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forest management

Alternative Silvicultural Approaches to Managing Jack Pine Plantations for Endangered Species Habitat and Forest Products

Daphna Gadoth-Goodman and David E. Rothstein

Since the early 1980s, *ca* 1,550 hectares (3,800 ac) 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 (KW; *Setophaga kirtlandii*). Because these plantations do not appear capable of producing merchantable sawlogs by their planned 50-year harvest age, we investigated the potential to implement reduced rotation lengths in these stands to produce biomass and/or pulpwood. We used space-for-time substitution to assess biomass and volume accrual over time, using our own locally derived allometric biomass equations. The predicted optimal rotation age for biomass was 20 years, and the predicted optimal rotation age for pulpwood volume was 28 years. We compared the total land area required for management under these rotation scenarios to continue establishing 1,550 hectares (3,800 ac) of KW habitat annually. Management on the current 50-year cycle requires *ca* 77,500 hectares (191,500 ac). Management for pulpwood would reduce this to *ca* 43,400 hectares (107,250 ac), and management for biomass would require *ca* 31,000 hectares (76,600 ac). Our results suggest that rotation lengths in these plantations could be substantially reduced, allowing for reductions in the total land area dedicated to warbler habitat, allowing for diversification of management at the landscape scale.

Study Implications: Jack pine ecosystems in the northern Lower Peninsula have been managed for the last 30 years with an approach based primarily on the habitat needs of the Kirtland's warbler (KW; *Setophaga kirtlandii*). The KW management system has been revenue negative for many years; however, it is coming under increasing strain because of declining availability of older (>60 years) stands with larger, more marketable trees. Lack of economic return from KW plantations is a significant concern for the long-term viability of the KW (US Fish and Wildlife Service 2018), as high-density KW plantations appear unable to produce merchantable sawtimber within the planned 50-year rotation. Our findings indicate that reducing rotation lengths in a portion of the stands currently managed for KW to *ca* 30 year would maximize production of pulpwood while reducing the total land area required to be under KW management at any given time. This would provide land managers flexibility to diversify management goals at the landscape level by freeing up land area to produce more valuable timber species, which could, in turn, subsidize costs associated with annual KW habitat creation. Furthermore, extending rotation lengths and diversifying cover types on a portion of the area currently managed for KW would allow managers to better emulate the presettlement stand age distribution and cover type distribution across the landscape.

Keywords: jack pine, Kirtland's warbler, rotation length, biomass, pulpwood

Modern ecological forestry emphasizes the implementation of management strategies that emulate natural disturbance regimes and stand-development processes (Franklin et al. 2007, Long 2009). Clearcut harvesting is used to manage forest types historically perpetuated by stand-replacing wildfire and can be maintained on a rotation period that is similar to the historical fire return interval (Long 2009, Michigan Department of Natural Resources (MDNR) 2014). Nevertheless, the distribution of stands on managed landscapes differs significantly from that found on landscapes naturally maintained by wildfire (Wagner 1978, Lecomte 2006). A fully regulated landscape of forest stands on a fixed harvest rotation will eventually yield a

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Affiliations: *Daphna Gadoth-Goodman (daphna.gadoth@gmail.com) and David E. Rothstein (rothste2@msu.edu), Department of Forestry, Michigan State University, East Lansing, MI 48824-1222.*

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rectangular stand age distribution in which stand ages are distributed evenly with no stands exceeding the age of the rotation period (Gustafson and Crow 1998, Lecomte 2006). In contrast, natural landscapes maintained by wildfire contain a significant proportion of stands that exceed the average fire return interval (Johnson 1992, Bergeron 1999, Lecomte 2006). Therefore, large-scale implementation of fixed-rotation management on such a landscape tends to homogenize the prevalence of age classes that fall within the rotation period.

This phenomenon has been documented in the northeastern region of Michigan's Lower Peninsula, where thousands of hectares of jack pine (*Pinus banksiana*) are managed on a 50-year rotation to provide critical, early-successional endangered species habitat (MDNR 2014, Tucker et al. 2016). Jack pine forests in this region naturally occur in even-aged stands and were historically perpetuated by stand-replacing fires on an average return interval of *ca* 60 years (Cleland et al. 2004). Fire-suppression efforts in the early- to mid-1900s led to widespread habitat loss for a diversity of early-successional-adapted wildlife, driving one bird species, the Kirtland's warbler (*Setophaga kirtlandii*; hereafter referred to as "KW"), to near extinction by the mid-1970s (MDNR 2014). Since 1981, land-management agencies have implemented a management program in which a composite land area of *ca* 1,550 hectares (3,800 ac) of high-density jack pine plantations are harvested and re-established as KW habitat annually. This ensures a continuous supply of early-successional forest sufficient for KW population recovery (Kepler et al. 1996, 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 × 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 a fifth 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.

Although these intensively managed stands, which now cover approximately 77,000 hectares, have led to the successful recovery of a critically endangered species, they have dramatically altered the distribution and diversity of forest stands on the landscape (MDNR 2014, Tucker et al. 2016). 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 General Land Office Surveys. The authors found that 30+ years of extensive management had led to significant landscape homogenization over time, with a pronounced reduction in the prevalence of mature stands as well as reductions in other nonjack-pine cover types (Tucker et al. 2016). Thus, in this region, large-scale management for early-successional species of concern has resulted in a reduction in landscape diversity and habitat availability for later-successional species.

Because KW is a conservation-reliant species, continuous management for sufficient early-successional habitat on the landscape is critical to maintain its population (Bocetti et al. 2012). Although these birds cease to inhabit stands >23 years of age, a 50-year commercial harvest rotation was implemented based on the notion that plantations would provide habitat during earlier stages of stand development, and be of merchantable size for commercial cutting at harvest age (Byelich et al. 1985, Meyer 2010). However, it has become apparent that these high-density plantations are not capable of producing merchantable sawlogs as they approach rotation age (J. Hartman, MDNR pers. commun.). We are unaware of any studies in the current literature that address volume accumulation by jack pine in this region of northern Lower Michigan. Given that jack pine planted for KW habitat is planted at a much higher density than what would be practiced in a traditional timber plantation (1.5 m × 1.8 m versus 1.8 m × 2.4 m; Benzie 1977, MDNR 2014), it may be necessary to manage for alternative products, such as biomass or pulpwood, which may allow for a shorter rotation length.

To meet the KW recovery objective of establishing *ca* 1,550 hectares (3,800 ac) of plantations per year, a 50-year rotation requires *ca* 77,500 hectares (191,500 ac) to remain under KW management at any given time (MDNR 2014). Increasing the rate of habitat turnover under a reduced-rotation management scheme could have added benefits of reducing the total land area required to be under KW management. Furthermore, land managers would gain the opportunity to increase rotation lengths, or transition to other cover types, in other areas of the landscape to better emulate historic age class and cover type variability. Assessing the viability of reduced rotations to manage KW plantations for alternative products requires that we first understand aboveground production over time in this novel silvicultural system. Our specific objectives were:

1. To estimate harvestable biomass and pulpwood volumes at different stages of stand development in high-density KW plantations.
2. To determine the 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 reducing rotation lengths in KW plantations on biomass, merchantable volume, and early-successional habitat provisioning over the coming decades.

Methods

Study Area Description

All study sites were located within the KW management areas of northeastern Lower Michigan, USA (Figure 1). 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, we designated three geographic regions of study to analyze whether variations in production could be attributed to variations in soils and climate. The regions selected represent three distinct subsections defined in the Ecosystem Classification of the State of Michigan by Albert (1995): Highplains, Presque Isle, and Arenac.

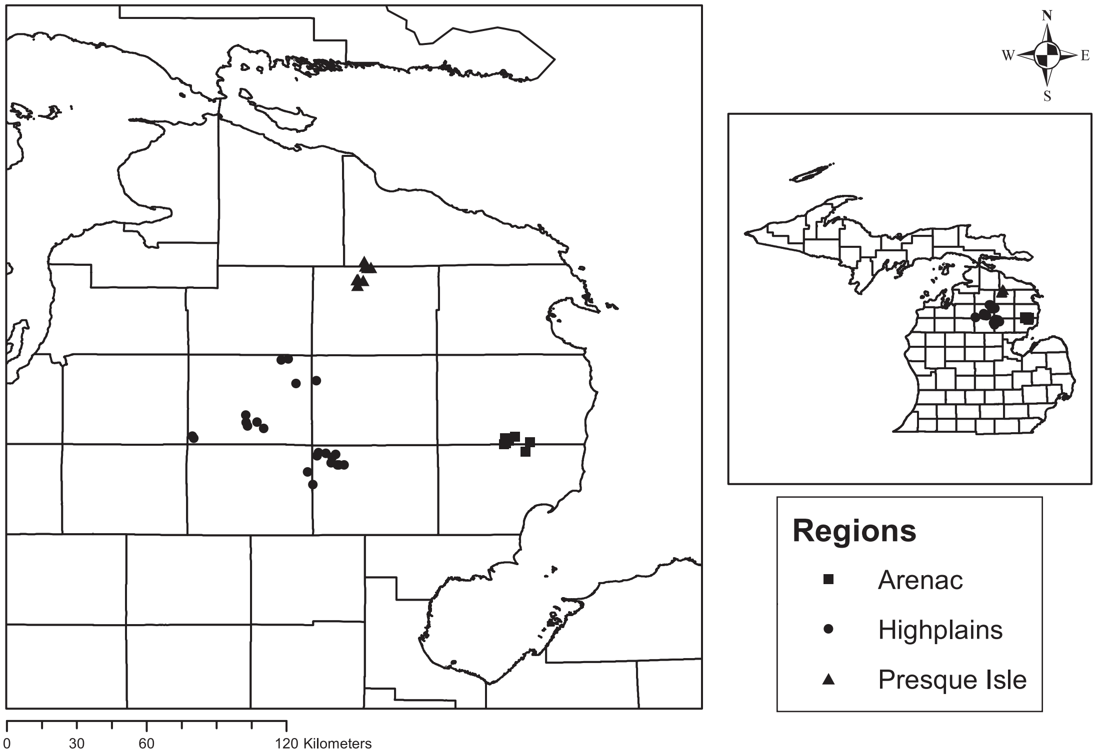

Figure 1. Locations and regions of sampled stands in northern Lower Michigan.

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 to 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 to 130 days (Albert 1995).

In 2015, we established a single chronosequence within each of the three regions, sampling from several plantations (hereafter referred to as "stands") across a range of ages to assess changes in productivity over time. We selected a total of nine stands from the Highplains region, eight stands from the Presque Isle Region, and seven stands from the Arenac region (Table 1). Sampled stand areas ranged from 8.5 to 368.3 hectares. Because large-scale KW habitat establishment began in 1981, few mature high-density plantations were available at the time of sampling, resulting in a limited-age-range data set, which did not exceed 52 years. In 2016, we 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).

Allometric Equation Development

To estimate biomass as a function of stand age, we first developed local allometric equations to predict biomass of individual stems as a function of diameter at breast height (dbh; 1.37 m; 4.5 ft). Because the geography, climate, and silvicultural practices of the KW management system are distinct from traditional jack pine systems, we opted to develop our own allometric equations, as opposed to adopting pre-existing equations from geographically distant areas such as Canada and Minnesota. In 2015, we destructively sampled a total of 26 living stems from a total of 14 stands within two of the selected regions: Highplains and Presque Isle. Stems sampled from the Highplains region ranged in dbh from 0.7 to 22.9 cm (0.3 to 9.0 in.) (0.7, 2.5, 2.7, 5.0, 6.5, 7.6, 8.5, 9.5, 10.7, 12.2, 12.8, 17.7, and 22.9 cm), whereas those harvested from Presque Isle ranged in dbh from 2.0 to 21.5 cm (0.8 to 8.5 in.) (2.0, 3.3, 4.5, 5.0, 5.8, 7.6, 8.2, 10.1, 11.4, 12.3, 16.5, 17.5, and 21.5 cm). Initially, destructive samples were not collected from the Arenac region because stands in this region fall under United States Forest Service (USFS) jurisdiction, and attaining permission to harvest was difficult. Once no significant differences were observed between the Highplains and Presque Isle regions, we elected not to harvest from the Arenac region altogether (analysis described in the following paragraph). In 2016, we destructively sampled eight dead stems from three stands, aged 20, 28, and 41 years, within the Highplains region to develop an allometric equation specific to standing dead trees predicting biomass from diameter. The dbh values for harvested dead stems ranged from 2.4 to 18.47 cm (0.9 to 7.2 in.) (2.4, 4.3, 5.9, 7.2, 8.1, 11.3, 13.2, and 18.4). We did not attempt to sample standing dead trees across a range of decay classes; rather we sampled recently dead trees (bark and fine twigs intact) that were likely to be included in a biomass-harvesting operation.

Harvested stems were cut into 1.22 m (4 ft) vertical sections; branches (including twigs and needles) were then separated from each vertical bole section, and a portable field scale was used to determine the fresh mass of each section's bole and branches. We then collected a subsample of representative branches and a 5–7 cm (2–3 in.) thick stem disc from the bole of each vertical section and recorded their fresh weights in the field. All bole and

Table 1. Stand ages, areas, basal areas, stem densities, and diameters at breast height of sampled stands across the three study regions.

Region	Stand age (years)	Stand area (ac)	Basal area (m^2 ha^{-1})	Stem density (stems ha^{-1})	Mean diameter at breast height (cm)
Arenac	10	230	9.2	3,426	5.7
Arenac	13	266	8.7	3,287	5.6
Arenac	19	316	15.7	3,056	7.7
Arenac	22	215	18.8	3,287	8.3
Arenac	28	177	25.2	3,148	9.9
Arenac	32	124	18.9	2,963	9.1
Arenac	35	186	19.7	3,009	9.7
Arenac mean values (SD)	22.7 (9.45)	216.3 (62.69)	16.6 (5.9)	3,168 (171)	8.0 (1.8)
Highplains	8	518	2.9	3,500	2.9
Highplains	11	553	4.3	3,361	3.8
Highplains	15	330	9.3	4,861	4.7
Highplains	17	386	11.0	3,278	6.4
Highplains	18	301	11.5	3,639	6.0
Highplains	19	280	8.1	3,639	5.1
Highplains	19	910	15.8	2,861	8.0
Highplains	20	137	13.8	2,472	8.1
Highplains	20	310	17.6	3,417	8.2
Highplains	22	118	13.4	3,163	7.3
Highplains	22	198	15.3	2,833	8.1
Highplains	24	275	25.4	3,500	9.7
Highplains	28	70	20.5	2,889	9.7
Highplains	31	91	16.8	1,917	11.8
Highplains	31	104	22.1	2,250	11.6
Highplains	31	188	20.4	3,139	9.5
Highplains	31	115	26.5	2,278	12.5
Highplains	33	124	16.5	2,667	10.5
Highplains	34	76	26.7	2,556	12.1
Highplains	35	237	16.4	3,194	9.4
Highplains	41	175	19.3	2,917	9.9
Highplains	52	183	22.8	2,083	12.8
Highplains mean values (SD)	25.5 (10.27)	258.1 (197.70)	16.2 (6.6)	3,019 (654)	8.5 (2.9)
Presque Isle	7	65	1.0	3,194	1.6
Presque Isle	10	90	4.8	3,972	3.6
Presque Isle	13	162	7.8	4,389	4.5
Presque Isle	16	134	7.8	3,833	4.7
Presque Isle	20	190	12.7	3,417	6.6
Presque Isle	23	38	22.1	3,194	9.1
Presque Isle	30	21	18.0	2,750	9.4
Presque Isle	32	79	18.5	2,833	9.2
Presque Isle mean values (SD)	18.9 (9.08)	97.4 (59.64)	11.6 (7.4)	3,448 (574)	6.1 (2.9)
Mean values across all regions	22.4	190.6	14.8	3,212	7.5

branch subsamples were returned to the lab and dried in a forced-air oven at 65° C (150° F) before recording their dry weights. The dry-mass-to-green-mass proportions were used to calculate the total dry mass of each section, which were then summed to estimate total aboveground biomass of each respective stem. Tree biomass estimates and dbh were log-transformed, and we ran separate linear regressions on transformed live and dead stem data to determine parameters for each respective allometric equation. Log-biomass estimates for live and dead stems were obtained using the common linear function (Picard et al. 2012):

$$\ln(B) \quad = a + [b \times \ln(D)], \qquad (1)$$

where ln(B) is natural log of B, biomass (kg), a is the y-intercept of the regression line, b is the slope, and ln(D) is the natural log of diameter D at breast height (cm). Additionally, ANCOVA was performed on live-stem data to test for statistical differences in the biomass–diameter relation across the two regions sampled (Highplains and Presque Isle). The level of significance set for all statistical analyses was $\alpha = 0.05$.

Stand Inventory

Within each stand, we established between three and five 6 × 12 m (20 × 40 ft) or 0.0072 hectares (0.018 ac) 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, we recorded species, dbh, and status (live or dead). The individual biomass of each living and dead stem was estimated with their respective allometric equation, and these then summed for each plot to estimate plot-level standing biomass. 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 percent of the total habitat land area (MDNR 2014).

To estimate pulpwood volume production over time, we first calculated the volumes of live stems from inventory data using equations and procedures outlined by Hahn (1984). All dead stems were excluded from volume estimates, as they are not considered a source of merchantable timber, and thus their contribution to stand-level pulpwood volume is of little relevance to management decisions. Additionally, merchantable volume was estimated only for stems that met the one-stick minimum size requirement for pulpwood production: 2.44-m (8-ft) pulp stick below a 10.16-cm (4-in.) top. We then summed the merchantable volumes of each stem within a given plot to estimate plot-level volume and averaged the plot-level estimates within each stand to achieve mean stand-level volume estimates. These estimates of merchantable volume per unit area only apply to planted areas of KW habitat and do not account for the approximate 20 percent total land area left unplanted as foraging gaps. Only 20 of the 37 stands had any saw log size trees, and within these 20 stands, saw log volumes were extremely low (mean 1.6 MBF ac^{-1}; median 1.2 MBF ac^{-1}). Therefore, saw log volume was not considered in this study.

Production over Time

For the purposes of this study, stand age refers to the number of years since stand establishment and was acquired from stand inventory GIS databases provided to us by MDNR and USFS. To estimate biomass or merchantable volume as a function of stand age, a nonlinear relation was described using a modification of the Richards logistic function (Richards 1959):

$$B_t \text{ or } V_t = a\left[1 - e^{(-b*t)}\right]^c \tag{2}$$

where B_t represents aboveground biomass (Mg ha^{-1}) for planted areas at time t, V_t represents aboveground pulpwood volume (m^3 ha^{-1}) for planted areas at time t, a represents the potential maximum biomass (Mg ha^{-1}) or pulpwood (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 biomass or pulpwood volume accumulation, and c is a parameter controlling the inflection point of the curve. To test the validity of this function for our data, we compared the mean squared error (MSE) and standard error of the residuals (S) to those produced by fitted linear and logarithmic models produced with the same dataset.

Differences in biomass and pulpwood volume production across regions were estimated by analyzing differences of least-squares means. We obtained parameters for the functional forms of each Richard's 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 merchantable volume data.

Because the age range of our data set was limited to 52 years, we wanted to examine the potential influence of older stands on our production estimates. We repeated the model-fitting processes described above with the addition of data from five older jack pine stands in the region from a prior study (Spaulding and Rothstein 2009). These stands were aged 50, 55, 60, 65, and 69 years. We reran regression analyses on the expanded dataset for linear, logarithmic, and Richards curves, and compared model parameters and statistics of fit to that of our original data set of dedicated KW plantations. The results showed minimal deviations in model parameters and fit statistics with or without including these older stands (see Supplementary Table S1), so we proceed to report results only from our sampled stands. Finally, because our oldest dedicated KW plantation (52 years) was much older than the rest of our stands, we ran our models with and without this stand to assess its potential influence on parameter estimates.

We also explored the potential for covariates to improve our predictions of biomass and volume production in the modified Richard's models. Covariates 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 DI describes the amount of water that a soil supplies to plants 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 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).

We 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}. Soil taxonomic classifications for each plot were obtained from USDA Web Soil Survey data (Soil Survey Staff 2016). These taxonomic classifications were then used to assign appropriate DI and PI values to each plot (Schaetzl et al. 2009; Schaetzl et al. 2012). Within 30 of the 37 stands sampled, DI and PI values did not vary across plots. For the seven stands in which these indices varied across plots, the mode index value was used for analyses. Stand-level DI values ranged from 14 to 35, and stand-level PI values ranged from 4 to 9. We regressed each covariate against the residuals of the biomass and merchantable volume curves to test for statistical significance and whether there was a need to include any in the final growth models. However, none of these regressions yielded statistically significant results for either biomass or merchantable volume growth. Therefore, these covariates were not included in the final model.

Mean Annual Increment and Optimal Rotation Ages

To identify an optimal rotation length for biomass production, we analyzed Mean Annual Increment (MAI) values for biomass and merchantable volume estimates produced by our growth models. 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). We first calculated MAI values for biomass and merchantable volume estimates at each year from 0 to 60 years. We then determined the derivative of the growth function for biomass and merchantable volume, and calculated estimates for these derivative functions at each year from 0 to 60 years. Finally, the MAI curves were plotted against the derivative growth function curves to identify the optimal rotation lengths for biomass or merchantable volume production.

Regional Impact Assessment

Following determination of optimal rotation ages for biomass and merchantable volume production in KW stands, we performed a regional impact assessment to compare three 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. We assessed the potential ecosystem service outputs of each rotation length for a 1,550-hectare (3,800-ac) area over the course of 100 years. A land area of 1,550 hectares (3,800 ac) was selected 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, we 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, the cumulative potential biomass output over a 100-year period, the potential pulpwood volume output per rotation, and the cumulative potential pulpwood volume output over a 100-year period. For this analysis, all potential biomass and pulpwood volume yield outputs were calculated to account for the unplanted foraging gaps that are included in KW plantations, assuming these make up 20 percent of the total land area (MDNR 2014).

Additionally, we calculated the cumulative number of years that the land would provide suitable breeding habitat for KW over a 100-year period. KW nest in stands between the ages of 5 and 23 years (Meyer 2010), so this figure was calculated 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, we 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 1,550 hectares (3,800 ac), as outlined in the KW Breeding Range Conservation Plan (MDNR 2014) by multiplying the rotation length (years) by 1,550 hectares.

Results

Allometric Biomass Equations

ANCOVA of the log-transformed biomass-to-diameter relations of live stems in the Highplains and Presque Isle regions showed no significant difference between the two regions ($P = .097$), 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 percent difference from combined equation estimates in stands older than 20 years (Table 2). Therefore, we 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 × $\ln D$ (cm)]; adjusted $R^2 = .929$; $P < .001$. We compared estimates of biomass produced by this equation to six other pre-existing allometric equations for jack pine derived from areas throughout the northeastern United States and Canada (reported in Ter-Mikaelian and Korzukhin 1997). Differences in estimates between our locally derived equation and nonlocal equations were relatively modest for younger stands, but quite large for older stands. For example, applying nonlocal equations to inventory data from a single 20-year old stand resulted in biomass estimates that were on average 7 percent higher than that produced by our local equation (range = –22 percent to 25 percent). In contrast, application of nonlocal equations to inventory data from the 52-year old stand resulted in biomass estimates that were on average 24 percent higher than that produced by our local equation (range = –13 percent to 40 percent).

Table 2. 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.

	Stand age (years)		
	23	32	41
Combined equation (Mg ha^{-1})	60.6	61.6	64.8
Highplains equation (Mg ha^{-1})	63.5	63.8	66.1
Presque Isle equation (Mg ha^{-1})	58.1	60.6	65.7
Percentage difference, Highplains	–4.6	–3.4	–1.9
Percentage difference, Presque Isle	4.3	1.8	–1.4

Note: Differences between region-specific equation outputs and the combined equation outputs are expressed as percentages. The Arenac region is excluded from this analysis because destructive samples were not collected, and a region-specific allometric equation could not be developed.

To further strengthen the accuracy of plot-, stand-, and landscape-level biomass estimates, we 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 we expected that these stems would contain lower levels of biomass than their live-stem counterparts of equal diameter. The linear regression we 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 × $\ln D$ (cm)]; adjusted $R^2 = .960$; $P < 0.001$.

Production over Time

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

In a comparison between fitted linear, logarithmic, and nonlinear Richards models, MSE and S values indicated that the Richards model performed best for both the biomass and merchantable volume datasets (Table 3). 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} (31.7 US tons ac^{-1}; Figure 2A). The pattern of biomass accrual over time conformed well to the modified Richards function for logistic growth (Richards 1959): B_t (Mg ha^{-1}) = $70.856[1–e^{(–0.118 \times t)}]^{4.201}$; $R^2 = .828$; $P < .001$. Excluding the 52-year-old stand had minimal influence on model output: B_t (Mg ha^{-1}) = $70.826[1–e^{(–0.118 \times t)}]^{4.206}$; $R^2 = .821$; $P < .001$.

To compare the optimal rotation lengths for biomass and pulpwood production in KW stands, we developed a similar growth curve to map pulpwood volume accumulation over time (Figure 2B). The minimum size requirements for

Table 3. Comparison of fitted modified Richard's model with fitted linear and logarithmic models for biomass and volume.

	Equation	Mean squared error	Standard error of the residuals
Biomass models			
Linear	$B_t = 8.59206 + (1.66340 \times t)$	126.33	10.93
Logarithmic	$B_t = –68.8153 + (38.0804 \times \ln t)$	82.66	8.84
Richard's	$B_t = 70.8556 \times [1–e^{(–0.1180 \times t)}]^{4.2010}$	72.93	8.19
Volume models			
Linear	$V_t = –33.16424 + (2.89070 \times t)$	336.81	17.85
Logarithmic	$V_t = –146.8 + (59.3667 \times \ln t)$	398.30	19.41
Richard's	$V_t = 71.1178 \times [1–e^{(–0.3546 \times t)}]^{1,932.7}$	225.40	14.39

Note: Lower statistical values indicate a better model fit.

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} (10.2 CCF ac^{-1}; Figure 2B). Stand-level pulpwood volume was described using a modified Richards function for logistic growth (Richards 1959): V_t (m^3 ha^{-1}) = $71.118(1–e^{(-0.355 \times t)})^{1,932.7}$; R^2 = .817; $P < .001$. Excluding the 52-year-old stand had minimal influence on model output: V_t (m^3 ha^{-1}) = $68.216[1–e^{(-0.402 \times t)}]^{4,981}$; R^2 = .818; $P < .001$. The shape of the curve for stand-level pulpwood volume growth differed greatly from that of biomass production, showing no accumulation until *ca* 20 years after planting. We found that the upper and lower 95 percent confidence limits for the pulpwood volume function indicate a lower precision than that for the biomass regression (Figures 2A and 2B). Model comparisons and fit statistics are shown in Table 3.

Optimal Rotation Ages

We 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 3A). Stands at this age contained an average of 47 Mg ha^{-1} (21 US tons ac^{-1}) of aboveground biomass in planted zones of KW habitat. Additionally, we observed the culmination of MAI for the pulpwood volume curve to occur 28 years after establishment and determined this to be the optimal rotation length to maximize pulpwood yields (Figure 3B). At this age, stands are expected to yield approximately 65 m^3 ha^{-1} (9.3 CCF ac^{-1}) of pulpwood volume in planted areas of KW habitat.

Regional Impact Assessment

We compared the potential ecosystem service outputs that could be provided from 1,550 hectares (3,800 ac) of KW habitat managed under three different rotation scenarios over a 100-year period (Table 4). The three rotation lengths of interest were 20 years

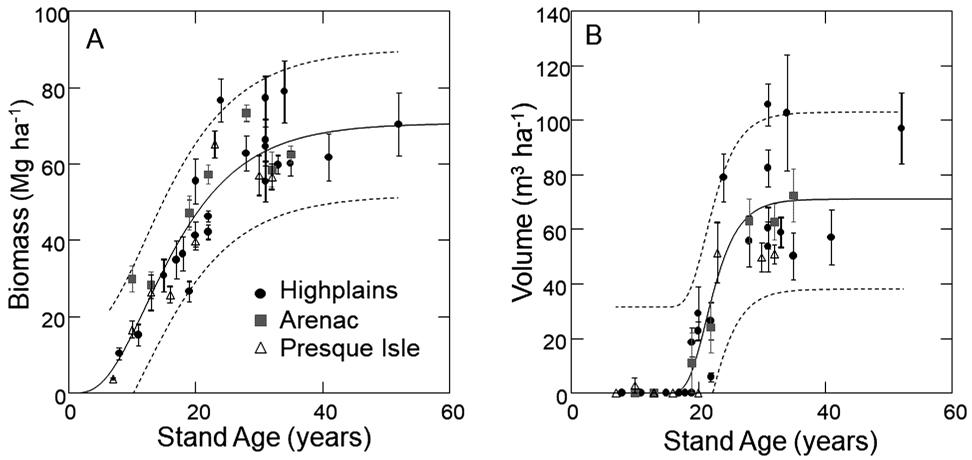

Figure 2. Aboveground dry biomass (A) and merchantable pulpwood volume (B) as a function of stand age. Biomass accounts for both living and standing dead trees. Merchantable pulpwood volume is estimated for all living stems with a minimum 2.44 m length to a 10.16 cm top. Symbols represent stand means (±1 SE). Solid curves represent the nonlinear regression lines described in the text. Dashed lines represent the upper and lower 95 percent confidence limits across the age range of the dataset.

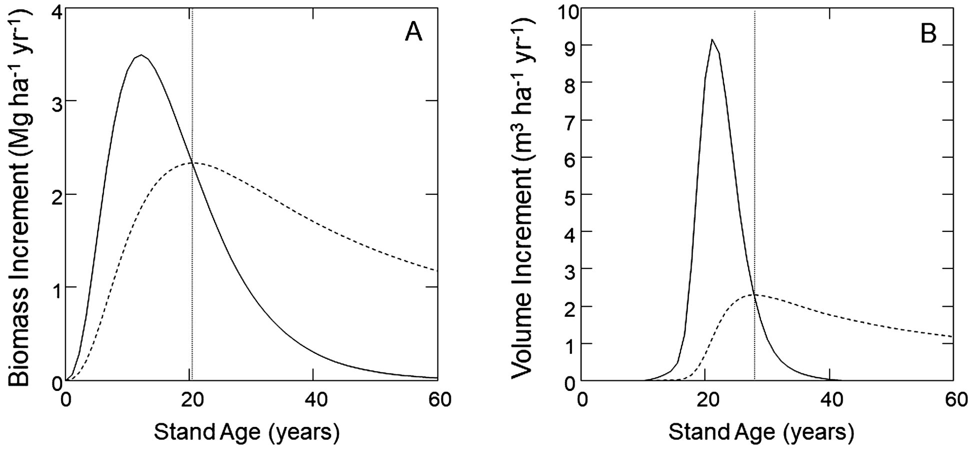

Figure 3. Derivatives of (A) biomass and (B) merchantable pulpwood volume growth curves plotted against their respective MAI curves over time. Solid curves represent the growth curve derivatives, and dashed curves represent MAI over time. Vertical lines represent the stand age at which culmination of MAI occurs, where MAI equals the derivative of the growth function.

Table 4. Potential ecosystem service outputs of 1,550 hectares (3,800 ac) of managed Kirtland's warbler habitat over 100 years, under three different rotation lengths.

	Rotation length (years)		
	20	28	50
No. of rotations per 100 years	5	3	2
Biomass per rotation, Gg (US tons)	58 (63,934)	75 (82,673)	87 (95,901)
Cumulative biomass, Gg 100 year^{-1} (US tons 100 year^{-1})	290 (319,670)	225 (248,020)	174 (191,802)
Volume per rotation, 10^3 m^3 (CCF)	18 (6,356)	80 (28,252)	88 (31,077)
Cumulative volume, 10^3 m^3 100 year^{-1} (CCF 100 year^{-1})	88 (31,077)	241 (85,108)	176 (62,154)
Kirtland's warbler habitat duration, year 100 year^{-1}	80	69	38
Total required habitat area, hectares (ac)	31,000 (76,600)	43,400 (107,250)	77,500 (191,500)

(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). A land area of 1,550 hectares (3,800 ac) was selected 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 four fifths of a 1,550 hectares area (the approximate ratio of planted to unplanted foraging gaps within KW stands), equating to a total planted land area of 1,240 hectares.

Assuming establishment at year zero, management for biomass on a 20-year harvest cycle would undergo five full rotations within a 100-year period, followed by management for pulpwood, which would produce three harvests in this time, whereas management under the BAU rotation of 50 years would only be harvested twice (Table 4). A 20-year rotation would yield the greatest cumulative biomass over 100 years (*ca* 290 Gg or 320,000 US tons) and a 28-year rotation would yield the greatest cumulative pulpwood volume over this period (*ca* 241,000 m^3 or 85,000 CCF). Although management on a 50-year rotation produces the highest biomass and merchantable volume outputs per harvest cycle, cumulative yields over a 100-year period are predicted to be substantially lower than those produced by stands managed on reduced rotations.

For each rotation scenario, we calculated the total number of years that stands would provide 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 for 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, we determined the total land area that would be required under each management scheme to continue harvesting and re-establishing 1,550 hectares (3,800 ac) of KW habitat on an annual basis. The 50-year rotation requires a total of 77,500 hectares (191,500 ac) to be dedicated as KW habitat at any given time, whereas a 28-year rotation would reduce this to 43,400 hectares (107,250 ac). 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 hectares (76,600 ac) of designated habitat required to continue to meet current objectives (Table 4).

Discussion

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 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. 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 other cover types in the region in favor of jack pine, resulting in an estimated 29 percent decrease in red pine (*Pinus resinosa*) cover and a 67 percent reduction in barrens from their pre-European distributions (Tucker et al. 2016). Although the KW recovery effort has proven successful at restoring the endangered KW population, its widespread implementation has reduced landscape diversity, displacing other habitats once prevalent on the landscape.

Our results indicate that a shift to short-rotation management is a potential tool that could be used to maintain KW breeding habitat, while simultaneously maintaining forest product outputs and freeing up land area to diversify forest age classes and cover type composition across the landscape. Because KW habitat provisioning is restricted to young stands between the ages of 5 and 23 years (Meyer 2010), stands managed under the current approach only provide suitable nesting habitat for approximately a third of their 50-year rotation. Our field sampling of dedicated KW plantations demonstrates that biomass increment of these stands peaks at approximately the same time they age out of suitable KW nesting habitat (*ca* 20 year) and pulpwood increment peaks shortly thereafter (*ca* 28 year). If adequate markets for biomass or pulpwood were available regionally, short-rotation management could increase both product output and the rate of habitat turnover.

Our study indicates that optimal rotation lengths for biomass and pulpwood production (20 and 28 years, respectively) are much shorter than the current planned rotation length of 50 years. These results are largely consistent with other studies of stand development in jack pine and related species. Rothstein et al. (2004) studied the loss and recovery of carbon pools following stand-replacing fire in jack pine stands in the same region. They estimated overstory biomass in a chronosequence ranging in age from 1 to 72 years and found that growth over time in this system followed an S-shaped pattern with aboveground biomass increment peaking at 16 years and approaching an asymptotic value of 106 Mg ha^{-1} by age 40. Although their estimate of maximal biomass was higher than our estimate of 71 Mg ha^{-1}, their study used Perala and Alban's (1994) allometric equation to estimate jack pine biomass, which we found could lead to a nearly 40 percent overestimation of stand-level biomass in older KW stands when compared to estimates derived from our locally developed allometric equation.

We are not aware of any studies in the current literature that address volume accumulation by jack pine in northern Lower Michigan. However, several studies of jack pine volume production in Canada are available for comparison. Hébert et al. (2016) compared volume increment rates of individual stems in jack pine plantations of varying densities (1,111 to 4,444 trees ha^{-1}; 450 to 1,800 trees ac^{-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. 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 jack pine stands in Ontario, Canada. In another study in Ontario, Canada, Janas and Brand (1988) found that volume increment in high-density, fire-origin jack pine stands peaked at 18 years, and plantations of 2,200 trees ha^{-1} (890 trees ac^{-1}) peaked at 15 years. Overall, these studies provide strong support for our conclusion that rotation lengths in high-density KW plantations could be substantially reduced to maximize pulpwood volume yields prior to growth stagnation.

Reducing the total land area dedicated to KW habitat with the implementation of short-rotation management would allow for restoration of landscape age distributions and cover types that better emulate historical patterns and distributions. Silvicultural strategies that could be implemented on surplus KW stands include extending rotations to restore historical age class distributions and variability, and converting stands to cover types that are currently underrepresented on the landscape. This ecosystem-based approach should increase biodiversity at the landscape level through provisioning of diverse habitat types, including later-successional forests, which have key habitat features absent in younger stands (Lindenmayer et al. 2006, Franklin et al. 2007).

Furthermore, this mixed-management strategy could have additional benefits in terms of risk mitigation. At the stand level, shortened rotations mitigate risks associated with natural disturbances such as wind storms and insect pests and diseases that affect mature jack pine (Carey 1993, Felton et al. 2015). At the landscape level, increased heterogeneity of species compositions, age distributions, and cover types improves landscape resilience to species-specific pests and diseases, which can be devastating in regions with widespread monoculture plantings (Ennos 2014, Felton et al. 2015).

Prior to implementing shorter rotations in this system, it is important to consider the potential long-term consequences of repeated short-rotation harvests on site productivity and nutrient availability in these sandy, nutrient-poor soils. Several studies have shown that low-fertility sites, such as those used in KW management, are most likely to be negatively impacted by repeated intensive harvesting and associated nutrient removals over the long-term (Blanco et al. 2005, Kaarakka et al. 2014). Rothstein (2018) constructed basic nutrient budgets for jack pine stands in northern Lower Michigan based on literature data on soils and vegetation, combined with deposition data from the National Atmospheric Deposition Program. This work indicated that inputs for nitrogen, phosphorus, calcium, and magnesium were sufficient to balance removals in whole-tree harvesting, even over short rotations. In contrast, they found that it could take 70 years or more for potassium inputs to match removals in whole-tree harvest. Therefore, it would be important to monitor for changes in soil quality and productivity over time in intensively managed KW stands and adjust management accordingly; this could involve fertilization, or alternating harvesting methods and rotation lengths on a given site to balance production with long-term soil sustainability.

Another important caveat to consider in moving to shorter rotations is whether or not markets exist for biomass and small-diameter pulpwood to support this shift in management. Numerous cogeneration plants exist in the core KW habitat region (Leefers 2011), which have used logging residues from KW management for years. Where local capacity exists, land managers are finding it increasingly difficult to make jack pine timber sales with large chipping requirements because of reduced local demand for logging residues as fossil fuel prices have declined (J. Hartman, MDNR pers. commun.). This local experience is supported by academic studies of forest bioenergy markets, which find decreasing fossil fuel prices because of the boom in hydraulic fracking to be a major constraint to market demand for forest bioenergy (Carleton and Becker 2018, Young et al. 2018). Thus, without policy support for forest bioenergy use, a lack of demand for logging residues will likely constrain the implementation of short-rotation biomass harvests for the foreseeable future. Furthermore, demand for KW pulpwood can be affected by wood quality. Moving to shorter rotations will necessarily result in a product with high fractions of bark and branches, a major concern for marketability.

On the other hand, new markets for nontraditional forest products have the potential to support a system managed for maximal pulpwood volume on a *ca* 30-year rotation. The largest continuous particleboard plant in North America was recently constructed in Grayling, MI, in the heart of current KW management areas, providing a new market for small-diameter softwoods that could support new approaches to KW management (ARAUCO 2019). Thus, in the near term, if managers are seeking to shorten rotations on selected KW habitat, moving from a 50-year to 30-year rotation with the goal of providing pulpwood for this new mill appears likely to be the most viable scenario.

Conclusions

Implementation of short-rotation management in jack pine habitat plantations in Michigan's Lower Peninsula has the potential to provide multiple benefits. Reducing rotation lengths in a portion of these stands would expand the diversity of ecosystem services that can be produced from the entire landscape without negatively impacting its ability to provide critical early-successional habitat to 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. Land-management 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 planting. Diversification would also increase habitat variation and availability, improving landscape resilience through the restoration of later-successional forests and currently underrepresented cover types. Finally, moving from a 50-year to 30-year rotation with the goal of providing pulpwood for a new large-scale particleboard plant may be the most viable scenario for shortening rotations.

Supplementary Materials

Supplementary data are available at *Forest Science* online.

Supplement Table S1. Comparison of fitted modified Richard's models for biomass and volume, as well as estimated optimal rotation lengths (ORL), with or without the addition of data from five older stands sampled by Spaulding and Rothstein (2009).

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