

# Predicting the Recruitment of Established Regeneration into the Sapling Size Class Following Partial Cutting in the Acadian Forest Region: Using Long-Term Observations to Assess the Performance of FVS-NE

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**Abstract**—Forest managers are increasingly called upon to provide long-term predictions of forest development. The dynamics of regeneration establishment, survival and subsequent recruitment of established seedlings to larger size classes is a critical component of these forecasts, yet remains a weak link in available models. To test the reliability of FVS-NE for simulating sapling (stems  $\geq 0.5$  in dbh) recruitment dynamics in stands subject to repeated partial harvests, we compared model predictions with long-term observations ( $n = 729$  plots/5-yr interval combinations) from the Penobscot Experimental Forest (PEF) in central Maine. Two different parameterizations of FVS-NE were tested; the currently available production code and a yet to be released beta version that contains a number of structural changes. Because neither parameterization has a full-establishment model, regeneration composition and densities were from the research plots. Our analyses indicated that predicted rates of sapling recruitment were biased according to both models, averaging 47 percent (production) and 206 percent (beta) of the observed rate at the PEF ( $1.71 \pm 0.25$  ft<sup>2</sup>/ac/5-yr). Mortality rates among the newly recruited saplings were overestimated by both models, and species composition of the survivors did not closely match the observations. Correlation analysis on the residuals from the beta version pointed to a strong link between the overestimation of stems recruited to the sapling size class and the density of large regeneration input to the model. Limiting the density of regeneration entering the simulation to  $\leq 1,800$  TPA ( $\sim 2$  stems/milacre plot) largely eliminated the prediction bias, yet only modestly improved model accuracy ( $R^2$  0.398 vs. 0.341).

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## Introduction

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Reasonably accurate stand dynamic models are required in to assess the long-term consequences of different forest management scenarios. The Forest Vegetation Simulator (FVS) (Dixon 2002), developed and supported by the USDA Forest Service, is currently being used to provide evidence to support the sustainability of management plans developed for national forests across the United States. By definition, the terms *forest management* and *long-term* encompass the process of forest renewal, and suggest that prediction of regeneration is a requisite part of any such system (*sensu* Stage 1973). However, attempts to address this critical component remain problematic for developers. Among the 20 regional variants of FVS, only five support full establishment models. Users of variants lacking this functionality are required to specify measured or anticipated regeneration (with the exception of sprouting hardwoods) to obtain realistic long-term simulations following harvesting disturbances.

In the Northeastern United States, where rainfall is abundant and distributed fairly evenly throughout the year, growing season water deficits and associated regeneration failures are uncommon (Seymour 1992). In fact, regeneration is often viewed as overly dense and pre-commercial thinning is a common practice among landowners concerned with timber production in the conifer dominated forests of central and northern Maine (Seymour and Gadzik 1985). Evidence from a long-term USDA Forest Service compartment study at Penobscot Experimental Forest (PEF) in central Maine supports the hypothesis that abundant reproduction may be obtained following a broad range of silvicultural treatments (Brissette 1996). Under these conditions the imputation of regeneration to

the partial establishment model in FVS-NE following harvest may be justifiable, allowing it to develop under the influence of the residual overstory. Another generalization that may be drawn from the research carried out at the PEF is that heavier cutting results in a relative shift in species composition from shade-tolerant conifers to less tolerant hardwoods (Sendak and others 2003), which may allow users that lack specific regeneration data to impute a more realistic regeneration response based on the level of overstory disturbance.

Partial-cutting practices that give rise to multiaged stand structures have come to characterize contemporary forest management across much of the Northeast U.S. (Department of Conservation, Maine Forest Service 2005). Thus, newly regenerated cohorts typically develop under the influence of partial overstory shade before recruiting into the main canopy layer, or succumbing to competition induced mortality. A number of important regulators of stand development in FVS are based on quantitative relationships established in even-aged stands. Specifically, size-density relationships are constrained by Reineke's (1933) stand density index (SDI), and site quality is described by site index in the eastern TWIGS based variants. Both approaches are of questionable validity in the context of multiaged stand development.

In light of the issues laid out above, and in order to build on some recent validation work conducted with FVS-NE (Ray and others 2006), we sought to determine if the model would provide reasonably accurate and unbiased estimates of the rates of sapling recruitment observed under the range of partial-cutting treatments at the PEF. Specifically, we compared model predicted rates of ingrowth to the 1-in dbh class with observations from nested fixed-area plots remeasured at 5-yr intervals over a 25–30 yr period. Observed self-thinning within these cohorts was compared with model-predicted competition induced mortality. Results obtained from the currently available production code of FVS-NE were compared with those from an unreleased beta version that incorporates some major structural changes.

## Methods

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### The Dataset

Penobscot Experimental Forest (PEF) is the location of a long-term silvicultural compartment study established as a collaborative effort between the U.S. Forest Service and the forest products industry in the early 1950s. The 4,000-ac property is located in central Maine, U.S.A (44°52'N, 68°38'W) within the Acadian Forest Region. Species composition is characterized by a mixture of shade-tolerant northern conifers, most notably red spruce (*Picea rubens*), balsam fir (*Abies balsamea*) and eastern hemlock (*Tsuga canadensis*); and faster growing hardwoods, primarily red maple (*Acer rubrum*), paper birch (*Betula papyrifera*) and aspen (*Populus* spp.). Precipitation averages 42 inches annually and is evenly distributed throughout the growing season. Soils are of glacial till origin and tend to be somewhat poorly drained, particularly in the flat areas where the compartment study is located. We estimate the average site index for balsam fir at 55 ft at a breast height age of 50 yrs.

The growth and development of individual trees in response to six partial-cutting treatments (2 reps/treat) has been documented before and after harvests and at about 5-yr intervals between harvests since the mid-1970s. Species, diameter at breast height (dbh, 4.5-ft), and status (i.e. ingrowth/live/dead/harvested) were noted at each inventory. Stems  $\geq 4.5$ -in dbh have consistently been tracked on circular 5<sup>th</sup> ac plots, while smaller stems (0.5 to 4.5-in dbh) were historically measured on nested 20<sup>th</sup> ac plots; beginning in year 2000 individual stems between 0.5 and 2.5-in dbh have been tallied on a nested 50<sup>th</sup> ac plot due to perceived over sampling within that size class. Counts of regeneration by species within four height classes (0.5 to 1 ft, 1 to 2 ft, 2 to 4.5 ft, and >4.5 ft tall but <0.5 in dbh) have taken place since the mid-1960s on three milacre plots distributed around the perimeter of the 20<sup>th</sup> ac plot.

In the context of this study, we take a broad view of partial cutting as encompassing commercial timber harvests that remove sufficient stocking of overstory trees to facilitate the establishment/recruitment of a new/existing cohort. The six partial-cutting approaches documented at the PEF vary widely, both in terms of silvicultural intensity (commercial clearcutting vs. single-tree selection) and frequency of application (table 1). For a more detailed description of the PEF study system, the reader is referred to Sendak and others (2003).

**Table 1**—Summary description of the partial-cutting treatments at the Penobscot Experimental Forest (PEF). Note that the treatment codes correspond to the figures.

Treatment	Code	Description	Cutting cycle (yrs)	Harvests	Total plot count (2-reps)
Selection system	S05	Single-tree/small groups	5	10	33
	S10	Single-tree/small groups	10	5	35
	S20	Single-tree/small groups	20	3	37
Diameter-limit	FDL	Fixed diameter-limit	20 <sup>a</sup>	3	33
	MDL	Modified diameter-limit	20	3	32
Unregulated harvest	URH	Commercial clearcut	30 <sup>a</sup>	2	41
Natural area	NAT	Reference stand	n/a	n/a	20

<sup>a</sup>Historical cutting cycle lengths are not sustainable in the more exploitative treatments.

## The Forest Vegetation Simulator (FVS)

All simulations were carried out with FVS production code (FVS-NE<sub>p</sub>, revision date of 12.27.06) and an unreleased beta version (FVS-NE<sub>B</sub>) of the Northeastern Variant. A description of FVS-NE<sub>p</sub> is provided by Bush (1995), while FVS-NE<sub>B</sub> has yet to be documented. A summary of the major alterations implemented between versions is outlined in table 2. We used the recently available database extension (Crookston and others 2005) to manage data input and output streams.

Because FVS-NE does not support a full establishment model, we input regeneration measured on the milacre plots at the PEF. Only stems within the largest size class (4.5 ft tall to 0.5-in dbh, hereafter referred to as large regeneration) at the beginning of the projection interval were entered into the simulation. Large regeneration was generally well represented across treatments and remeasurement periods, and was considered the most likely pool of recruits to the 1-in dbh size class (i.e. sapling ingrowth). Large regeneration was added to the TREELIST after determining species specific dbh estimates based on the height/diameter (h/d) equations used in FVS-NE<sub>B</sub>. This involved first calculating the height of a 0.5-in dbh tree, determining the midpoint value between that height and the 4.5 ft lower cutoff for the large regeneration size-class, and then back calculating the corresponding dbh based on the initial equation. On average, large regeneration of conifer and broadleaf species was 6.5 and 5.4-ft tall and 0.33 and 0.23-in dbh, respectively. Site index for all runs was set at 55 ft for balsam fir based on observations from the even-aged treatment compartments located on similar sites at the PEF.

Short-term simulations corresponding to the nominal 5-yr inventory period at the PEF were used to evaluate FVS predictions of recruitment dynamics on the study plots. Approximately 1,200 plots per 5-yr interval combinations were simulated, or about five runs/plot. We believe these short interval projections provided the most objective means of evaluating model performance in the context of sapling recruitment. Specifically, this approach was taken to minimize the influence of a growth overestimation bias revealed previously in the overstory model (Ray and others 2006) that would otherwise suppress growth and/or increase mortality within the subordinate cohort. To further limit this possibility, the available diameter increment measurements were used to calibrate the large tree diameter growth model during each model run.

In summary, each simulation involved projecting the initial conditions (post-cut in cases where a harvest had taken place during the interval) on an individual research plot over a 5-yr period and generating an output TREELIST. Large regeneration present at the beginning of the run was assigned a number  $\geq 500$  so they could easily be located on the output (there were typically  $< 200$  trees on a given plot). Large regeneration that grew above the 0.5-in dbh threshold by the end of the simulation was considered recruitment to the sapling size class and converted to units of basal area (BA; ft<sup>2</sup>/ac/5-yr), which were then compared with observed rates on the same study plot. To be fair to the model, we did not include plots that lacked large regeneration at the beginning of a given measurement interval. Because the partial-establishment model in FVS requires that the user specify the regeneration, plots containing no regeneration have no chance of yielding ingrowth. Imposing this criterion resulted in a substantial reduction to the available plot by interval combinations, by approximately 35 percent, to 729 across all treatments.

**Table 2**—Comparison of changes to model components implemented between the production (FVS-NEP) and beta (FVS-NEB) versions of the model used in this study. A more complete description for FVS-NEP is available in Burke (1995).

Component	Production code	Beta code
Height-Diameter Allometry	Based on Ek's equations.	Based on Curtis-Arney or Wykoff equations.
Small Tree Model (<1-in dbh)		
Height	Uses aspen hg from UT variant (hardwoods) and conifer equations from NI variant (softwoods).	See large tree height growth (potential with a modifier value).
Diameter	Uses Wykoff h/d relationship to get growth.	Use h/d above to get DG.
Large Tree Model (>1-in dbh)		
Height	HG based on Ek's equations as modified by GMOD from large tree diameter growth	HG based on potential HG from site index curves as modified by relative height and GMODa from large tree DG.
Diameter	Uses TWIGS potential growth with GMOD modifier, lower limit of GMOD is set to 0.15.	Uses TWIGS potential growth with GMODa modifier, lower limit of GMOD is set to 0.5.
Mortality		
Background (<55 percent maxSDI)	1/10 of TWIGS mortality rate (survival model).	Utilizes background mortality rate equations from the SE Variant.
Density dependent (>55 percent maxSDI)	SDI-based, distributed based on the TWIGS survival function rates.	SDI-based, distributed based on species tolerance and relative height.

<sup>a</sup>GMOD in the beta version is influenced by competitors in 2 1-in classes below the dbh of the subject tree.

## Performance Criteria and Analyses

To get a sense of the suitability of the nested-plot design at the PEF for carrying out this analysis, we compared the occurrence of ingrowth on the larger 20<sup>th</sup> and 50<sup>th</sup>-ac plots to the presence/absence of large regeneration on the milacre plots; the assumption being that large regeneration is a prerequisite to recruitment over this timeframe. Alternatively, the patchy spatial distribution of stems of different sizes resulting from repeated partial cuts may result in poor correspondence between estimates from the two plot types. We also predicted a pre-recruitment dbh for saplings at the PEF by subtracting the average 5-yr post-recruitment diameter increment rate from their initial dbh (when they first appeared as saplings). This information was then used to assess the proportion of observed sapling recruitment that may have been smaller than our large regeneration category, and to identify stems that may have been overlooked during an earlier inventory (i.e. estimated dbh 5-yr prior >0.5-in).

To assess the performance of FVS-NE, we compared observed and predicted rates of sapling recruitment to the 1-in dbh class ( $\geq 0.5$ -in dbh) in units of BA. The Northeast TWIGS model (Teck and Hilt 1990, 1991) that underlies FVS-NE is based on basal area growth equations, providing the most direct link between model predictions and the observed values. Goodness of fit was assessed using reduced major axis regression to accommodate both measurement and prediction errors (Sokal and Rohlf 1981). We assessed mortality dynamics among the newly recruited stems by comparing the observed and predicted rates in these same units of measure. Finally, correlation analysis was used to relate residuals (observed-predicted recruitment rates) with various attributes of the remeasurement plots (i.e. large regeneration density, composition (broadleaf vs. conifer), Dq, SDI, etc.).

The sampling unit(s) employed in this study, in particular the use of individual plots to measure recruitment rates over 5-yr intervals, raise some concerns about pseudoreplication in the context of significance testing, e.g. the average plot was represented by three remeasurement intervals. Thus, the alpha level used to assess the P-values associated with the correlation analysis should be evaluated with this in mind, that is, P-values close to 0.05 are probably not significant. Note that our intent here was simply to identify important trends in relation to model bias. Averaging across plots within a compartment was done to minimize the influence of zero values, and is consistent with the stand-level estimates generated from a typical inventory driven FVS run.

## Results

### Assessing the Sampling Design

Nested fixed-area plots are commonly used to sample vegetation of substantially different stature (e.g. FIA). Establishing the cutoffs between the size classes sampled on smaller versus larger plots involves striking a compromise between sampling effort and variability. At the PEF, three, and more recently four different nested fixed-area plots have been used. Because recruitment to the sapling size class involves growth across one of these plot size cutoffs (i.e. from the milacre to the larger 20<sup>th</sup> or 50<sup>th</sup> (since 2000) ac plot), we were mindful of avoiding spurious conclusions based on an incompatibility between our research questions and the sampling design.

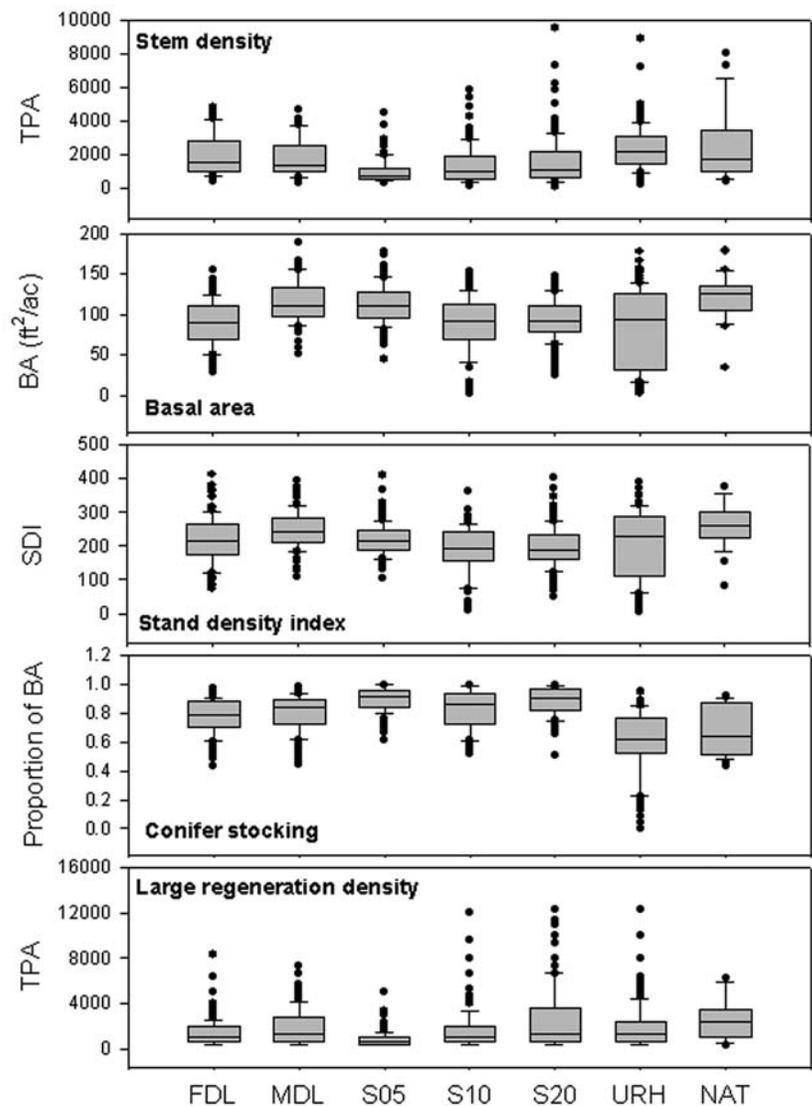
Observations from the six partial-cut treatments and an untreated reference stand indicated that sapling recruitment took place on more than half of the plot/interval combinations (653 of 1,182). Large regeneration was present at the beginning of a measurement interval on 68 percent of the total plot/interval combinations; thus, ingrowth 'appeared' on 32 percent of all plots. Among the 729 plot/interval combinations for which large regeneration was present (the dataset used for simulations in order to assess model performance), approximately 60 percent registered some sapling recruitment during the subsequent 5-yr interval. By comparison, the model(s) predicted sapling recruitment on 35 percent (FVS-NE<sub>p</sub>) and 68 percent (FVS-NE<sub>B</sub>) of these plots. Assessed across all plots that had large regeneration present, and on which sapling recruitment was recorded, model predictions of the presence or absence of sapling recruitment were consistent with observations for 29 percent (FVS-NE<sub>p</sub>) and 56 percent (FVS-NE<sub>B</sub>) of plot/interval combinations.

A total of 8,729 (28 percent of total records) saplings identified as recruits on the PEF plots had multiple dbh measurements allowing estimation of pre-recruitment diameters. The resulting backward extrapolations suggested that approximately 10 percent of the observed recruitment may have been shorter than 4.5-ft tall (i.e. resulted in negative dbh estimates). Stems in this category were primarily associated with fast growing broadleaf species in the commercial clearcutting treatment (URH; table 1). These backward projections also indicated that up to 44 percent of saplings that appeared as new recruits may have been overlooked during the first measurement interval when they crossed the  $\geq 0.5$ -in dbh threshold. Assuming some of these saplings estimated to have been  $\geq 0.6$ -in dbh or  $\geq 0.7$ -in dbh were actually below the 0.5-in dbh threshold, then only 29 percent or 18 percent are implied to have been overlooked, respectively. The average initial diameters of 0.31-in (broadleaves) and 0.23-in (conifers) back calculated for the newly recruited saplings was very similar to predictions from the allometric equations in FVS-NE<sub>B</sub> (see "Methods").

Perhaps more important in the context of evaluating model performance, however, was confirmation that large regeneration was sufficiently abundant on the milacre plots, and thus included in the TREELIST to account for the observed rates of sapling recruitment. Correspondence between nested plots was considerably better based on this criterion, with 96 percent of all simulated plot/interval combinations having at least as many large regeneration stems as recruited saplings. The percentage of plots with adequate large conifer regeneration was also 96 percent, whereas 92 percent of plots with large broadleaf regeneration were similarly represented.

### Characteristics of the Simulation Plots

There was considerable overlap in the range of conditions present on the study plots with large regeneration (fig. 1). The overall average stem density of  $1,810 \pm 207$  (TPA;  $\geq 0.5$ -in dbh) was highest on the reference plots (NAT;  $2,577 \pm 416$  TPA) and lowest for the 5-yr selection treatment (S05;  $996 \pm 65$  TPA). Basal area was highest on the reference plots (NAT;  $120.7 \pm 5.4$  ft<sup>2</sup>/ac) and lowest in the commercial clearcuts (URH;  $81.8 \pm 4.0$  ft<sup>2</sup>/ac), compared to the average across treatments of  $100.3 \pm 6.0$  ft<sup>2</sup>/ac. Stand density index (SDI) ranged from  $187.9 \pm 6.4$  in the 10-yr selection treatment (S10) up to  $262.7 \pm 13.4$  on the reference plots, averaging  $219.4 \pm 10.4$  across treatments. The plot level values for SDI seldom exceeded the 55 percent of SDI<sub>max</sub> threshold of 293 (determined as a weighted average value for red spruce/balsam fir/eastern hemlock) used to trigger density dependent mortality in FVS (Dixon 2002). Northern conifers, including red spruce, balsam fir, eastern hemlock, northern white-cedar, and eastern white pine (*Pinus strobus*), accounted

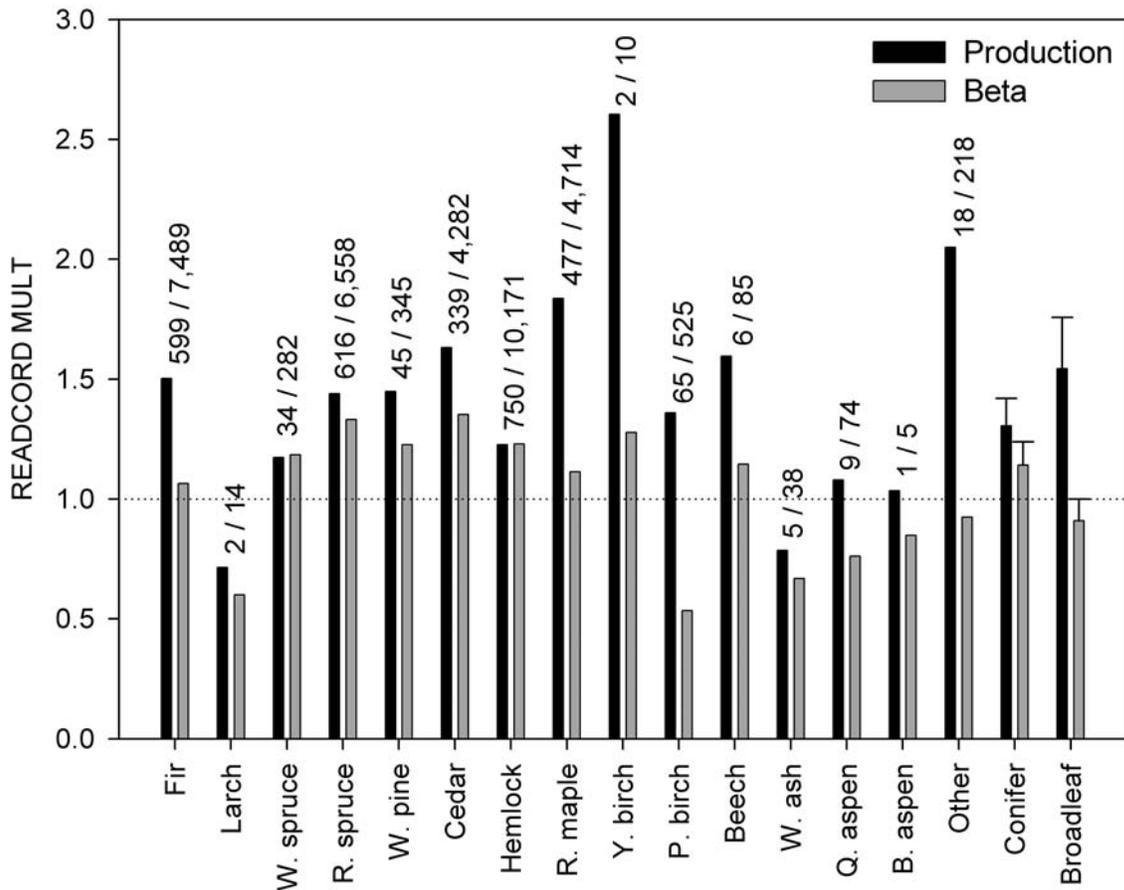


**Figure 1**—Summary of conditions on the partially cut and control plots at the PEF (treatment codes are in table 1). Variables presented in the top four panels are based on stems  $\geq 0.5$ -in dbh. The large regeneration category (bottom panel) corresponds to stems between 4.5-ft tall and 0.5-in dbh.

for approximately 80 percent of the BA stocking on the research plots, being highest ( $90 \pm 1$  percent) on the 5-yr selection and lowest on the commercially clearcut plots ( $60 \pm 2$  percent). Large regeneration was abundant on the simulated plots, averaging  $1,837 \pm 241$  TPA across treatments, and ranging from a high of  $2,639 \pm 345$  TPA on the control plots down to  $849 \pm 66$  TPA in the 5-yr selection treatment. Note that large regeneration was only present on plots in one of the reference compartments. Although no harvesting has been carried out in the reference compartment since the study was established in the early 1950s, natural disturbance, i.e. the eastern spruce budworm outbreak extending from the mid 70s into the early 80s, differentially impacted the development of the reference compartment with large regeneration.

### Calibration of Large Tree Diameter Growth

While a comprehensive evaluation of the performance of FVS-NE<sub>p</sub> against FVS-NE<sub>B</sub> is beyond the scope of this study, we used the large tree diameter growth calibration option on all runs and briefly summarize those results here (fig. 2). Fifteen species were sufficiently represented to provide calibrations (seven conifers, seven broadleaves and one misc. grouping), however, only two of the broadleaves (e.g. red maple and paper birch) were well represented. The summary READCORD factors were greater than 1.0 in most



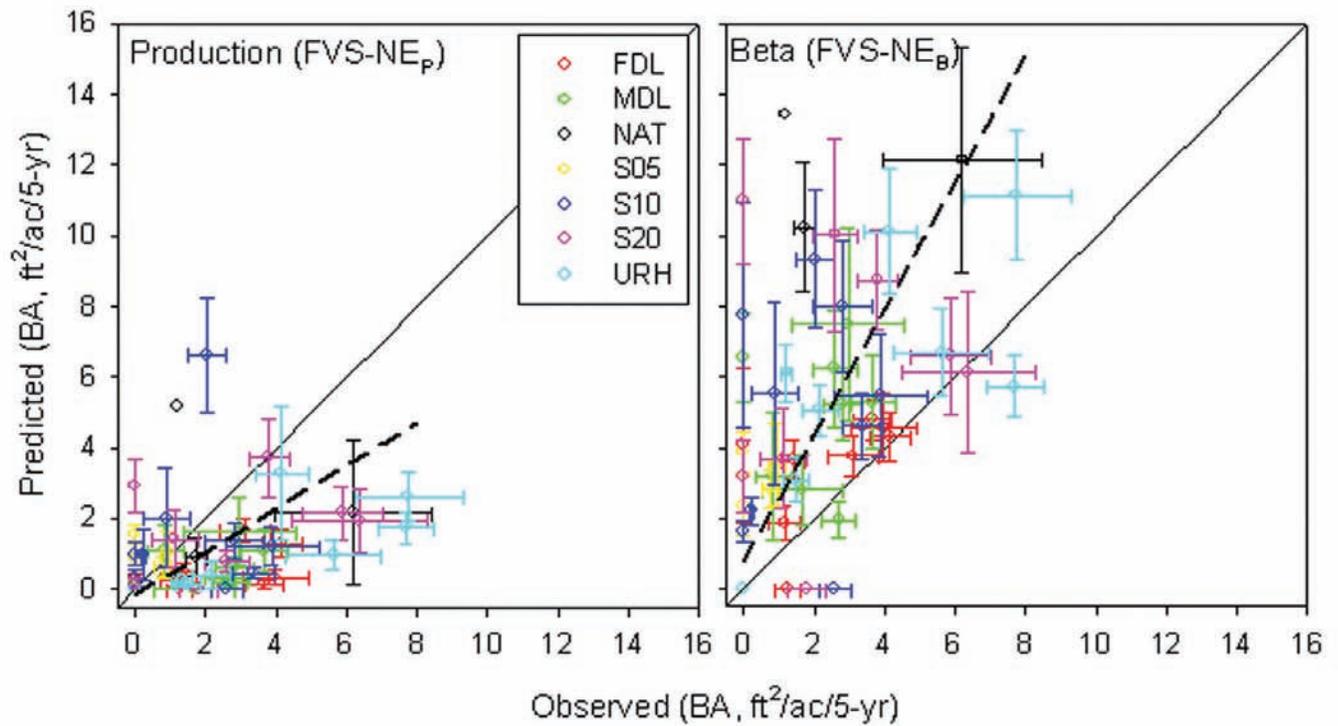
**Figure 2**--Comparison of summary calibration factors (READCORD MULT) obtained from the large tree diameter growth model running the production and beta coded versions of FVS-NE. The number of plot/interval combinations and individual tree records contributing information to the species level means, respectively, are presented above the bars. The mean and standard error are also presented for the conifer and broadleaf species groupings.

cases, suggesting that the uncalibrated model(s) tended to grow trees at the PEF too slowly. The multipliers were generally higher for the conifers than the broadleaves, and on average, estimates from FVS-NE<sub>B</sub> were closer to the observed diameter growth rates than FVS-NE<sub>P</sub>.

### Sapling Recruitment and Mortality Rates

Recruitment to the sapling size class was systematically underestimated by FVS-NE<sub>P</sub> and overestimated by FVS-NE<sub>B</sub> relative to observations from the PEF (fig. 3). Fit statistics associated with the RMA regression models confirm that the correspondence between observed and predicted values was poor (table 3). Averaged across treatments and intervals, the observed sapling recruitment rate of 1.71±0.25 ft<sup>2</sup>/ac/5-yr at the PEF was 96 percent above the FVS-NE<sub>P</sub> prediction (0.87±0.15 ft<sup>2</sup>/ac/5-yr) and 123 percent below the FVS-NE<sub>B</sub> estimate (3.96±0.45 ft<sup>2</sup>/ac/5-yr). The median values were less than the means in all cases, reflecting the right skewed distributions (PEF=1.12; FVS-NE<sub>P</sub>=0.31; FVS-NE<sub>B</sub>=3.51 ft<sup>2</sup>/ac/5-yr). The ratio of medians taken between FVS-NE<sub>B</sub> and PEF was more dramatic than for the means (3.1 vs. 2.3).

Mortality dynamics among the newly recruited saplings as portrayed by FVS-NE also differed substantially from observations. Specifically, whereas mortality claimed approximately 6 percent of sapling recruitment across all treatments at the PEF (0.13 ft<sup>2</sup>/ac/5-yr), the proportions forecast by FVS-NE were markedly higher, amounting to 28 percent (FVS-NE<sub>P</sub>=0.27 ft<sup>2</sup>/ac/5-yr) and 23 percent (FVS-NE<sub>B</sub>=0.98 ft<sup>2</sup>/ac/5-yr) of total



**Figure 3**—Comparison between observed (PEF) and predicted (FVS-NE<sub>p</sub>; FVS-NE<sub>b</sub>) rates of sapling recruitment (BA; ft<sup>2</sup>/ac/5-yr). Data points means and standard errors for all compartment/interval combinations associated with the partial-cutting treatments. The dashed line corresponds to the reduced major axis regression (RMA).

**Table 3**—Model parameters and fit statistics from reduced major axis (RMA) regression relating observed and predicted recruitment rates for both versions of FVS-NE tested; standard errors of the estimates are in parenthesis.

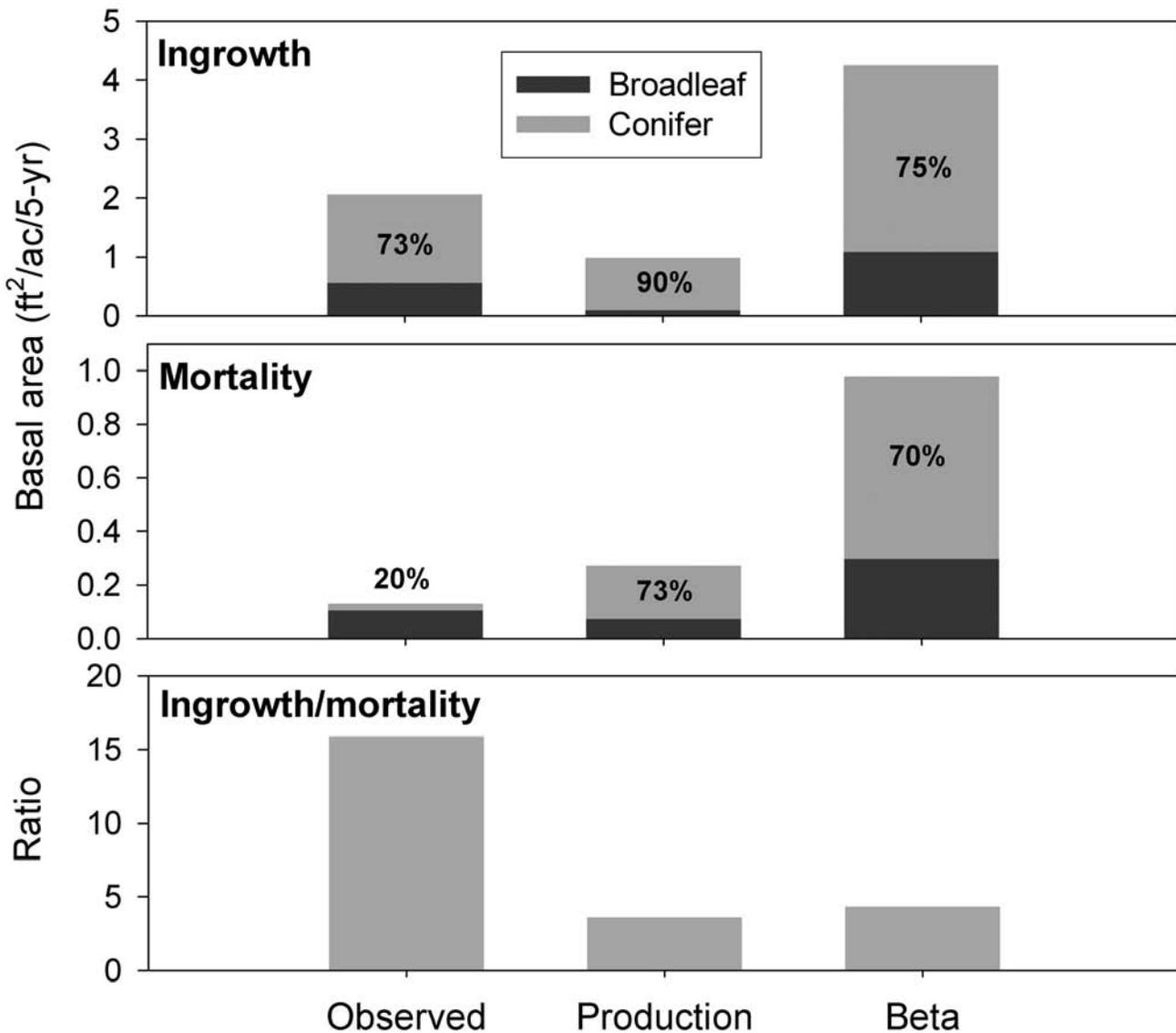
Model	Intercept	Slope	R <sup>2</sup>
Production code (FVS-NE <sub>p</sub> )	-0.176 (0.184)	0.6126 (0.069)	0.180
Beta code (FVS-NE <sub>b</sub> )	0.771 (0.480)	1.788 (0.180)	0.341

sapling recruitment (fig. 4). Compositionally, sapling recruitment was proportional to overstory make-up at the PEF, which averaged approximately 80 percent conifer BA (fig. 4). By contrast, mortality was considerably higher among broadleaf species at the PEF than predicted by FVS-NE (fig. 4). Thus, not only was the ratio of survival to mortality approximately four times higher according to the PEF dataset, but the ratio of conifer to broadleaf survival was considerably underestimated.

The predicted rates of sapling recruitment were seldom very accurate (table 3). For example, evaluated at the level of the individual plot/interval combination (n=729), only approximately 30 percent of predictions were within 10 percent of the observed value according to either FVS-NE<sub>p</sub> or FVS-NE<sub>b</sub>. As the accuracy criteria were relaxed to ±30 percent and ±50 percent of the observed sapling recruitment rate, approximately 40 percent and 50 percent of the plot/interval combinations projected with FVS-NE<sub>b</sub>, respectively, fell into those ranges; predictions from FVS-NE<sub>p</sub> were somewhat less accurate.

### Diameter Distributions

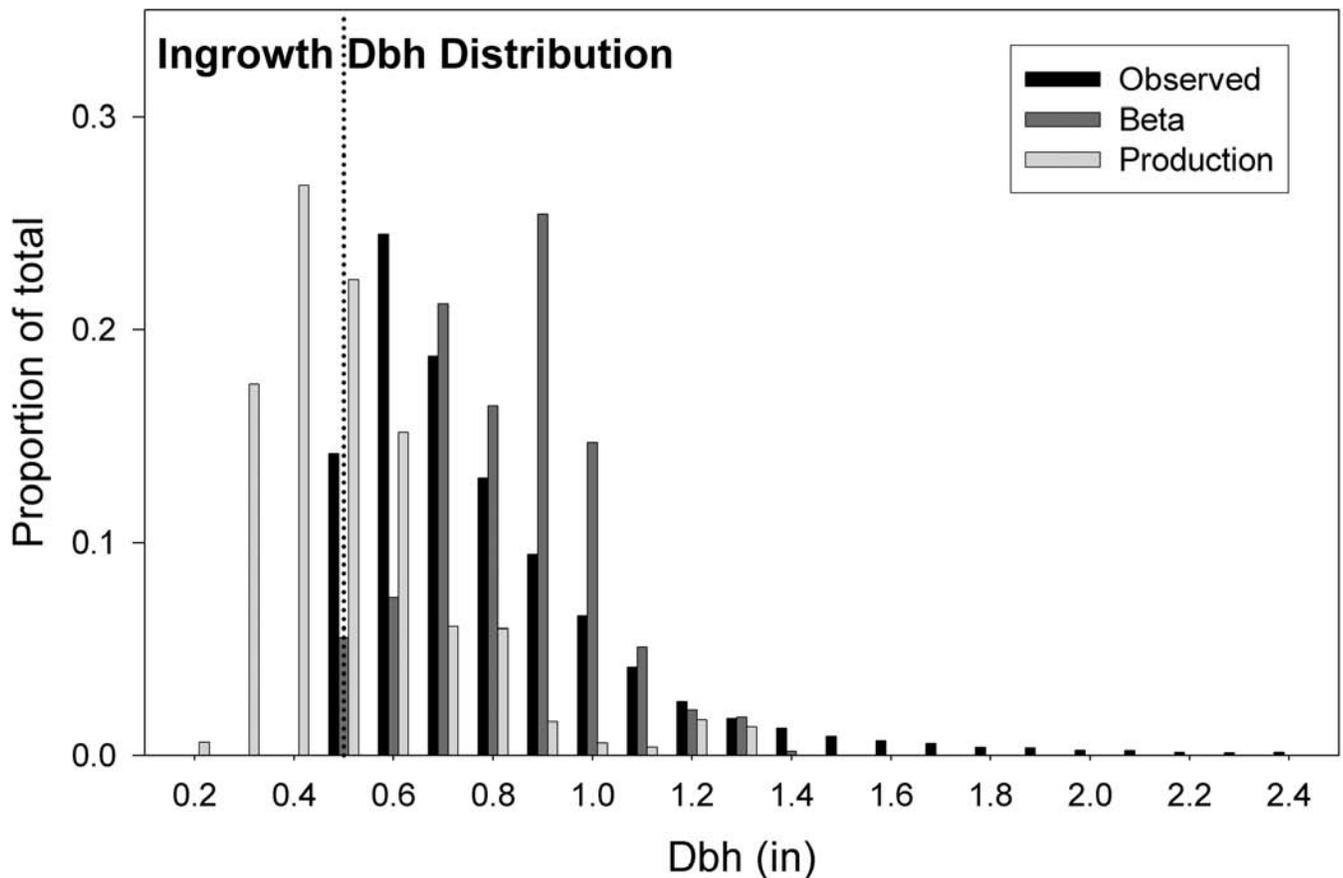
A composite diameter distribution across all treatment/plot/interval combinations was derived for all three data sources (PEF, FVS-NE<sub>p</sub>, FVS-NE<sub>b</sub>). The FVS data came from the TREELIST output at the end of the simulation period, which allowed large



**Figure 4**—Average ingrowth and mortality rates, and the proportion of those totals accounted for by broadleaf and conifer (percentage shown) species at the PEF (observed) and according to the FVS-NE models (production and beta; top two panels). The bottom panel presents the ratio between ingrowth and mortality for each of the estimates.

regeneration (always <0.5-in dbh at the beginning of the interval) to persist below the recruitment threshold over the course of the 5-yr projection. Similar information was not available for the research plots at the PEF, because only counts of stems between 4.5-ft tall and 0.5-in dbh were taken.

There was a dramatic separation between the two FVS predicted diameter distributions, with peak frequencies occurring at 0.4-in dbh for FVS-NE<sub>p</sub> and 0.9-in dbh for FVS-NE<sub>b</sub>; the peak in the observed distribution was intermediate at 0.6-in dbh (fig. 5). Approximately half of the surviving large regeneration projected by FVS-NE<sub>p</sub> remained below the threshold for sapling ingrowth established in this study. By contrast, all surviving stems projected with FVS-NE<sub>b</sub> had grown up above 0.5-in dbh over the subsequent 5-yr intervals. The long tail on the diameter distribution for the PEF data likely reflects some measurement errors, where ingrowth trees were inadvertently overlooked during the inventory period when they initially crossed that size-class threshold, being added to the inventory during a subsequent remeasurement.

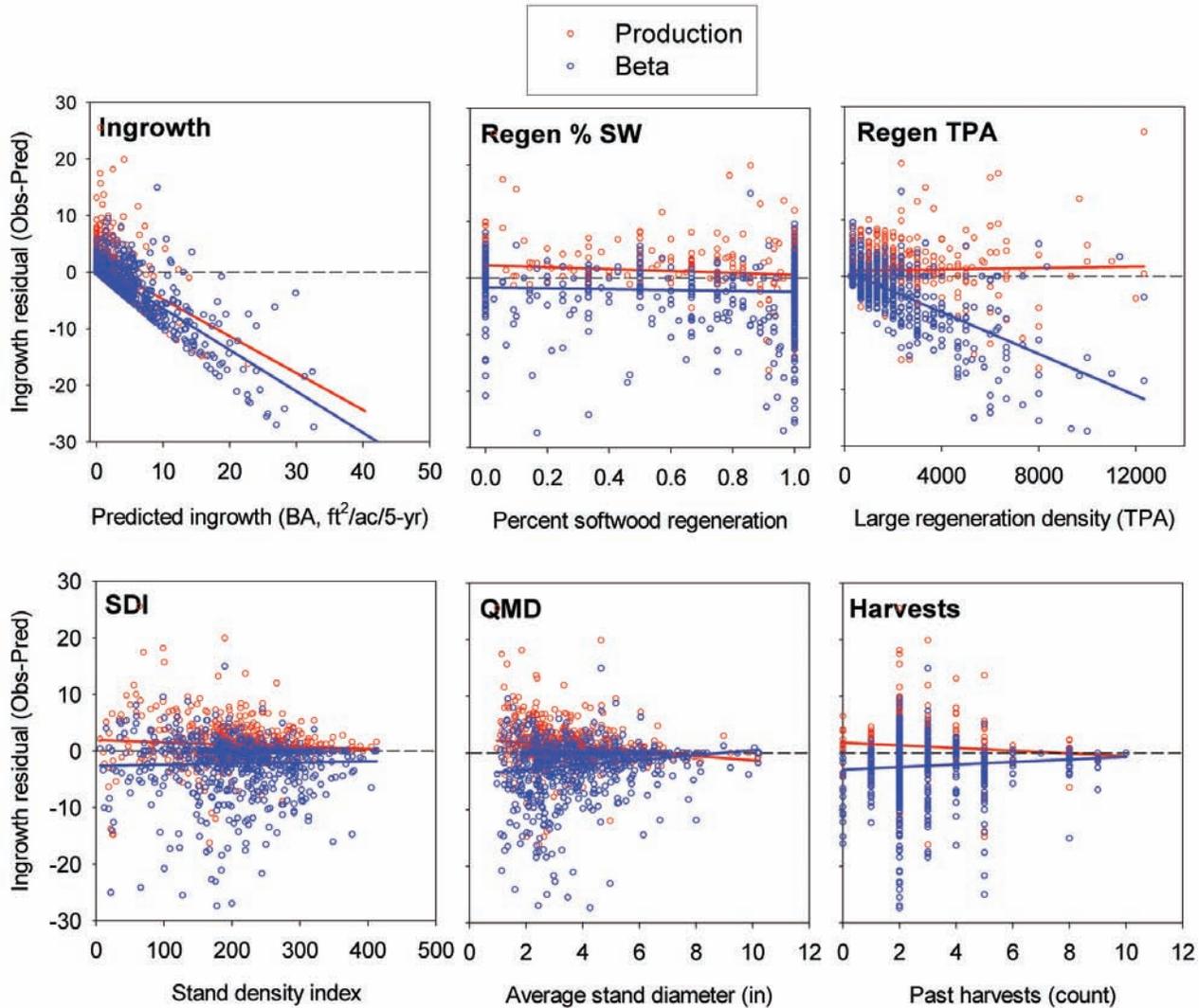


**Figure 5**—Composite diameter distribution comparing sapling recruitment in the partially cut treatments at the PEF with that forecast by the production (FVS-NEP) and beta (FVS-NEB) versions of the model. The vertical line at 0.5-in corresponds to the lower end of the 1-in dbh class threshold established for sapling recruitment.

### Correlates of Model Bias

Prediction bias was strongly correlated with the absolute amount of recruitment to the sapling size class forecast by the models (fig. 6). The characteristic of individual plot/interval combinations most closely associated with the overall negative bias in FVS-NE<sub>B</sub> (model overestimates) was the quantity of large regeneration present at the beginning of the simulation ( $R=-0.67$ ;  $P<0.001$ ); the residuals from FVS-NE<sub>P</sub> were uncorrelated with this variable. According to the linear fit presented in the correlation matrix, plots with abundant large regeneration, perhaps in excess of 2,000 stems/ac, and certainly beyond 4,000 or 8,000 stems/ac, were associated with substantial overestimates of sapling recruitment on the order of 10 to 20 ft<sup>2</sup>/ac/5-yr.

Attempts to uncover the factor(s) behind the positive residuals (model underestimates) associated with FVS-NE<sub>P</sub> involved the consideration of more independent variables, none of which explained a very high proportion of the total error (fig. 6). Increasing the percentage of large regeneration accounted for by conifer species on a plot, the average plot diameter ( $D_q$ ) based on trees above sapling size, and the cumulative number of harvests carried out in a compartment, were all modestly negatively related with prediction bias for FVS-NE<sub>P</sub>; in other words, predictions were more similar to observation as the proportion of conifer regeneration increased, on plots with more large trees, and following multiple harvests.



**Figure 6**—Scatterplot matrix relating ingrowth rate residuals (observed-predicted) with characteristics of the inventory plots at the PEF. A linear smoother was fit through the data clouds.

## Discussion

The rate at which advance regeneration was recruited to the sapling size class on partially cut plots dominated by shade-tolerant northern conifers at the PEF was not closely approximated by FVS-NE running either the production (FVS-NE<sub>p</sub>) or beta coded (FVS-NE<sub>B</sub>) versions of the model. The tendency was for FVS-NE<sub>p</sub> to underestimate ( $-0.84$  ft<sup>2</sup>/ac/5-yr) and FVS-NE<sub>B</sub> to overestimate ( $+2.12$  ft<sup>2</sup>/ac/5-yr) the observed rates ( $1.71$  ft<sup>2</sup>/ac/5-yr). Although shortcomings associated with the nested-plot sampling design used at the PEF tempered expectations about the correspondence between observed and predicted values, we believe that the magnitude of the differences revealed here suggest other factors are involved. The fact that nearly all of the plot/interval combinations (96 percent) had sufficient large regeneration present at the beginning of a simulation to yield the observed ingrowth is offered in support of this contention. Given the plan to transition to the beta coded version of the FVS model (FVS-NE<sub>B</sub>), the following discussion focuses on the behavior of that new parameterization.

## Changes to the Model

Alterations to the model structure implemented between FVS-NE<sub>p</sub> and FVS-NE<sub>B</sub> (table 2), while difficult to view in isolation, can be expected to exert substantial influence on the prediction of small tree dynamics. Most notable among these was the shift away from a generic height growth model for conifers and broadleaves (Bush 1995) to regionally appropriate species-specific h/d allometry and growth functions. Also, the consideration of species shade-tolerance characteristics and relative height in the allocation of SDI based density dependent mortality. Even so, while these changes represent clear improvements from a theoretical standpoint, there appear to be some issues with their current behavior, at least in relation to predicting sapling recruitment dynamics in the Acadian Forest Region.

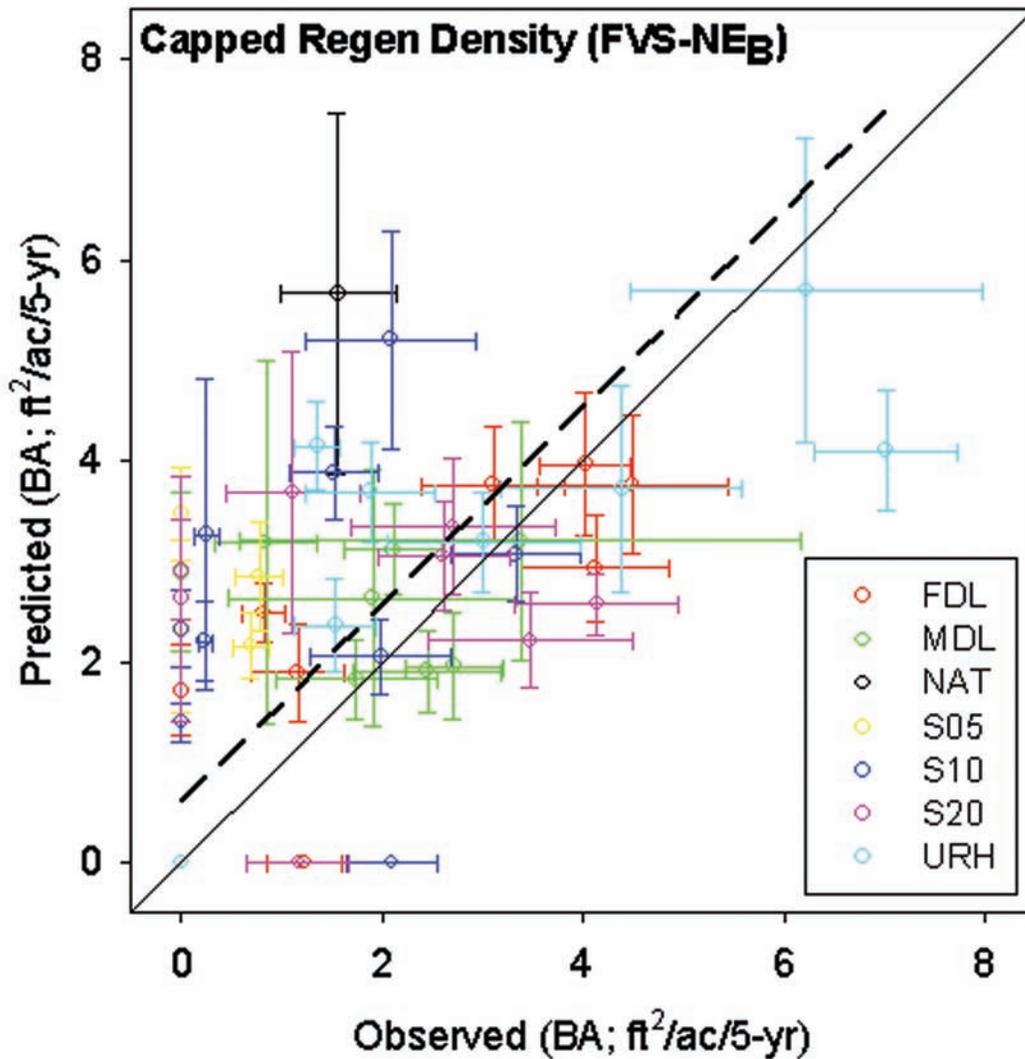
For example, we believe that the growth modifier (GMOD) used to adjust the SI based potential height growth in the 'small' tree model may be set too high in the new model. Specifically, raising the minimum value of GMOD from 0.15 in FVS-NE<sub>p</sub> to 0.5 in FVS-NE<sub>B</sub> is inconsistent with the growth dynamics of the shade-tolerant northern conifers that dominate reproduction following partial-cutting in the Acadian Forest Region (Brissette 1996). Evidence from a recent study of sapling growth rates under the influence of partial canopy cover suggests that the signature shade-tolerant species in this system (i.e. spruce/fir/hemlock) are able to persist while growing at rates well below 10 percent of their potential (Moore et al, in press).

Assessing changes to the mortality function was complicated by the fact that relatively few of the plot/interval combinations had SDIs exceeding 55 percent of RD, the level that triggers density dependent mortality in FVS. Consistent with expectations, mortality rates predicted by FVS-NE<sub>B</sub> were twice as high for plots with RD>55 percent than below that threshold (1.25 vs. 0.58 ft<sup>2</sup>/ac/5-yr), also providing an indication of the level of background mortality forecast by the new model. These estimates did not correspond very well, however, with mortality dynamics measured on the PEF plots, where average rates were only 1.3 times higher on the plots with RD<55 percent. The tendency for FVS-NE<sub>B</sub> to overestimate mortality, and to kill-off a disproportionate number of shade-tolerant conifers relative to broadleaves on these multiaged plots (fig. 4), suggests addressing this component of model behavior may require more than simply increasing the threshold for density dependent mortality.

## The Issue of Regeneration Density

The fact that overestimation of sapling recruitment by FVS-NE<sub>B</sub> was strongly related to the amount of large regeneration at the beginning of the simulation (fig. 6) points to another facet of FVS-NE<sub>B</sub> that is worthy of consideration: the possibility of developing rules for passing only a subset of the 'best,' i.e. most likely to survive, individuals tallied in the inventory to the model. According to the field procedures used by Ferguson and Carlson (1993, p. 4), after all the established regeneration were tallied by species, the two tallest trees, regardless of species, and the tallest individual of each species, were identified on their 300<sup>th</sup> ac circular plots. At a minimum, the four tallest trees taller than a species specific establishment threshold were sought. In our study, regeneration was sampled on three milacre plots per overstory plot, corresponding to 90 percent of the ground area occupied by a 300<sup>th</sup> ac plot. The regeneration sampling protocol at the PEF, that of counts by size class interval, disallowed the identification of best trees based on differences in relative height, because all stems of a given species within the large regeneration class had the same estimated height.

As noted previously, regeneration density in the Acadian Forest Region is typically quite high, owing both to favorable growing season water balance and high shade-tolerance of the component species. The average density of large regeneration on the plots entered into the simulations (i.e. those that contained large regeneration at the beginning of the projection interval) was 1,747 TPA, which corresponds to between five and six trees on a 300<sup>th</sup> ac plot, and is in line with levels recommended for input to the model. Approximately 70 percent of the plots included in this analysis had large regeneration densities at or below this level. A follow-up analysis suggested that model bias could be largely eliminated by restricting the comparison between sapling recruitment rates predicted by FVS-NE<sub>B</sub> and those observed at the PEF, to plots with no more than 1,800 TPA (6 stems on a 300<sup>th</sup> ac plot, or ~2/milacre) of large regeneration (fig. 7). Model accuracy was improved somewhat (R<sup>2</sup> up from 0.341 to 0.398), according to the restricted model.



**Figure 7**—Relationship between observed (PEF) and predicted (FVS-NEB) sapling recruitment rates for plots with no more than 1,800 TPA of large regeneration. Data points means and standard errors from the compartment/interval combinations associated with the partial cutting treatments (codes are provided in Table 1). The dashed line corresponds to the reduced major axis regression (RMA);  $n=65$ , intercept= $0.613 \pm 0.211$ , slope= $0.998 \pm 0.098$ ,  $R^2 = 0.398$ .

A notable improvement was also achieved in terms of the overestimation of sapling mortality. Whereas mortality estimates averaged 8 times higher ( $0.67$  vs.  $0.08$   $\text{ft}^2/\text{ac}/5\text{-yr}$ ) when the full range of large regeneration density was considered, this multiplier was reduced to 3 ( $0.18$  vs.  $0.06$   $\text{ft}^2/\text{ac}/5\text{-yr}$ ) when the density of large regeneration was constrained.

The rationale presented for restricting the amount of regeneration projected by FVS to only the best trees, while a convenient simplifying assumption in terms of forecasting future timber yields, may be limiting in the context of other values. The linkage between early successional forest structure and viability of the threatened Canada Lynx (*Lynx canadensis*) population in Northern Maine (Hoving and others 2004) illustrates this point. Specifically, the snowshoe hare (*Lepus americanus*) populations on which the Lynx feeds appear to depend on the dense conifer cover provided by sapling sized spruce-fir stands (Fuller and others 2004). According to a recently established SDI relationship for the spruce-fir forest type in Maine (Ray and Seymour 2006), fully stocked (defined here as between 55 and 85 percent of SDI<sub>max</sub>) sapling stands with average diameters ( $D_q$ ) between 1- and 4-in dbh can have from 16.9 times down to 1.2 times, respectively,

the stem densities attainable if regeneration input to FVS were to be capped at 1,800 TPA. That such high stem densities are less likely to develop under partial canopy cover (30 percent of the samples in this study) suggests this issue may be more relevant in the context of even-aged stand development.

## Towards a Full Establishment Model

The fact that FVS-NE lacks a full establishment model represents a limitation in terms of making long-term projections of multiaged stand dynamics. Partial-cuttings patterned on those at the PEF, carried out at 5- to 20-yr intervals could result in stands consisting of 5–20 cohorts over a 100-yr management cycle. Ignoring this dynamic will result in unrealistic projections over considerably shorter timeframes, depending on the partial-cutting scenario envisioned.

It is fortunate, from a forest renewal perspective at least, that regeneration tends to proliferate in response to a wide range of harvest initiated disturbances in the Acadian Forest Region (Seymour 1992, Brissette 1996). This allows users interested in simulating long-term partial-cutting scenarios to input regeneration into the model, based on information from inventory plots or even personal experience, with a fair degree of confidence that regeneration will fill growing space not occupied by the overstory. However, resolving the issue of species composition remains a daunting challenge. On this issue, some guidance is provided by the observation that less shade-tolerant hardwoods tend to increase in abundance with disturbance intensity in the Acadian Forest Region (Sendak and others 2003).

Alternatively, information about stand structure, species composition, and site quality (e.g. soil texture and drainage) obtainable from the FIA Database and other sources could be correlated with seedling/sapling populations on those plots and developed into an automated regeneration algorithm, following the methodology for the Prognosis based Variants of FVS that support full establishment models (Ferguson and Crookston 1991). We believe this approach represents the best way forward, and would be the most expedient means of generating objective estimates of forest renewal in the context of long-term partial-cutting scenarios within the existing FVS framework. In the meantime, the Regeneration Imputation Extractor, REPUTE (Vandendrieshe 2005)—a recently developed FVS Post-Processor that creates ‘regeneration’ addfiles based on the sapling component of an existing stand table, and available to all Regional Variants of FVS—provides an option that may be used where direct measurements or expert knowledge is lacking.

## Summary and Recommendations

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The accurate portrayal of regeneration and sapling recruitment dynamics presents a significant challenge to modeling stand development over the long-term, particularly where management practices give rise to multiaged stand structures. The current and soon to be released version(s) of FVS-NE exhibit some serious limitations in this regard, and users seeking reliable predictions of sapling recruitment rates in response to partial-cutting within the shade-tolerant conifer dominated portion of the Acadian Forest Region should be cognizant of them. The fact that no strong correlates of model bias were detected for the predictions obtained from FVS-NE<sub>p</sub>, and perhaps more importantly that the parameterization of the small tree model is based on tenuous relationships (i.e. allometry and growth from western variants of FVS, table 2), questions the relevance of seeking improvements to that model. The overestimation of recruitment rates by FVS-NE<sub>b</sub>, in contrast, was closely linked to regeneration density input to the model, and prediction bias could be eliminated by capping the amount of regeneration input to FVS-NE at ~1,800 TPA. Prediction accuracy was only modestly improved, however, and the regeneration density-constrained estimates still only explained approximately 40 percent of the total variation. Further, evidence from past work suggests that the elevation of the growth modifier function (GMOD) in FVS-NE<sub>b</sub> from 0.15 to 0.5 is unrealistically high for the shade-tolerant conifers that dominate our study system. It follows that lowering GMOD to reflect observed sapling recruitment dynamics while maintaining the regeneration density cap is likely to introduce an underestimation bias. Given that the present regeneration density cap is too low to accommodate some important attributes of forest structure in this forest, calibration of both parameters may be required to improve model performance. It is also apparent that the overall mortality rates predicted by FVS-NE<sub>b</sub>

are too high, and do not accurately reflect observed differences between shade-tolerant conifers and less tolerant broadleaves in this forest. Finally, we believe that the development of a full establishment model for FVS-NE, based on modifications to the existing framework for the Prognosis Model, would represent a significant step forward in our ability to forecast medium and long-term stand dynamics in response to contemporary forest management scenarios (i.e. partial-cuttings that result in multiaged stands) in the Northeast.

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