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Development and evaluation of an individual tree growth and yield model for the mixed species forest of the Adirondacks Region of New York, USA

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Abstract

Background: Growth and yield models are important tools for forest planning. Due to its geographic location, topology, and history of management, the forests of the Adirondacks Region of New York are unique and complex. However, only a relatively limited number of growth and yield models have been developed and/or can be reasonably extended to this region currently.

Methods: In this analysis, 571 long–term continuous forest inventory plots with a total of 10 – 52 years of measurement data from four experimental forests maintained by the State University of New York College of Environmental Science and Forestry and one nonindustrial private forest were used to develop an individual tree growth model for the primary hardwood and softwood species in the region. Species–specific annualized static and dynamic equations were developed using the available data and the system was evaluated for long–term behavior.

Results: Equivalence tests indicated that the Northeast Variant of the Forest Vegetation Simulator (FVS–NE) was biased in its estimation of tree total and bole height, diameter and height increment, and mortality for most species examined. In contrast, the developed static and annualized dynamic, species–specific equations performed quite well given the underlying variability in the data. Long–term model projections were consistent with the data and suggest a relatively robust system for prediction.

Conclusions: Overall, the developed growth model showed reasonable behavior and is a significant improvement over existing models for the region. The model also highlighted the complexities of forest dynamics in the region and should help improve forest planning efforts there.

Keywords: Individual tree growth model, Mixed species, Forest vegetation simulator

Background

The forests in the Adirondacks Region of New York are a complex mixture of hardwood and softwood species that have a long and varied history of natural disturbance occurrences (Lorimer and White 2003) and human management (McMartin 1994). The region is considered an ecotone at the southernmost end of the eastern forest–boreal ecoregion with over 25 different tree species present and is particularly sensitive to variation in local climate (Beier et al. 2012). Due to variation in elevation and geology, a variety of forest communities occur in this region ranging from high alpine to northern hardwood (Leopold et al. 1988). Historically, research in the region was concentrated on spruce–fir (*Picea – Abies*) with increasing attention on northern hardwoods (Berven et al. 2013). The forest currently faces a number of issues including climate change (Beier et al. 2012), beech bark disease (McGee 2000), high fern cover (Engelman and Nyland 2006), and atmospheric deposition (Chen et al. 2004), which are all likely to affect future stand dynamics and management options. Consequently, there is a strong

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need to understand and project the potential influence of alternative forest management strategies.

Growth and yield models are important tools for effective and sustainable forest management and have a long history of development (Weiskittel et al. 2011a). However, a relatively limited number of growth and yield simulators exist for the Adirondacks Region. Aldridge (1982) developed stand–level basal area and volume projections equations, but they were only applicable to northern hardwood stands in the region. Likewise, Pan and Raynal (1995) presented individual tree volume growth equations for three plantation conifers in the region. Today, the most commonly used models in the region currently are Northeast–TWIGS (NE–TWIGS; Hilt and Teck 1989) and the Northeast variant of the Forest Vegetation Simulator (FVS–NE; Dixon et al. 2007). Recent work has suggested NE–TWIGS and FVS–NE to have some important limitations in the region (Ray et al. 2009). For example, Russell et al. (2013) indicated FVS–NE predictions of total height as well as diameter and height increment were statistically not equivalent for many of the common species in the Adirondacks. Based also on recent US Forest Service Forest Inventory and Analysis (FIA) data, Pandit et al. (2012) also indicated that FVS–NE had biased short–term predictions of stand–level basal area growth in New York, especially in the elm–ash (*Ulmus–Fraxinus*) and oak–hickory (*Quercus–Carya*) forest types.

The goal of this project was to develop an individual–tree growth and yield simulator that is specific to the Adirondacks Region of New York. Specific objectives were to: (1) test the component equations of Northeast (FVS–NE) for bias in the Adirondacks Region; (2) refit component equations (total height, bole height, diameter increment, height increment, and mortality) as necessary; and (3) evaluate and present long–term prediction behavior for forest types common to the region.

Methods

Study area

The Adirondacks Region of New York is located in Upstate New York and is characterized by a unique mountain range that varies in elevation from 350 to over 1500 m. Climate and soil conditions vary dramatically with elevation, but the average monthly summer high and winter low temperatures are 26 and −15 °C, respectively. Total annual precipitation is around 1044 mm with a nearly equal distribution of precipitation during the year (monthly mean ± SD; 87.1 ± 19.3 mm). Soils in the region are generally young, thin, sandy, acidic, and infertile.

Common forest types in the region include black spruce (*Picea mariana* (Miller) B.S.P) – northern white cedar swamps (*Thuja occidentalis* L.), red spruce (*Picea rubens* Sarg.) – balsam fir (*Abies balsamea* L.) flats, red spruce – balsam fir – red maple (*Acer rubrum* L.) – yellow birch (*Betula alleghaniensis* Britton), and sugar maple (*Acer saccharum* Marsh.) – American beech (*Fagus grandifolia* Ehrh.) – yellow birch. Other species present include white spruce (*Picea glauca* (Moench) Voss.), eastern white pine (*Pinus strobus* L.), Norway spruce (*Picea abies* (L.) Karst.), red pine (*Pinus resinosa* Ait.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), paper birch (*Betula papyrifera* Marsh.), gray birch (*Betula populifolia* Marsh.), quaking aspen (*Populus tremuloides* Michx.), bigtooth aspen (*Populus grandidentata* Michx.), black cherry (*Prunus serotina* Ehrh.), northern red oak (*Quercus rubra* L.), and white ash (*Fraxinus americana* L.).

Based on their frequency and occurrence, this analysis focused on the top eight hardwoods (American beech, ash, black cherry, quaking aspen, red maple, red oak, sugar maple, yellow birch) and top six softwoods (balsam fir, eastern hemlock, red pine, spruce, white cedar, white pine). The other species present were grouped into either "other hardwoods" (OH) or "other softwoods" (OS).

Data

The data used in this analysis was obtained from long–term continuous forest inventory (CFI) plots. In addition to the privately owned Shirley Forest (SF), this data included four experimental forests maintained and managed by the State University of New York College of Environmental Science and Forestry (SUNY–ESF), namely Dubuar Memorial Forest (DMF), Huntington Wildlife Forest (HWF), Pack Demonstration Forest (PDF), and Pack Experimental Forest (PEF). Large differences in site quality, based on observed dominant height, are apparent among the experimental forests. For example, Germain et al. (2016) reported white pine site index (dominant/co-dominant height at base age 50 in m) values of 25 and 16 for HWF and PDF respectively. Given differences in location and sampling, each of these forests are described separately below.

Dubuar memorial forest

Dubuar Memorial Forest is a 1068 ha forest in St. Lawrence County and is near Wanakena, NY. In 1982, approximately 72 potential plot locations were selected to be sampled across the entire property with an even distribution between hardwood and softwood forest types. Exact plot locations were referenced to the north–south/east–west grid system already surveyed on the property. The plots have been measured in 1989, 1996, and 2006 with a total of 5765 observations.

Each CFI plot is a fixed–area series of concentric circles including a 0.08 ha (1/5 acre) for sawtimber

[>27.9 cm (>11 in.) DBH for hardwoods and >22.8 cm (>9 in.) DBH for softwoods], a 0.04 ha (1/10 acre) for poletimber [>12.7 cm (>5 in.) DBH], and a 0.001 ha (1/300 acre) for saplings [>2.5 cm (>1 in.) DBH and <12.7 cm (<5 in.) DBH]. Measurement of saplings was only completed in 1982. A subsample of trees were selected for total and bole height measurements. Bole height (BHT) was defined as the distance between a 30 cm stump and either a 10 cm upper–stem diameter outside bark or where the central stem terminates due to forking.

Huntington wildlife forest

Huntington Wildlife Forest is an approximately 6000 ha forest in Essex and Hamilton Counties and near Newcomb, NY. In 1970, 290 plots were established in a systematic grid. The plots have been measured in 1970, 1981, 1991, 2001, and 2011 for a total of 21,170 observations. Each CFI plot is a fixed–area series of concentric circles including a 0.08 ha (1/5 acre) for sawtimber [26.9 cm (>10.6 in.) DBH] and a 0.2 ha (1/20 acre) for poletimber [>11.7 cm (>4.6 in.) DBH and <26.9 cm (<10.6 in.) DBH]. A subsample of trees were selected for total and bole height measurements.

Pack demonstration forest

Pack Demonstration Forest is a 977 ha forest in Warren County near Warrensburg, NY. In 1983, a total of 95 plots were established in a systematic grid. The plots have been measured in 1993 and 2003 for a total of 5795 observations. Each CFI plot is a fixed–area, circular 0.04 ha (1/10 acre) plot with trees >9.1 cm (>3.6 in.) DBH being measured. A subsample of trees were selected for total and bole height measurements.

Pack experimental forest

Pack Experimental Forest is located in St. Lawrence County near Cranberry Lake. In 1989, a total of 27 plots were established in a systematic grid. The plots have been measured in 1989, 1996, and 2006 for a total of 1706 observations. Like Dubuar Memorial Forest, the Pack Experimental Forest uses CFI plots that are a fixed–area series of concentric circles including a 0.08 ha (1/5 acre) for sawtimber [>27.9 cm (>11 in.) DBH for hardwoods and >22.9 cm (>9 in.) DBH for softwoods] and a 0.04 ha (1/10 acre) for poletimber [>12.7 cm (>5 in.) DBH]. A subsample of trees were selected for total and bole height measurements. In contrast to the other experimental forest mentioned above, the Pack Experimental Forest has not received any active forest management in recent decades due to limited access.

Shirley forest

Shirley Forest is a privately owned forest with several locations in Essex County west of Lake Champlain with a total of 93 potential plots established in the 1960s and 1970s. The majority of plots have been measured in 1962/63, 1967/68, 1973/74, 1977/79, 1984/86, 1995/98, 2002/05, and 2011/2014 for a total of 11,060 observations. The circular fixed–area CFI plots were 0.08 ha (1/5 acre) in size and trees with DBH > 12.7 cm (>5 in.) were measured. No height and bole height measurements were taken. SF has received active forest management on a regular basis with harvest operation taking place approximately every 10 to 20 years.

Analysis

All available measurements from the five studied forests not taken after cleaning or harvesting operations were standardized, merged into a common format, and converted to metric units. This resulted in a dataset with 45,496 observations with 16.6% and 15.7% having total and bole height measurements, respectively (Table 1). Table 2 displays the same tree measurement statistics of Table 1 by the key tree species. Missing individual tree total and bole height values were imputed by using a plot– and species–specific mixed–model as outlined by Robinson and Wykoff (2004). Stand– and tree–level attributes were then summarized for each plot and included stem density (TPH, # ha^{-1}), additive stand density index (SDI, # ha^{-1}), quadratic mean diameter (QMD, cm), total basal area (BA, $m^2 \cdot ha^{-1}$), basal area in larger trees (BAL, $m^2 \cdot ha^{-1}$), and percent basal area in hardwood species (PBAHW, %) (Table 3).

Since tree age measurements were not available, climate site index (CSI, m) of Weiskittel et al. (2011b) was used in place of traditional site index, which is similar to the Acadian variant of FVS (Weiskittel et al. 2012). CSI is a base–age 50 years estimate of site index based on downscaled climate variables (http://forest.moscowfsl.wsu.edu/climate/) and a random forest nonparametric regression model built on field–observed values (Table 3). The general approach to model and derive CSI has been described in detail previously (Jiang et al. 2015). Since FVS–NE requires traditional site index, it was assumed that CSI was an equivalent estimate for the fastest–growing species on the plot. FVS–NE then uses the estimate for the fastest–growing species on the plot to convert to species–specific values based on nine species groups (Dixon et al. 2007).

To evaluate the suitability of FVS–NE component equations, an equivalence test (Robinson and Froese 2004) with 15% allowable error was conducted.

Table 1 Individual tree attributes by forest, which are Dubuar Memorial Forest (DMF), Huntington Wildlife Forest (HWF), Pack Demonstration Forest (PDF), Pack Experimental Forest (PEF), and Shirley Forest (SF)

Attribute[a]	N	Mean	SD	Minimum	Maximum
Dubuar Memorial Forest (DMF)					
DBH	5765	28.39	9.76	12.70	79.76
HT	1058	21.22	4.95	3.96	36.58
BHT	1053	15.23	5.08	1.83	30.18
ΔDBH	2423	0.24	0.16	0	1.02
ΔHT	435	0.19	0.18	0	0.98
PS	2831	87.35	13.00	21.43	100.00
Huntington Wildlife Forest (HWF)					
DBH	21170	31.62	13.97	11.18	100.84
HT	4302	21.45	5.01	1.52	38.10
BHT	3938	15.42	4.98	1.52	29.57
ΔDBH	11357	0.28	0.17	0	1.27
ΔHT	1827	0.18	0.15	0	0.91
PS	13167	88.05	11.53	0	100.00
Pack Demonstration Forest (PDF)					
DBH	5795	21.17	11.64	9.14	88.39
HT	869	20.08	6.15	5.49	37.80
BHT	851	13.83	6.34	2.44	30.18
ΔDBH	2083	0.18	0.13	0	0.99
ΔHT	327	0.17	0.14	0	0.82
PS	2422	88.62	8.43	61.73	100.00
Pack Experimental Forest (PEF)					
DBH	1706	29.12	11.61	12.70	80.01
HT	359	21.49	3.62	10.97	31.09
BHT	359	14.79	3.52	3.96	25.60
ΔDBH	803	0.26	0.15	0	1.12
ΔHT	147	0.24	0.24	0	0.96
PS	1037	80.12	12.08	40.00	100.00
Shirley Forest (SF)					
DBH	11060	23.94	9.47	9.40	95.50
ΔDBH	8772	0.31	0.24	0	1.49
PS	9334	94.72	11.80	0	100.00
Overall					
DBH	45496	27.92	12.77	9.14	100.84
HT	7557	21.17	5.24	1.52	38.10
BHT	7150	14.63	5.27	1.22	30.18
ΔDBH	25438	0.28	0.19	0	1.49
ΔHT	2736	0.18	0.16	0	0.98
PS	28791	89.17	12.01	0	100.00

[a]*DBH* is diameter at breast height (cm), *HT* is total height (m), *BHT* is bole height (m), *ΔDBH* is annual diameter increment (cm yr^{-1}), *ΔHT* is annual height increment (m yr^{-1}), and *PS* is probability of survival (here percentage of live trees per plot by measurement period, %)

Equations were then fit to the Adirondacks data and included individual tree total and bole height, diameter and height increment, and mortality. Each of these equations was fit to the primary species using nonlinear mixed effects modeling (NLME) with each forest being treated as random (Pinheiro et al. 2016). Extending the random effects structure by including plots and trees did not improve prediction accuracy. The specific equations are further described separately below. All analyses were conducted using the programming software R version 3.3.1 (R Core Team 2016).

The primary species included in this analysis were American beech (AB), ashes (AS, including white and black ash (*Fraxinus nigra* Marshall)), black cherry (BC), balsam fir (BF), eastern hemlock (EH), quaking aspen (QA), red maple (RM), red pine (RN), red oak (RO), sugar maple (SM), spruces (SP, including black, red, and white spruce), northern white cedar (WC), white pine (WP), yellow birch (YB, also including river birch (*Betula nigra* L.)), other hardwood species (OH), and other softwood species (OS). However, species specific equations could not be derived for all attributes.

Total height

Based on the findings of Rijal et al. (2012b), a modified Chapman–Richards equation form was used for the prediction and imputation of total tree height (HT, m):

$$\mathrm{HT} = b_{10}\cdot(1-\exp(-b_{11}\cdot\mathrm{DBH}))^{(b_{12}+b_{13}\cdot\ln(\mathrm{BA}+1)+b_{14}\cdot\ln(\mathrm{BAL}+1))} \quad (1)$$

where DBH is diameter at breast height (cm), BA is total basal area ($m^2 \cdot ha^{-1}$), and BAL is the basal area in larger trees ($m^2 \cdot ha^{-1}$). Unlike Rijal et al. (2012b), climate site index was not found to be a significant predictor in preliminary analysis. In addition, an additive term (e.g. 1.3 m) for when DBH is equal to zero was not included as prior work has suggested that this constraint may cause poorer model performance across the full range of DBH (Newton and Amponsah 2007).

Bole height

Although Rijal et al. (2012a) modeled height to crown base and our Adirondacks data contained measurements of bole height (defined as the first live branch or a 10.2 cm (4 in) top), its applicability was still tested. However, rather than using a modified Chapman–Richards equation form similar to Rijal et al. (2012a), a modified logistic similar to Hann et al. (2003) was used for the prediction and imputation of bole height (BHT, m):

Table 2 Tree–level attributes by species examined in this analysis

Attribute[a]	N	Mean	SD	Minimum	Maximum
American beech (AB)					
DBH	6350	25.11	10.13	9.14	69.85
HT	928	18.48	4.44	2.44	32.00
BHT	840	11.50	4.43	1.52	26.52
ΔDBH	2974	0.30	0.16	0	1.04
ΔHT	331	0.23	0.19	0	0.91
Ash (AS)					
DBH	883	27.41	12.76	9.14	81.28
HT	263	22.67	5.17	6.40	33.53
BHT	250	14.31	5.52	1.83	28.35
ΔDBH	521	0.30	0.21	0	0.89
ΔHT	60	0.22	0.17	0	0.70
Black cherry (BC)					
DBH	666	28.70	12.65	9.14	80.01
HT	212	20.05	5.12	7.62	29.26
BHT	206	13.22	4.95	2.74	23.47
ΔHT	58	0.16	0.15	0	0.61
Balsam fir (BF)					
DBH	945	21.74	8.31	9.14	55.12
HT	131	17.12	5.36	5.18	28.65
BHT	121	11.43	5.87	1.83	21.64
ΔDBH	365	0.31	0.20	0	1.14
ΔHT	30	0.29	0.17	0	0.82
Eastern hemlock (EH)					
DBH	4180	28.70	13.72	9.14	95.76
HT	635	19.59	5.06	5.49	34.14
BHT	605	14.92	5.22	1.22	28.65
ΔDBH	2750	0.30	0.17	0	1.02
ΔHT	308	0.17	0.14	0	0.67
Other hardwoods (OH)					
DBH	3112	22.37	9.30	9.14	72.39
HT	309	19.39	5.95	4.57	33.53
BHT	297	12.41	5.68	1.22	26.21
ΔDBH	2145	0.23	0.18	0	1.02
ΔHT	48	0.22	0.19	0	0.74
Other softwoods (OS)					
DBH	1281	26.94	8.53	9.14	58.67
HT	440	21.47	5.39	5.49	36.58
BHT	431	13.90	4.73	2.44	24.99
ΔDBH	456	0.23	0.14	0	0.83
ΔHT	87	0.20	0.16	0	0.76
Quaking aspen (AS)					
DBH	792	24.35	9.96	9.14	65.53
ΔDBH	455	0.36	0.23	0	1.14
ΔHT	14	0.21	0.23	0	0.64

Table 2 Tree–level attributes by species examined in this analysis *(Continued)*

Red maple (RM)					
DBH	4549	28.24	10.63	9.14	72.90
HT	827	21.39	4.14	1.52	30.18
BHT	783	14.42	4.13	1.52	24.99
ΔDBH	2502	0.25	0.15	0	0.62
ΔHT	304	0.19	0.19	0	0.96
Red pine (RN)					
DBH	1693	28.75	9.71	9.14	61.47
HT	313	23.00	4.05	9.75	35.05
BHT	310	17.47	4.53	2.44	28.65
ΔDBH	822	0.20	0.13	0	0.81
ΔHT	122	0.21	0.17	0	0.98
Red oak (RO)					
DBH	907	25.14	9.30	9.14	73.41
ΔDBH	478	0.35	0.23	0	1.30
ΔHT	35	0.13	0.14	0	0.46
Sugar maple (SM)					
DBH	6289	33.44	16.01	9.14	94.23
HT	1672	23.40	4.72	7.62	38.10
BHT	1604	16.09	5.04	2.13	28.35
ΔDBH	3799	0.26	0.17	0	1.27
ΔHT	592	0.16	0.15	0	0.83
Spruce (SP)					
DBH	3051	25.73	10.99	9.14	64.01
HT	498	18.96	5.69	4.27	32.61
BHT	443	14.88	5.66	1.52	28.04
ΔDBH	1499	0.18	0.12	0	0.53
ΔHT	203	0.14	0.13	0	0.52
White cedar (WC)					
DBH	423	28.28	8.31	11.68	56.13
ΔDBH	332	0.17	0.12	0	0.72
ΔHT	12	0.19	0.13	0	0.49
White pine (WP)					
DBH	5790	27.07	13.52	9.14	95.50
HT	340	23.25	7.18	5.79	37.80
BHT	329	17.98	7.11	2.44	30.18
ΔDBH	3754	0.38	0.27	0	1.49
ΔHT	122	0.21	0.17	0	0.65
Yellow birch (YB)					
DBH	4585	31.88	14.15	9.14	100.84
HT	989	21.37	4.18	7.62	34.14
BHT	931	14.52	4.29	2.13	25.60
ΔDBH	2586	0.25	0.17	0	1.27
ΔHT	412	0.16	0.15	0	0.64

[a]*DBH* is diameter at breast height (cm), *HT* is total height (m), *BHT* is bole height (m), *ΔDBH* is annual diameter increment (cm yr^{-1}), and *ΔHT* is annual height increment (m yr^{-1}), see Table 8 for probability of survival (PS, %)

$$\mathrm{BHT} = \frac{\mathrm{HT}}{\left(1 + \exp\left(\begin{array}{c} b_{20} + b_{21}\cdot\mathrm{HT} + b_{22}\cdot\ln(\mathrm{BAL}+0.1) + b_{23}\cdot\ln(\mathrm{BA}) + \\ b_{24}\cdot\ln\left(\frac{\mathrm{DBH}}{\mathrm{HT}}\right) + b_{25}\cdot\mathrm{CSI} \end{array}\right)\right)} \quad (2)$$

where CSI is climate site index (m), and all other variables are defined above.

Diameter increment

A variety of model forms and potential covariates were tested for individual tree diameter increment predictions, but it was found that it was best modeled using an equation form similar to Hann et al. (2003):

$$\Delta\mathrm{DBH} = \exp\left(\begin{array}{c} b_{30} + b_{31}\cdot\ln(\mathrm{DBH}) + b_{32}\cdot\mathrm{DBH} + b_{33}\cdot(\mathrm{BAL}) + \\ b_{34}\cdot\sqrt{\mathrm{BA}} + b_{35}\cdot\mathrm{CSI} \end{array}\right) \quad (3)$$

where ΔDBH is the annual diameter increment ($\mathrm{cm}\cdot\mathrm{yr}^{-1}$) and all other variables have been defined above. Preliminary analysis indicated that neither bole nor crown ratio (CR, (HT−BHT)/HT) were effective predictors. In addition, variables expressing species composition such as PBAHW and relative density (Stout and Nyland 1986; Woodall et al. 2005) were not found to be influential.

Since annual parameters were desired but the observed variables were on longer growth intervals (2–17 years) parameters were annualized using an iterative technique of Weiskittel et al. (2007). Based on Cao (2000) the right side of the equation was a function which summed the estimated annual ΔDBH estimates over the number of growing seasons during the observed growth period using the updated parameter estimates from the NLME optimization algorithms. For each growing season during the growth period, DBH was subsequently updated, while BAL and BA were linearly interpolated between their beginning values and ending values. Final equations were fitted using initial parameter estimates derived using non–linear least square modeling and assuming SI was constant over time. Although this assumption of linear growth is likely too simplified for highly irregular and longer remeasurement intervals (>10 years), the iterative approach used in this analysis does produce model behavior similar to a more sophisticated optimization approach and is more effective than using the remeasurement interval as a covariate (e.g. Juma et al. 2014).

Height increment

A variety of height increment models including the one used in FVS–NE and those presented in Russell et al. (2014) were tested. The following form was shown to perform best:

$$\Delta\mathrm{HT} = \exp\left(\begin{array}{c} b_{40} + b_{41}\cdot\mathrm{HT} + b_{42}\cdot\ln(\mathrm{HT}) + b_{43}\cdot\left(\frac{\mathrm{DBH}}{\mathrm{HT}}\right) + \\ b_{44}\cdot(\mathrm{BAL}) + b_{45}\cdot\mathrm{BA} + b_{46}\cdot\ln(\mathrm{BA}) \end{array}\right) \quad (4)$$

where ΔHT is the annual height increment ($\mathrm{m}\cdot\mathrm{yr}^{-1}$) and all other variables have been defined above. Like diameter increment, the parameters were annualized using an iterative technique of Weiskittel et al. (2007). Initially, the model was fit for each species individually. However, no or poor model convergence resulted, likely because of small sample sizes for most species and high variability (Table 2). Instead, the model was fit by treating b_{40} and b_{41} as random parameters that varied by species similar to the approach outlined in Russell et al. (2014). CSI and variables describing species composition were not found to be significant predictors.

Mortality

A logistic function was used to model the probability of individual tree survival:

$$PS = \left(1 + \exp\left(-\left(\begin{array}{c} b_{50} + b_{51}\cdot\mathrm{DBH} + b_{52}\cdot\ln(\mathrm{DBH}) + b_{53}\cdot\mathrm{CR} + b_{54}\cdot\mathrm{BAL} + \\ b_{55}\cdot\sqrt{\mathrm{BA}} + b_{56}\cdot\mathrm{CSI} \end{array}\right)\right)\right)^{-1} \quad (5)$$

where PS is the probability of annual survival and all other variables have been defined above. The parameters were annualized using an iterative technique of Weiskittel et al. (2007).

Evaluation

For all developed equations presented above, biological consistency with expectation, parameter significance, sign, and magnitude as well as degree of multicollinearity were evaluated. Equation fit statistics assessed were mean bias (MB; observed – predicted) and root mean square error (RMSE). MB and RMSE were computed using the fixed–effects only. For the mortality equation, a receiver operator curve (ROC) was constructed and area under the curve (AUC) computed (Hein and Weiskittel 2010). To determine the optimal cutpoint for the species–specific survival equations (Rota and Antolini 2014), the function 'coords' of the R package 'pROC' was used (Robin et al. 2011).

Table 3 Key plot– and tree–level attributes by forest

Attribute[a]	N	Mean	SD	Minimum	Maximum
Dunbar Memorial Forest (DMF)					
TPH	197	496.3	253.0	37.1	1779.2
SDI	197	540.4	243.1	26.9	1211.5
QMD	197	29.3	5.9	13.1	46.4
BA	197	29.4	13.8	1.1	70.6
BAL	197	17.1	8.2	0.3	42.8
PBAHW	197	56.4	44.6	0	100.0
CSI	72	17.2	0.3	16.4	18.1
Huntington Wildlife Forest (HWF)					
TPH	1207	447.0	238.8	12.4	1803.9
SDI	1207	466.9	183.0	14.3	1090.5
QMD	1207	34.3	7.0	11.7	67.8
BA	1207	26.2	10.6	0.5	67.4
BAL	1207	14.9	6.6	0	41.8
PBAHW	1207	79.5	27.0	0	100.0
CSI	281	16.9	0.5	15.6	18.7
Pack Demonstration Forest (PDF)					
TPH	171	837.4	381.4	24.7	2223.9
SDI	171	710.0	255.2	11.2	1346.5
QMD	171	24.6	5.7	14.1	44.8
BA	171	38.4	15.3	0.5	89.6
BAL	171	27.7	11.5	0	66.0
PBAHW	171	34.4	31.6	0	100.0
CSI	77	17.3	0.5	16.4	18.3
Pack Experimental Forest (PEF)					
TPH	74	413.6	121.2	160.6	741.3
SDI	74	465.5	99.2	269.1	695.8
QMD	74	31.6	4.8	23.9	48.8
BA	74	25.9	6.1	15.5	43.6
BAL	74	15.5	4.2	8.6	29.8
PBAHW	74	94.5	20.0	0	100.0
CSI	25	17.0	0.3	16.3	17.5
Shirley Forest (SF)					
TPH	328	416.6	214.3	37.1	1630.9
SDI	328	405.9	172.4	18.9	1074.4
QMD	328	26.1	4.7	15.8	40.4
BA	328	21.7	9.8	0.8	51.8
BAL	328	14.2	6.5	0.3	36.0
PBAHW	328	46.2	33.9	0	100.0
CSI	93	17.6	1.4	15.7	20.3

[a]*TPH* is trees per ha (# ha^{-1}), *SDI* is stand density index (# ha^{-1}), *QMD* is quadratic mean diameter (cm), *BA* is total stand basal area (m^2 ha^{-1}), *BAL* is basal area in larger trees (m^2 ha^{-1}), *PBAHW* is the percent basal area in hardwood species (%), and *CSI* is the climate site index (m)

Simulations

To evaluate the long–term behavior of the equations, a simulation model was constructed by linking all of the component equations and using them to project each plot from its initial to final measurement. Missing total tree heights at the start of each plot specific simulation run were predicted using Eq. [1], while subsequent height growth was predicted with Eq. [4]. Due to its importance on long–term simulations, the prediction of tree mortality was handled in two ways, namely an expansion factor method and a fixed cutpoint (Weiskittel et al. 2011a). In the expansion factor method, the tree's expansion factor was annually multiplied by the probability of survival (Eq. [5]), while in the fixed cutpoint method an entire tree record was killed if the probability of survival exceeded the optimal cutpoint derived from the species specific survival equations. Plots that were harvested or showed signs of either excessive mortality (>20% of total basal area) or excessive ingrowth (≥5 trees) were included up until the occurrence of the event. MB and RMSE were computed for key stand–level attributes like stem density and basal area. Finally, some common forest types in the region were projected for 50 years assuming similar initial starting conditions.

Results

Total height

A total of 7575 observations were available for the total height equation with most of the observations being sugar maple (22.1%), yellow birch (13.1%), American beech (12.3%), and red maple (10.9%). For most species, an equivalence test suggested that the observed values and the predicted values from FVS–NE were not statistically different at the 15% levels of allowable error (Table 4). Species–specific equations were developed and resulted in RMSE between 2.5 to 4.5 m. For a given set of covariates, sugar maple had the greatest total height, while eastern hemlock had the smallest (Fig. 1).

Bole height

A total of 7150 observations were available for the bole height equation with most of the observations being sugar maple (22.4%), yellow birch (13.0%), American beech (11.7%), and red maple (11.0%). For all species, an equivalence test suggested that the observed values and those predicted by FVS–NE were statistically different at the 15% levels of allowable error (Table 5). Species–specific equations were developed and resulted in RMSE between 1.6 to 3.8 m. For a given set of covariates, sugar maple and white pine showed the highest bole height for the majority of DBH range examined, while eastern hemlock showed the lowest (Fig. 1).

Table 4 Results of the equivalence test of the Northeast (NE) Variant of FVS for total height (m) and the parameter estimates and fit statistics for Eq. [1]. Mean bias (MB; observed – predicted) and root mean square error (RMSE) were computed using the fixed effects only. Both mean difference and MB were computed as observed – predicted. The null hypothesis for the equivalence test is that $\mu_1 \neq \mu_2$

SPP[a]	N	FVS–NE		Equation [1]						
		Mean ± SE difference (m)	Result of equivalence test	b_{10}	b_{11}	b_{12}	b_{13}	b_{14}	MB (m)	RMSE (m)
AB	928	−0.45 ± 0.11	rejected	33.6020	0.0201	1.0584	−0.0498	−0.0889	0.0009	2.9021
AS	263	3.33 ± 0.21	not rejected	42.0612	0.0093	0.7372	−0.0916	–	0.0011	2.8813
BC	212	2.00 ± 0.26	rejected	30.2327	0.0243	1.4215	−0.2522	–	0.0814	2.6475
BF	131	1.33 ± 0.27	rejected	42.0696	0.0121	0.8860	−0.0720	–	0.0011	2.8830
EH	635	−1.43 ± 0.12	rejected	48.0279	0.0117	1.2979	−0.0981	−0.0429	−0.4499	2.7909
OH	309	0.23 ± 0.22	rejected	35.4457	0.0242	1.0128	–	−0.0755	0.1742	3.7033
OS	440	2.82 ± 0.22	not rejected	26.1875	0.0819	3.5310	–	−0.3375	0.7962	4.5155
RM	827	2.49 ± 0.11	rejected	29.9463	0.0331	1.2740	−0.0892	−0.0878	−0.0496	2.7841
RN	313	4.19 ± 0.16	not rejected	29.9419	0.0752	3.5272	–	−0.5136	−0.4386	2.7722
SM	1672	2.21 ± 0.08	rejected	38.0384	0.0211	1.0325	−0.0544	−0.0639	−1.0922	2.9732
SP	498	0.36 ± 0.13	rejected	42.3324	0.0217	1.4738	−0.0453	−0.1076	−0.4566	2.5105
WP	340	1.85 ± 0.20	rejected	37.7213	0.0289	1.8887	−0.1368	−0.1392	0.3715	3.1214
YB	989	0.58 ± 0.10	rejected	29.5755	0.0286	1.0028	−0.0299	−0.0886	0.0001	2.7534

[a]*SPP* Species are *AB* American beech, *AS* ash, *BF* balsam fir, *EH* eastern hemlock, *OH* other hardwoods, *OS* other softwoods, *RM* red maple, *RN* red pine, *SM* sugar maple, *SP* spruce, *WP* white pine, and *YB* yellow birch

Diameter increment

A total of 25,438 observations were available for the diameter increment equation with most of the observations being sugar maple (14.9%), white pine (14.8%), American beech (11.7%), and yellow birch (10.2%). An equivalence test suggested that for all species, the observed values and the predicted values from FVS–NE were statistically different at the 15% levels of allowable error (Table 6). Species–specific equations were developed and resulted in RMSE between 0.11 and 0.22 $cm \cdot yr^{-1}$. For a given set of covariates, red maple and American beech showed the greatest diameter

Table 5 Results of the equivalence test Northeast (NE) Variant of FVS for bole height (m) and the parameter estimates and fit statistics for Eq. [2]. Mean bias (MB; observed – predicted) and root mean square error (RMSE) were computed using the fixed effects only. Both mean difference and MB were computed as observed – predicted. The null hypothesis for the equivalence test is that $\mu_1 \neq \mu_2$

SPP[a]	N	FVS–NE		Equation [2]							
		Mean ± SE difference (m)	Result of equivalence test	b_{20}	b_{21}	b_{22}	b_{23}	b_{24}	b_{25}	MB (m)	RMSE (m)
AB	840	4.93 ± 0.13	not rejected	−1.3767	−0.0613	−0.0408	–	−1.2310	0.9215	−0.0268	1.8829
AS	250	2.70 ± 0.27	not rejected	−4.5957	−0.0449	–	–	−0.2274	1.7595	−0.0026	2.5730
BC	206	2.93 ± 0.25	not rejected	−7.2046	−0.0490	–	–	−0.2216	2.6474	0.0077	2.2417
BF	121	6.03 ± 0.45	not rejected	−5.7095	−0.0991	–	–	−1.1598	2.5493	−0.0657	1.8356
EH	605	8.48 ± 0.16	not rejected	−12.3299	−0.0654	−0.0418	–	−1.1709	4.7187	−0.0341	1.6112
OH	297	3.15 ± 0.23	not rejected	−2.1695	−0.0546	–	−0.1961	−0.5721	1.2364	−0.1407	1.9742
OS	431	5.03 ± 0.18	not rejected	0.0110	−0.0160	−0.0184	−0.1176	–	–	−1.0851	3.8629
RM	783	5.27 ± 0.10	not rejected	0.7482	−0.0322	–	−0.1254	−0.4321	–	0.7071	2.1710
RN	310	9.04 ± 0.22	not rejected	0.0821	−0.0206	–	−0.1456	−0.4580	–	0.3897	2.1899
SM	1604	5.11 ± 0.09	not rejected	−2.1520	−0.0229	–	−0.0701	−0.2583	0.8273	0.4317	2.5170
SP	443	8.85 ± 0.21	not rejected	0.8253	−0.0604	−0.0350	–	−1.1086	–	0.6008	1.6807
WP	329	8.98 ± 0.29	not rejected	−4.3500	−0.0437	−0.0279	–	−0.7877	1.6198	−0.0769	1.6524
YB	931	4.48 ± 0.09	not rejected	−1.2995	−0.0442	−0.0316	−0.0660	−0.8534	0.8015	−0.0228	1.7532

[a]*SPP* Species are *AB* American beech, *AS* ash, *BF* balsam fir, *EH* eastern hemlock, *OH* other hardwoods, *OS* other softwoods, *RM* red maple, *RN* red pine, *SM* sugar maple, *SP* spruce (SP), *WP* white pine, and *YB* yellow birch

Table 6 Results of the equivalence test of Northeast Variant (NE) of FVS for diameter increment (cm yr^{-1}) and the parameter estimates and fit statistics for Eq. [3]. Mean bias (MB; observed – predicted) and root mean square error (RMSE) were computed using the fixed effects only. Both mean difference and MB were computed as observed – predicted. The null hypothesis for the equivalence test is that $\mu_1 \neq \mu_2$

SPP[a]	N	FVS–NE		Equation [3]							
		Mean ± SE difference (m)	Result of equivalence test	b_{30}	b_{31}	b_{32}	b_{33}	b_{34}	b_{35}	MB (cm)	RMSE (cm)
AB	2974	0.23 ± 0.003	not rejected	−3.4430	1.4219	−0.0727	−0.0250	–	–	−0.0054	0.1508
AS	521	0.20 ± 0.009	not rejected	−6.1840	0.0195	−0.0020	−0.0211	–	1.800	0.0339	0.2030
BF	365	0.23 ± 0.010	not rejected	−2.5924	1.2056	−0.0556	−0.0064	−0.2013	–	0.0488	0.1972
EH	2750	0.19 ± 0.003	not rejected	−1.7508	0.5775	−0.0113	−0.0057	−0.1795	–	0.0126	0.1437
OH	2145	0.12 ± 0.004	not rejected	−1.5197	0.3231	−0.0225	−0.0286	–	–	−0.0048	0.1685
OS	456	0.16 ± 0.007	not rejected	−3.4203	1.0599	−0.0301	−0.0183	−0.0541	–	−0.0060	0.1234
QA	455	0.21 ± 0.011	not rejected	−2.3591	1.0659	−0.0653	−0.0469	–	–	0.0239	0.2122
RM	2502	0.18 ± 0.003	not rejected	−4.1465	0.2889	−0.0148	−0.0156	–	0.8415	0.0157	0.1445
RN	822	0.09 ± 0.005	not rejected	−7.6829	2.7843	−0.1017	−0.0210	–	–	0.0359	0.1259
RO	478	0.24 ± 0.011	not rejected	−2.3680	0.8776	−0.0537	−0.0159	–	–	0.0356	0.2218
SM	3799	0.19 ± 0.003	not rejected	−2.6059	0.4614	−0.0176	−0.0156	−0.1351	0.3294	0.0411	0.1616
SP	1499	0.11 ± 0.003	not rejected	−4.5654	0.3646	−0.0098	−0.0258	–	0.7272	0.0482	0.1259
WC	332	0.10 ± 0.007	not rejected	−2.8205	0.4290	−0.0042	−0.0111	–	–	0.0011	0.1108
WP	3754	0.25 ± 0.004	not rejected	−4.5354	0.9649	−0.0208	−0.0230	−0.0986	0.6226	0.0237	0.2197
YB	2586	0.11 ± 0.003	not rejected	−1.0956	0.4043	−0.0186	−0.0123	−0.1808	–	0.0043	0.1595

[a]*SPP* Species are *AB* American beech, *AS* ash, *BF* balsam fir, *EH* eastern hemlock, *OH* other hardwoods, *OS* other softwoods, *QA* quaking aspen, *RM* red maple, *RN* red pine, *RO* red oak, *SM* sugar maple, *SP* spruce, *WC* white cedar, *WP* white pine, and *YB* yellow birch

Table 7 Results of the equivalence test of the Northeast (NE) variants of FVS for height increment and the parameter estimates and fit statistics for Eq. [4]. Mean bias (MB; observed – predicted) and root mean square error (RMSE) by species are presented. Both mean difference and MB were computed as observed – predicted. The null hypothesis for the equivalence test is that $\mu_1 \neq \mu_2$. Columns marked with an asterisk (*) were those that were treated as a random effect and presented as the fixed + species random effect

SPP[a]	N	FVS–NE		Equation [4]								
		Mean ± SE difference (m)	Result of equivalence test	b_{40}*	b_{41}*	b_{42}	b_{43}	b_{44}	b_{45}	b_{46}	MB (m)	RMSE (m)
AB	331	0.059 ± 0.010	not rejected	−2.0016	−0.1519	0.8261	−0.0583	−0.0121	−0.0049	0.3741	0.0009	0.1640
AS	60	0.168 ± 0.020	not rejected	−2.4663	−0.1134	0.8261	−0.0583	−0.0121	−0.0049	0.3741	0.0171	0.1555
BC	58	−0.011 ± 0.020	not rejected	−2.6260	−0.1227	0.8261	−0.0583	−0.0121	−0.0049	0.3741	−0.0081	0.1399
BF	30	0.102 ± 0.042	not rejected	−2.7233	−0.1037	0.8261	−0.0583	−0.0121	−0.0049	0.3741	0.0253	0.1537
EH	308	0.001 ± 0.008	rejected	−2.8409	−0.1169	0.8261	−0.0583	−0.0121	−0.0049	0.3741	−0.0042	0.1337
OH	48	0.133 ± 0.025	not rejected	−2.7560	−0.1111	0.8261	−0.0583	−0.0121	−0.0049	0.3741	0.0231	0.1820
OS	85	0.029 ± 0.021	not rejected	−2.7532	−0.1081	0.8261	−0.0583	−0.0121	−0.0049	0.3741	0.0004	0.1471
QA	14	0.134 ± 0.061	not rejected	−2.6734	−0.1114	0.8261	−0.0583	−0.0121	−0.0049	0.3741	0.0189	0.2232
RM	304	0.058 ± 0.011	not rejected	−2.4157	−0.1284	0.8261	−0.0583	−0.0121	−0.0049	0.3741	0.0142	0.1801
RN	122	0.094 ± 0.015	not rejected	−2.8316	−0.0979	0.8261	−0.0583	−0.0121	−0.0049	0.3741	0.0110	0.1636
RO	35	0.033 ± 0.025	not rejected	−3.0972	−0.1040	0.8261	−0.0583	−0.0121	−0.0049	0.3741	−0.0314	0.1420
SM	592	0.093 ± 0.006	not rejected	−2.5667	−0.1180	0.8261	−0.0583	−0.0121	−0.0049	0.3741	0.0024	0.1436
SP	203	−0.023 ± 0.010	not rejected	−3.1431	−0.1069	0.8261	−0.0583	−0.0121	−0.0049	0.3741	−0.0094	0.1235
WC	12	0.043 ± 0.035	not rejected	−2.8164	−0.1139	0.8261	−0.0583	−0.0121	−0.0049	0.3741	−0.0481	0.1123
WP	122	0.141 ± 0.015	not rejected	−3.1466	−0.0836	0.8261	−0.0583	−0.0121	−0.0049	0.3741	0.0087	0.1596
YB	412	0.090 ± 0.007	not rejected	−2.0130	−0.1526	0.8261	−0.0583	−0.0121	−0.0049	0.3741	0.0010	0.1277

[a]*SPP* Species are *AB* American beech, *AS* ash, *BC* black cherry, *BF* balsam fir, *EH* eastern hemlock, *OH* other hardwoods, *OS* other softwoods, *QA* quaking aspen, *RM* red maple, *RN* red pine, *RO* red oak, *SM* sugar maple, *SP* spruce, *WC* white cedar, *WP* white pine, and *YB* yellow birch

Table 8 Parameter estimates for individual tree survival (Eq. [5]), the area under the curve (AUC) and optimal cutpoint (OCP) for the developed equation and the ones used in the Northeast Variant of FVS (FVS–NE) by species

SPP[a]	*N*		FVS–NE	Equation [5]							
	Alive	Dead	AUC	AUC	OCP	b_{50}	b_{51}	b_{52}	b_{53}	b_{54}	b_{55}	b_{56}
AB	2991	596	0.6885	0.7740	0.8028	7.4069	−0.0855	–	2.9649	−0.1041	–	–
AS	541	59	0.5439	0.6962	0.8900	−2.6972	−0.0511	2.7220	3.1868	–	−0.2677	–
BF	364	145	0.6190	0.6936	0.7480	5.4321	−0.0618	–	–	−0.0383	–	–
EH	2752	88	0.5098	0.6301	0.9584	−1.9897	−0.0809	3.1020	–	–	–	–
OH	2159	315	0.6872	0.7313	0.8760	−0.7529	−0.0709	2.5867	–	-	–	−0.1076
OS	470	79	0.5585	0.6767	0.8718	15.1544	−0.2712	2.4283	–	−0.2753	–	–
QA	465	109	0.6645	0.7304	0.8296	0.2811	−0.0517	1.7626	–	–	−0.2104	–
RM	2587	284	0.4793	0.6926	0.8906	11.2896	−0.1113	–	–	−0.1480	–	–
RN	845	58	0.4866	0.9483	0.9365	8.9149	0.2446	–	–	–	–	−0.5346
RO	530	12	0.5741	0.7962	0.9757	−6.2021	−0.0889	4.5545	–	–	–	–
SM	3842	359	0.4556	0.7453	0.9314	3.7231	−0.1037	1.9431	–	−0.1096	–	–
SP	1613	240	0.5690	0.7034	0.8911	7.1204	−0.0591	–	–	−0.0794	–	–
WC	324	11	0.4753	0.8157	0.9541	10.5219	0.1672	–	–	–	−1.6906	–
WP	3782	222	0.7106	0.7980	0.9212	4.3116	−0.0242	2.0274	–	–	–	−0.2974
YB	2601	348	0.5150	0.7298	0.9081	8.9994	−0.0607	–	–	−0.1359	–	–

[a]*SPP* Species are *AB* American beech, *AS* ash, *BF* balsam fir, *EH* eastern hemlock, *OH* other hardwoods, *OS* other softwoods, *QA* quaking aspen, *RM* red maple, *RN* red pine, *RO* red oak, *SM* sugar maple, *SP* spruce, *WC* white cedar, *WP* white pine, and *YB* yellow birch

increment at smaller tree sizes (DBH < 25 cm), while white pine and eastern hemlock showed the greatest diameter increment for larger tree sizes (DBH > 25 cm; Fig. 2). Spruces had the slowest diameter increment across a range of tree sizes.

Height increment

A total of 2744 observations were available for the height increment equation with most of the observation being sugar maple (21.6%), yellow birch (15.3%), American beech (12.1%), and eastern hemlock (11.2%). For all

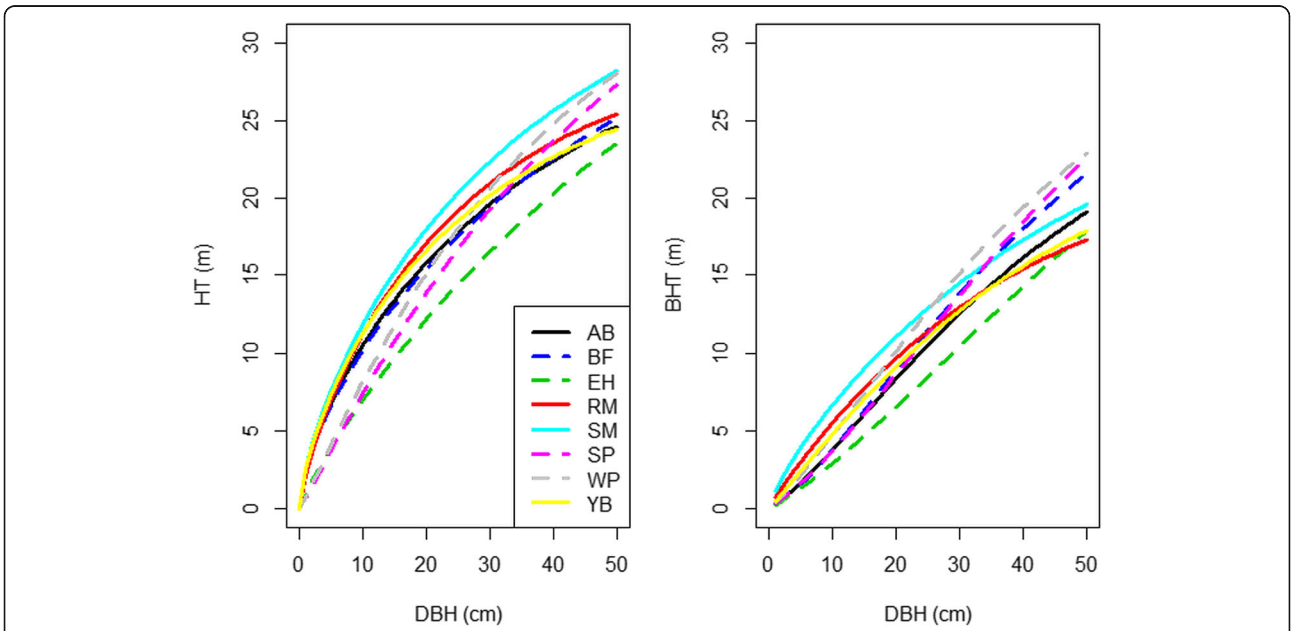

Fig. 1 Predictions of total height (HT, m) and bole height (BHT, m) across diameter at breast height (DBH, cm) for different species using Eqs. [1] and [2], respectively. Other equation covariates were set at mean levels, which were 10 m^2 ha^{-1}, 25 m^2 ha^{-1}, and 17 m for basal area in larger trees, total basal area, and climate site index, respectively. Species are American beech (AB), balsam fir (BF), eastern hemlock (EH), red maple (RM), sugar maple (SM), spruce (SP), white pine (WP), and yellow birch (YB)

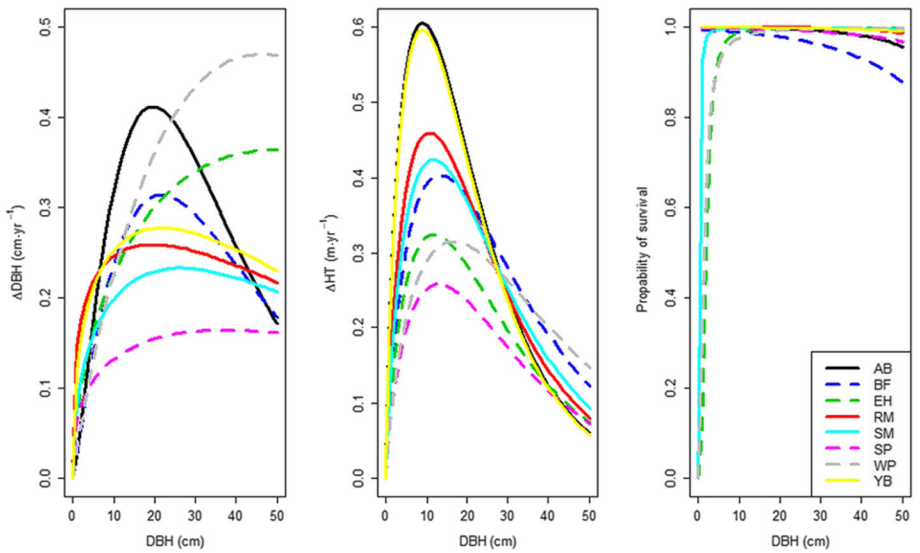

Fig. 2 Predictions of annual diameter (ΔDBH, cm yr^{-1}), height increment (ΔHT, m yr^{-1}), and annual probability of survival across diameter at breast height (DBH, cm) for different species using Eqs. [3], [4], and [5] respectively. For all equations, basal area in larger trees, total basal area, crown ratio, and climate site index were fixed at 10 m^2 ha^{-1}, 25 m^2 ha^{-1}, 0.33, and 17 m, respectively. For height increment, total height (HT, m) was varied as fixed percentage of the DBH (HT = DBH × 0.6). Species are American beech (AB), balsam fir (BF), eastern hemlock (EH), red maple (RM), sugar maple (SM), spruce (SP), white pine (WP), and yellow birch (YB)

species except eastern hemlock, an equivalence test suggested that the observed values and those predicted by FVS–NE were statistically different at the 15% level of allowable error (Table 7). As mentioned in the Methods section, a preliminary species–specific equation did not converge for the majority of species so an equation was fitted by using species as random effect. This resulted in an adequate fit with RMSE ranging from 0.16 to 0.25 m·yr^{-1}.

For a given set of covariates, yellow birch and American beech had the greatest height increment for smaller tree sizes (DBH < 25 cm), while spruce had the smallest height increment (Fig. 2). On larger trees (DBH > 25 cm), white pine and balsam fir had the greatest height increment and American beech and yellow birch had the lowest. Since small–sized suppressed yellow birch individuals were not available for our analysis, predicted height growth thus might be too optimistic.

Survival

A total of 28,791 observations were available for the survival analysis with most of the observation being sugar maple (14.6%), white pine (13.9%), American beech (12.5%), and yellow birch (10.2%). Balsam fir (28.5%), quaking aspen (19.0%), American beech (16.6%), and other softwoods (14.4%) showed the highest percentage of dead trees. A species–specific survival equation fit to the data showed a much higher AUC (0.74 ± 0.08; 0.63 – 0.95) compared to FVS–NE predictions (0.57 ± 0.09; 0.46 – 0.69, Table 8). The determined optimal cutpoint varied by species and ranged from 0.75 to 0.98. Across the various tree sizes examined, red maple showed the highest level of survival, while American beech and balsam fir displayed some of the lowest predicted survival rates (Fig. 2).

Long–term simulations

Based on the initial plot tree list, the component equations described above were used to project the plot from its first to last measurement. The simulations ranged from 7 to 41 years in length with an average of 22.1 ± 11.3 years. Tree–level mortality was estimated using either the expansion factor reduction or species–specific optimal cutpoints derived from the survival equations (Eq. [5]). At the tree–level, the equations did not show a high degree of bias with prediction of crown recession having the highest error. A minor decreasing trend in error across total tree height was apparent. Across species, the best performance was achieved for eastern hemlock and red maple, while the poorest performance was for spruce. At the stand–level, using the optimal species cutpoint for mortality was shown to be superior as the mean percent bias ranged from −2.4% to 4.6% with the error being the highest for total stem density (Table 9). Only minor trends were evident across the range of observed values or projection lengths (Fig. 3).

For the different forest types tested, growth was fairly linear for the 50 year projections when using either the expansion factor method or the optimal cutpoint method (Fig. 4). Overall, the hardwood dominated stand types showed greater growth when compared to the

Table 9 Stand–level projection mean bias (MB; observed – predicted), root mean square error (RMSE), and percent bias (%Bias) for total stem density (# ha^{-1}), quadratic mean diameter (QMD; cm), and basal area (m^2 ha^{-1}) by tree mortality method and forest, which are Dubuar Memorial Forest (DMF), Huntington Wildlife Forest (HWF), Pack Demonstration Forest (PDF), Pack Experimental Forest (PEF), and Shirley Forest (SF)

Forest	*N*	Years simulated (min – max)	Stem density			QMD			Basal area		
			MB	RMSE	%Bias	MB	RMSE	%Bias	MB	RMSE	%Bias
Expansion Factor method											
DMF	10	8.9 (7 – 17)	6.69	64.18	5.00	−0.29	1.47	−0.90	−0.28	3.10	1.22
HWF	59	20.1 (10 – 31)	174.81	214.62	30.08	−3.21	5.83	−10.64	5.31	7.04	18.19
PDF	71	10.0 (10 – 10)	130.67	188.45	13.95	−0.98	1.85	−4.41	0.80	3.79	0.70
PEF	2	8.5 (7 – 10)	87.72	89.38	17.85	−1.34	1.49	−4.98	2.59	3.21	9.04
SF	103	8.7 (3 – 24)	22.06	48.47	6.39	−0.11	1.54	−0.59	0.81	2.38	4.39
Overall	245	11.8 (3 – 31)	90.23	150.35	14.32	−1.13	3.20	−4.17	1.86	4.35	6.55
Optimal Cutpoint method											
DMF	10	8.9 (7 – 17)	−18.53	77.85	−1.01	−0.28	1.46	−0.86	−1.54	3.93	−4.03
HWF	59	20.1 (10 – 31)	74.97	136.73	12.48	−2.97	5.67	−9.96	−1.09	5.28	−1.81
PDF	71	10.0 (10 – 10)	58.82	143.28	5.84	−0.96	1.83	−4.29	−1.39	4.09	−4.99
PEF	2	8.5 (7 – 10)	49.42	55.25	10.13	−1.30	1.47	−4.86	−0.19	0.35	−1.16
SF	103	8.7 (3 – 24)	−5.64	53.52	−0.32	−0.08	1.55	−0.48	−0.51	2.83	−0.85
Overall	245	11.8 (3 – 31)	32.38	109.22	4.61	−1.05	3.14	−3.92	−0.95	3.94	−2.42

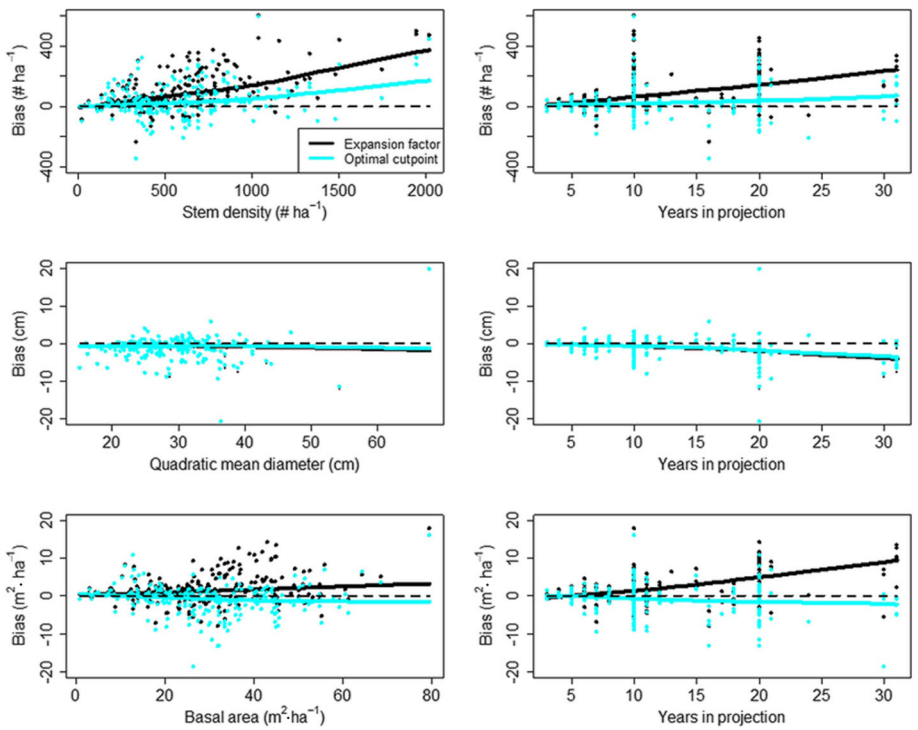

Fig. 3 Prediction bias (observed – predicted) for stem density (# ha^{-1}), quadratic mean diameter (cm), and total basal area (m^2 ha^{-1}) over observed values (left) and years in projection (right) using the different methods for simulating individual tree mortality. The expansion factor method is where the predicted probability of survival is multiplied by the tree's current expansion factor, while the optimal cutpoint method is where an entire tree record is killed when the predicted probability of survival falls below the species optimal cutpoint

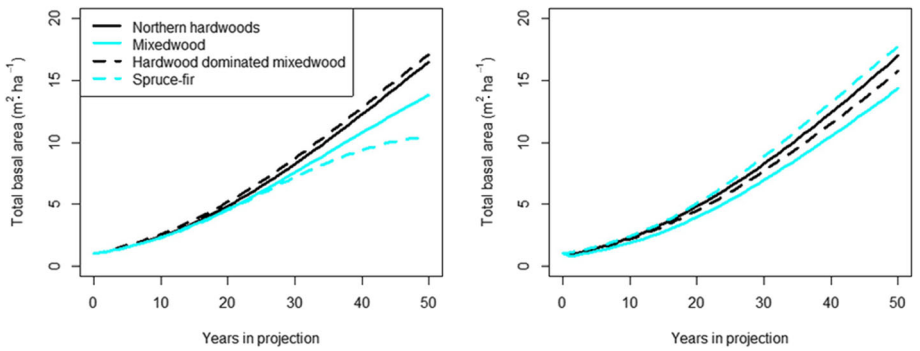

Fig. 4 Fifty year projections of total basal area (m^2 ha^{-1}) of common forest types using the developed equations and the expansion factor method (*left*) or the optimal cutpoint method (*right*), respectively. Each forest type was initialized with 500 stems per ha of 5 cm diameter at breast height. Northern hardwoods was an equal mixture of American beech, black cherry, red maple, sugar maple, and yellow birch. Mixedwood was red spruce, balsam fir, eastern hemlock, and red maple with some American beech, white pine, and yellow birch. Hardwood dominated mixedwood was American beech, eastern hemlock, red spruce, sugar maple, and yellow birch. Spruce–fir was an equal mixture of red spruce and balsam fir

softwood dominated ones. The total basal area values (10.5 – 17.1 and 15.7 – 17.7 $m^2 \cdot ha^{-1}$) and basal area growth rates (0.19 – 0.32 and 0.27 – 0.33 $m^2 \cdot ha^{-1} \cdot yr^{-1}$ for the expansion factor and the optimal cutpoint method, respectively) were all within reason of the general expectations for the region.

Discussion

To our knowledge, this effort represents the first attempt to develop an individual tree growth model specific to the range of tree species present in the Adirondacks Region of New York. Other efforts to model growth and yield in the region have only focused on plantation conifer species (Pan and Raynal 1995), hardwood species under a specific set of stand conditions like sugar maple in uneven–aged selection stands (Kiernan et al. 2009a, b), or pure hardwood stands (Aldridge 1982). Based on the assessment of the existing FVS–NE component equations, the Adirondacks Region appear to be a distinct ecological area that is deserving of a growth model specific to the present conditions. This is likely because the Adirondacks Region generally shows a higher potential productivity, a greater hardwood composition, and more intensive history of high–grading when compared to certain other parts of the Northeast. In particular, the Adirondacks Region has a disturbance regime predominated more by wind and ice (Lorimer and White 2003) and a history of highly selective logging in previously cutover old–growth hardwood stands (Berven et al. 2013), which both create relatively complex and mixed species stands.

The Adirondacks forest data used in this analysis represents the tremendous value of an intensive and well–maintained CFI system as it provided between 2 to 52 years of regular tree–level remeasurement data. The plots were well maintained, relatively large (0.04 – 0.08 ha), and representative of the conditions of the studied region. Initially, US Forest Service Forest Inventory and Analysis (FIA) data in New York was also considered in this analysis, but it was deemed of limited value given the relatively small plot size used (0.016 ha), the low number of remeasurements, and the general lack of total tree height measurements. Overall, the data used was determined to be of a sufficient size and scope with a full range of stand structure and compositions present. As common, plots in late–successional stands were not frequent and this may limit the growth model's ability to extrapolate to those conditions. However, the lack of forest management on the Pack Experimental Forest has created some mature stands with dynamics controlled primarily by natural factors. However, these CFI were relatively smaller than plots used in research, which may influence the estimate of key stand– and tree–level variables used during modeling.

In general, the component equations fit well and showed adequate performance when conducting long–term simulations. Consistent with other tree–level growth models, total height equations fit the best, while height increment and mortality equations were the most problematic. For total and bole height, FVS–NE tended to underpredict these values, which has important consequences for future projections. In contrast, Rijal et al. (2012a, b) found that FVS–NE generally overestimated total height in the Acadian Region, while Russell et al. (2013) indicated both under– and over–estimation across the primary species in the Northeast US. The underprediction here was likely reflective of the better growing conditions in the lower elevations of the Adirondacks Region. Given the use of bole height (defined as the first live branch or a 10.2 cm (4 in) top), prediction using height to crown base or crown ratio equations of FVS–NE were expected to be biased, which was confirmed by the data. However, the fitted bole height equation fit the data well, but utilizing it to estimate a modified form of crown

ratio proved not very useful for the other equations developed in this analysis.

In this analysis, the diameter and height increment equations proved particularly challenging due to remeasurement data only being available for trees > 10 cm in DBH and a general lack of height remeasurement data, respectively. However, relatively well–behaved and logical increment equations were constructed. In fact, to ensure proper fit and behavior of the height increment equation, it was estimated by treating species as a random effect rather than determining parameters by species like the diameter increment equation. Developing height increment equations by treating species as a random effect has been shown to be an effective technique when compared to fitting the equations by species (Russell et al. 2014). This is because all of the existing data can be used and species–specific parameters still extracted, which is particularly important for minor species that may not have observations across their full range. Consistent with Russell et al. (2014), this was found to be the case in this analysis. Using binary indicators for species to fit the equation was also an alternative option, but was determined to be inefficient given the number of species being examined and not further explored.

For mortality, the AUC for most species was approximately 0.75, which represents an acceptable to excellent discrimination of alive and dead trees (Hosmer and Lemeshow 2000). Thus, the equation was a significant improvement over the FVS–NE individual tree mortality equations. A variety of other model forms and implementation techniques were evaluated, but significant improvements were not achieved. Based on the observed stand–level bias, the equation appears to perform reasonably well, particularly if the whole tree approach with optimal species cutpoints was used. Like this study, a previous study has also found that using a fixed cutpoint rather than the tree expansion factor reduction method was superior (Crecente–Campo et al. 2009). In contrast, Rathbun et al. (2010) found just the opposite and suggested the tree expansion factor method to be superior, which indicates that additional research on the influence of how tree mortality is implemented in growth models, especially for long–term projections, is needed. However, both Crecente–Campo et al. (2009) and Rathbun et al. (2010) examined relatively short–term trends in mortality (1 – 17 years), while this analysis included plots simulated for over 40 years. Regardless, the findings highlights the sensitivity of models projections to mortality and likely a more sophisticated approach like a linked stand– and tree–level approach (e.g. Zhang et al. 2011) is warranted. However, a linked approach would require the development of a stand–level mortality equation, which can be problematic for multi–cohort, mixed–species stands (Weiskittel et al. 2011a).

Despite the difficulty of fitting individual component equations, the developed growth model shows good performance across a range of stand conditions. Using some of the longest validation data available in the Northeast (>50 years), the model showed only minor signs of increasing bias with greater projection lengths. The simulations for the different common forest types in the region were logical and met expectations as the hardwood dominated stands showed the greatest growth and spruce–fir the least. In this region, northern hardwood and mixedwood stands tend to occur on the best sites with deep and well–drained soils, while spruce–fir tend to occur in more poorly–drained flats. The observed annual total basal area growth rates were also consistent with typical regional values (e.g. Solomon 1977), while differences found between expansion factor and optimal cutpoint method in the 50 year projections again reflect the significance of the mortality approach applied.

Conclusions

Given the importance and uniqueness of the Adirondacks Region, an individual tree growth and yield model was developed based on existing, long–term CFI data (>50 years) for the region. The developed equations performed well despite high variability in the data and incomplete histories of past stand disturbances and harvesting practices. When the equations were combined into a growth and yield system, long–term behavior was consistent with observed trends and general expectations. Interestingly, long–term model performance was improved when using a whole–tree rather than expansion factor approach to individual tree survival. In addition, projections for the common forest types for the region indicated that mixed hardwood stands tended to outperform mixed and/or pure softwoods stands. Important next steps include evaluating the model's behavior in stands with varying management regimes, developing equations to predict ingrowth (e.g. Li et al. 2011), and assessing alternative approaches to forecasting mortality (e.g. Zhang et al. 2011).

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Authors' contributions

AW wrote the manuscript and assisted with the analysis. CK completed the analysis and prepared all manuscript tables and figures. JPM and MO provided input on the manuscript text and modeling approaches used. All authors read and approved the final manuscript.

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Competing interests
The authors declare that they have no competing interests.

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