNR	2	44.3976	-84.3872	2639	2111	11	9	2639	2111	0	0
33	11	Highplains	MDNR	3	44.4013	-84.3806	3611	2889	13	10	3611	2889	0	0
33	11	Highplains	MDNR	4	44.4008	-84.3898	3750	3000	22	17	3750	3000	0	0
33	11	Highplains	MDNR	5	44.4088	-84.3764	4028	3222	22	18	3750	3000	0	0
34	10	Arenac	USFS	1	44.5411	-83.5867	3611	2889	29	23	3333	2667	0	0
34	10	Arenac	USFS	2	44.5406	-83.5846	3611	2889	24	19	3611	2889	0	0
34	10	Arenac	USFS	3	44.5370	-83.6031	3056	2444	36	29	3056	2444	0	0
35	10	Presque Isle	MDNR	1	45.1497	-84.1941	3889	3111	23	19	3889	3111	14	11
35	10	Presque Isle	MDNR	2	45.1514	-84.1996	3750	3000	13	10	3750	3000	0	0
35	10	Presque Isle	MDNR	3	45.1492	-84.1959	3889	3111	19	15	3889	3111	0	0
35	10	Presque Isle	MDNR	4	45.1496	-84.1978	4444	3556	11	9	4306	3444	0	0
35	10	Presque Isle	MDNR	5	45.1504	-84.1999	3889	3111	17	14	3611	2889	0	0
36	8	Highplains	MDNR	1	44.3570	-84.3669	3750	3000	14	11	3750	3000	0	0
36	8	Highplains	MDNR	2	44.3481	-84.3783	3472	2778	12	9	3472	2778	0	0
36	8	Highplains	MDNR	3	44.3453	-84.3366	3056	2444	7	6	2917	2333	0	0
36	8	Highplains	MDNR	4	44.3550	-84.3579	4167	3333	13	10	4167	3333	0	0
36	8	Highplains	MDNR	5	44.3529	-84.3525	3056	2444	6	5	3056	2444	0	0
37	7	Presque Isle	MDNR	4	45.2190	-84.1692	2917	2333	3	3	2778	2222	0	0
37	7	Presque Isle	MDNR	5	45.2170	-84.1702	3472	2778	4	3	3472	2778	0	0

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