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Self-thinning dynamics in a balsam fir (*Abies balsamea* (L.) Mill.) insect-mediated boreal forest chronosequence

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Abstract

Self-thinning dynamics were examined in a natural, 120-year, insect-mediated balsam fir (*Abies balsamea* (L.) Mill.) chronosequence in the humid boreal forests of western Newfoundland. The well-developed chronosequence representing the classic stages of stand development provided a unique opportunity to quantify balsam fir self-thinning dynamics and to independently test a first approximation stand density management diagram developed for mixed balsam fir-black spruce (*Picea mariana* (Mill.) B.S.P.) stands in western Newfoundland. A slope of −1.28 for the self-thinning tree volume–density line (as determined by reduced major axis) was significantly different than the theoretical self-thinning slope of −1.5. This compared very well with other self-thinning studies in *Abies* stands. Older stands judged as non-self-thinning had a shallower slope approaching unity. The mixed fir-spruce stand density management diagram was found to be a good reflection of stand dynamics and may act as an effective operational tool in tree density management. Balsam fir began to self-thin at 75 percentile heights of ~7 m, 60 years of age and stem densities approaching 31,000 stems ha^{-1}. Balsam fir ceased self-thinning in 90 year-old stands, with tree heights > 15 m and stem densities < 3000 stems ha. The relative accumulation of live and dead basal area across the chronosequence was best explained by the relative contribution of insect herbivory, self-thinning and density-independent mortality to tree death. The relative proportion of dead basal area declined steadily from a high of 80% in the youngest stands to a low of 20% in the 60-year-old stands, increasing to levels not exceeding 30% in the oldest stands. Stand break-up associated with the onset of density-independent tree mortality occurred in stands approaching 90 years of age.

Keywords: Newfoundland; Stand development; Reduced major axis; Spruce budworm; Hemlock looper

1. Introduction

The boreal forests of Canada are generally of fire origin, but in the moist eastern boreal forests dominated by late succession balsam fir (*Abies balsamea* (L.) Mill.), forest fires are less frequent (Johnson, 1995; Bergeron et al., 2001). This is particularly so in the "wet boreal" forests of western Newfoundland where fire is rare or non-existent (Meades and Moores, 1994; Thompson et al., 2003). In these generally humid forests of eastern Canada, insect herbivory, particularly by the spruce budworm (*Choristoneura fumiferana* (Clem.)), hemlock looper (*Lambdina fiscellaria fiscellaria* Guen.) and balsam fir sawfly (*Neodiprion abietis* Harris), is the dominant disturbance factor (Holling, 1992; Engelmark, 1999). Three major spruce budworm outbreaks starting in 1910, 1940 and 1970 affected about 10, 25 and 57 million hectares of forest, respectively (Blais, 1983; Morin and Laprise, 1990). The hemlock looper has caused extensive stand mortality in Newfoundland (Hudak et al., 1996) and to a lesser extent in New Brunswick (MacLean and Ebert, 1999). More recently, historically unprecedented outbreaks of balsam fir sawfly have occurred in western Newfoundland (Moreau, 2006).

The humid boreal forest landscape is dominated by stands originating from insect defoliation. The new stands are the result of the vigorous release of a well-established balsam fir seedling bank (Greene et al., 1999). This link between insect-mediated stand collapse and vigorous stand re-initiation is so tightly coupled that the balsam fir-spruce budworm ecosystem is best described as a disturbance-based, self-regulating, self-perpetuating system (Baskerville, 1975; MacLean, 1984).

It has been extremely difficult to examine the stand dynamics of insect origin stands in a chronosequence due to

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the long history of pulpwood harvesting in balsam fir stands of eastern Canada. Harvesting has been widespread, often damaging residual seedling banks and creating an unnatural and highly variable pattern of second-growth stand development.

An area was noted in western Newfoundland where an insect-mediated balsam fir chronosequence could be examined in a landscape that had never been logged. The Little Grand Lake Provisional Ecological Reserve is composed of a fine-scale mosaic of stands of diverse age, structure and developmental sequence (McCarthy, 2004). This landscape heterogeneity is controlled for the most part by recurrent stand-replacing outbreaks of the hemlock looper and spruce budworm (Otvos and Moody, 1978; Otvos et al., 1979). Periodic outbreaks that kill mature canopies and replace them with vigorous young stands have created a natural chronosequence of relatively homogeneous even-aged stands. The landscape-level mosaic patch structure has provided a unique opportunity to examine the relationship between insect herbivory and stand structure. In most other forest areas of Newfoundland, and indeed throughout much of eastern Canada, such an opportunity does not exist because of the confounding effect of extensive forest harvesting.

Balsam fir, given its ability to form persistent, well-developed seedling banks under mature canopies, responds vigorously to release after insect-mediated canopy disturbance and undergoes intense self-thinning during stand development. Density-dependent competition during self-thinning is generally considered to follow the −3/2 power law (Yoda et al., 1963).

Self-thinning in *Abies* stands has been traditionally examined in *Abies* wave forests (Oshima et al., 1958; Kuroiwa, 1959; Tadaki et al., 1977; Mohler et al., 1978; Kohyama and Fujita, 1981; Sprugel and Bormann, 1981; Sprugel, 1984; Moloney, 1986; Kohyama et al., 1990; Robertson, 1993) or in stands that provided a range in tree densities needed for the construction of stand density management diagrams (SDMDs) (Sturtevant et al., 1998; Wilson et al., 1999; Bégin et al., 2001; Solomon and Zhang, 2002).

This study examines self-thinning dynamics within a natural, insect-mediated 120-year chronosequence of balsam fir-dominated stands. The well-established chronosequence provides a unique opportunity to examine three main objectives: (1) the quantification of balsam fir self-thinning dynamics in an insect-mediated natural chronosequence of stands, (2) a comparison of self-thinning dynamics with published accounts of self-thinning in other *Abies* stands and (3) independent testing of a first approximation SDMD developed for mixed balsam fir-black spruce (*Picea mariana* (Mill.) B.S.P.) stands of western Newfoundland (Sturtevant et al., 1998). Using established self-thinning theory, it is possible to determine tree heights at which self-thinning begins, the beginning of stand break-up and consequent ‘‘gap dynamics’’ in the absence of insect herbivory, the accumulation of dead wood with stand development and the changing characteristics of stand and stock table development in these natural disturbance origin stands.

2. Materials and methods

2.1. Study area

The 106 km^2 study area (350–500 m above sea level) is located within the Little Grand Lake Provisional Ecological Reserve in western Newfoundland (48°38′ N, 57°49′ W). The study area is considered as transitional between the ‘‘west coast’’ climatic zone and the ‘‘western hills and mountains’’ variant of the ‘‘central uplands’’ climatic zone to the east (Banfield, 1983). Based on 1991–1997 data from a data collecting platform southeast of the study site (48°23′ N, 57°34′ W, 420 m asl), mean annual temperatures are 2.3 °C, with total precipitation of 1377 mm, of which 29% is snow (K. Rollings, *personal communication*).

The study site lies within the generally very rugged, productive Corner Brook boreal forest section B28b (Rowe, 1977) and on the western edge of the Corner Brook subregion of the western Newfoundland ecoregion (Damman, 1983; Meades and Moores, 1994). The Damman forest types found throughout the study area include *Dryopteris-Lycopodium*-balsam fir, *Dryopteris-Hylocomium*-balsam fir, *Hylocomium*-balsam fir, *Pleurozium*-balsam fir, *Kalmia*-black spruce and black spruce-feathermoss (Damman, 1967; Meades and Moores, 1994).

2.2. Plot selection, sampling and measurement

An extensive aerial and ground reconnaissance combined with photo interpretation of 1997 1:12,500 colour aerial photographs of the study area by the Newfoundland and Labrador Forest Service confirmed a landscape-level mosaic of stands ranging in age from age class 1 (0–20 years) to age class 7 (>120 years). Given the general inaccessibility of the study area and the desire to sample stands within a specific range of age variability and stand development, sample plots were chosen arbitrarily without preconceived bias (McCune and Grace, 2002). At least five candidate stands within each interpreted age class were identified on the aerial photos and located on the ground. The interpreted stand ages served only as a basis for sampling and, if need be, were subsequently refined by stand-level tree age analysis. A total of 50 stands were sampled (Fig. 1).

Prior to plot layout, a thorough reconnaissance was made of each candidate stand and its surrounding area. Only structurally homogeneous stands (*sensu* Poore, 1962) with no history of logging were sampled. Care was taken to minimize overlap of different aged stands. The first corner of each sample plot ranging from 100 to 750 m^2 was randomly located. All live and dead trees ≥1.3 m tall were flagged, numbered, identified to species and measured for caliper diameter (cm) at breast height (dbh) and mortality status. Tree height (0.1 m) was obtained by measuring the length of dominant or codominant trees felled for stem and dendrochronological analysis.

2.3. Self-thinning regression analysis

Empirical analysis and verification of the −3/2 self-thinning rule depends in particular on three components of the statistical