UNDERSTORY HEIGHT GROWTH DYNAMICS IN UNEVEN-AGED, MIXED-SPECIES NORTHERN CONIFER STANDS

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Introduction

There is a great deal of interest in maintaining complex mixed-species, uneven-aged stands in forestry today. These stands provide many non-timber values by conserving important ecological characteristics of the forest. High productivity is also important, as it is key to meeting timber supply objectives. Growth efficiency (GE) in uneven-aged stands, defined as stemwood volume increment per unit of foliage, is maximized by maintaining a high proportion of the stand leaf area in the overstory where tree-level GE is highest (Seymour and Kenefic 2002). Growth efficiency however has been demonstrated to decline with age (Seymour and Kenefic 2002). This presents a tradeoff in managing uneven-aged northern conifer stands where the species of interest, red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* (L.) Mill), and eastern hemlock (*Tsuga canadensis* (L.) Carr.) are all shade tolerants capable of surviving and responding to release after prolonged periods of suppression in highly shaded understories (Godman and Lancaster 1990; Seymour 1992). If their advancement through the understory is delayed by highly stocked upper strata, future GE potential of these stands could ultimately be reduced. To balance the need for well-stocked upper strata with timely progression of trees through the understory, one must quantify the relationship between overstory density and understory height growth.

The purpose of this study was to explore the growth dynamics of understory trees in uneven-aged, mixed-species northern conifer stands dominated by balsam fir, red spruce, and eastern hemlock. The objectives were to 1) model sapling height growth of these three species as a function of overstory density; and 2) use these relationships to determine maximum overstory densities that facilitate adequate understory height growth.

Methods

Four mixed-species stands under uneven-aged management were used in this study. Two stands were operated on a 5-year cutting cycle while two stands were operated on a 10-year cutting cycle. All four stands are part of the long-term USDA Forest Service experiment on the 1540-ha Penobscot Experimental Forest (PEF) in east-central Maine. The PEF is owned by the University of Maine.

Sampling Scheme

The sample for this study included 60 saplings per species equally divided between three height classes of 0.5-2 m, 2-4 m, and 4-6 m for a total sample of 167 trees (there were deficits in the two larger red spruce height classes). These trees were distributed throughout the four stands in order to evenly span the range of available light conditions. Open and closed conditions were represented on an equal basis, to the greatest extent possible. Saplings were excluded if they were growing on poorly or very poorly drained soils, if there was evidence of cutting within the last five years within 5.6 m of the tree, or if the overstory surrounding the sapling contained a large component of hardwoods.

Data Collection

Canopy closure was measured by taking a gap fraction measurement (DIFN) directly above each sample tree using a LI-COR LAI-2000 Plant Canopy Analyzer (LAI-2000) (LI-COR Inc., Lincoln,

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NE) between mid-August to mid-September in 2002. Gap fraction is the proportion of canopy openness (where 1.0 represents full canopy openness and 0.0 represents full canopy closure), which is achieved by comparing a below-canopy diffuse light reading with a simultaneous reading taken in the open. Height growth measurements (the first five internodal distances) were taken for each sample tree between mid-August and late September in 2002.

Data Analysis

Average annual height increment (AAHINC) was calculated by summing the measured internodal distances and dividing by the number of nodes. Several linear and non-linear models were used to predict AAHINC for each species using initial height (IH) and DIFN as predictor variables (Table 1). The following alternative hypotheses of height growth response with respect to increases in gap fraction were tested: 1) a linear increase, 2) a curvilinear monotonic increase, and 3) a peaking pattern at intermediate gap fraction values. The models were fit using SYSTAT v.10.2 (Systat Software Inc., Richmond, CA), with alpha=0.05.

Table 1.—Linear and nonlinear regression models tested to predict balsam fir, red spruce, and eastern hemlock height growth from initial height and gap fraction.

Hypothesis	Model
1	$AAHINC = b_0 + b_1 DIFN + b_2 IH$
2	$AAHINC = b_0 * DIFN^{b1} * (IH)^{b2}$
3	$AAHINC = b_0 + b_1 DIFN + b_2 DIFN^2 + b_3 IH$

Results

Annual Height Growth Models

Both IH and DIFN were significant in predicting sapling height growth for all three species. Monotonically increasing power functions of height growth with respect to DIFN best modelled height growth for all three species (Table 2).

Table 2.—Best fit regression model and corresponding R^2 value for each species describing sapling height growth as a function of initial sapling height and gap fraction.

Species	Best fit model	R^2
Balsam fir	$AAHINC = 0.270 * (DIFN1)^{0.607} * (IH)^{0.344}$	0.681
Red spruce	$AAHINC = 1.289 * \exp[-1.822 * (DIFN1)^{-0.238} * (IH)^{-0.173}]$	0.702
Eastern hemlock	$AAHINC = 0.174 * DIFN1^{0.309} * (IH)^{0.275}$	0.502

Discussion

The findings of this research demonstrate that overstory canopy closure, defined as gap fraction, significantly affects height growth of balsam fir, red spruce and eastern hemlock saplings in uneven-aged, mixed-species northern conifer stands. For saplings up to 6.0 m tall, height growth continues to respond positively to decreases in overstory competition until conditions of full canopy openness are met. Average conditions of canopy closure in these stands significantly reduce the rate of height growth, and prolong the time it takes for saplings to reach heights of 6.0 m compared to even-aged stands. Model predictions show that balsam fir, red spruce and eastern hemlock can grow from heights of 0.5 m to 6.0 m in approximately 35-45 years under average understory conditions in these stands. This is a delay of about 15-20 years compared to a red spruce tree growing in an even-aged stand of site index 50 (Carmean *et al.* 1989).

While sapling height growth is reduced in these stands, they are still capable of advancing from seedlings and small saplings to larger saplings and pole-sized trees beneath well stocked, efficient overstories which are also simultaneously producing stemwood volume. This is an important benefit of uneven-aged management and this trade-off with reduced sapling height growth should be considered in any silvicultural decisions. Non-timber objectives are also important benefits of uneven-aged management that offset the reductions in sapling height growth.

The monotonically increasing nature of the best models for sapling height growth makes it difficult to suggest any particular goal for overstory density to balance the trade-off between efficient overstory leaf area allocation and sufficient sapling height growth. It is apparent, however, that gains in the advancement of saplings through the understory are progressively reduced as higher levels of canopy openness are obtained.

Acknowledgments
The authors would like to thank other committee members Dr. Jeremy Wilson and Dr. Michael Day. Thanks is also expressed to field assistants Leah Phillips, Justin DeRose, and Ted Chernesky and the USDA Forest Service, Northeastern Research Station.

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