EFFECTS OF NATURAL DISTURBANCES CAUSED BY THE SIBERIAN MOTH, *DENDROLIMUS SUPERANS SIBIRICUS* (TSCHETVERIKOV), AND FIRE ON THE DYNAMICS OF BOREAL FORESTS IN KRASNOYARSK KRAI, RUSSIA

by

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DEDICATION

This dissertation is dedicated to my wonderful wife, Olga Agalakova, for her unwavering support and continued patience.

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List of Abbreviations

A. Br.	Alexander Braun, botanical author
AMSL	above mean sea level
ANOVA	analyses of variance
Brid.	Samuel Elisee von Bridel, botanical author
cm	centimeter(s)
CWD	coarse woody debris
DBH	diameter at breast height
Du Tour	Du Tour de Salvert, botanical author
Ehrh.	Frederick Ehrhart, botanical author
Fuchs	Hans Peter Fuchs, botanical author
ha	hectare(s)
Hedl.	J. T. Hedlung, botanical author
Hedw.	Johann Hedwig, botanical author
Holub.	Josef Holub, botanical author
kg	kilogram(s)
Koelle.	Johann Ludwig Christian Koelle, botanical author
L.	Carl Linnaeus, botanical author
Ledeb.	Carl Friedrich Ledebour, botanical author
m	meter(s)
Mayr.	Heinrich Mayr, botanical and entomological author
Mg	megagram(s), metric ton(s)
Mill.	Philip Miller, botanical and entomological author
Mitt.	William Mitten, botanical author
Moench.	Conrad Moench, botanical author
Nakai.	Takenoshin Nakai, botanical author
Newm.	Edward Newman, botanical author
Pursh	Frederick Traugott Pursh, botanical author
Ratz.	Ratzeburg, entomological author
Roth	Albrecht Wilhelm Roth, botanical author
Sarg.	Charles Sprague Sargent, botanical author
Schimp.	Wilhelm Philipp Schimper, botanical author
SE	standard error
Trin.	Carl Bernard von Trinius
Voss	Andreas Voss, botanical author

Abstract

EFFECTS OF NATURAL DISTURBANCES CAUSED BY THE SIBERIAN MOTH, *DENDROLIMUS SUPERANS SIBIRICUS* (TSCHETVERIKOV), AND FIRE ON THE DYNAMICS OF BOREAL FORESTS IN KRASNOYARSK KRAI, RUSSIA

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The effects of fire and Siberian moth, *Dendrolimus superans sibiricus* (Tschetverikov), (Lepidoptera:Lasiocampidae) defoliation on overstory and understory composition and structure, carbon flux, and conifer regeneration were examined in the boreal forests of Krasnoyarsk Krai, Russia to better understand the impact the Siberian moth may have if introduced in North American forests.

Sampling was conducted in the following stand types: (1) undisturbed fir-spruce, (2) recent fire, five or fewer years ago, (3) severe defoliation by the Siberian moth in the 1995-97 outbreak with no fire, (4) severe defoliation by the Siberian moth in the 1995-97 outbreak, with a large post-outbreak fire scar, and (5) severe defoliation in the 1954-57outbreak that burned in the 1960's.

A steady state of forb domination between older defoliated stands and recently defoliated stands suggests that the Siberian moth may be responsible for a disruption of succession in Siberian boreal forests. No live conifer stems were sampled or observed in any of the recently defoliated and older defoliated stands.

The implications for carbon flux in large areas with complete mortality caused by the Siberian moth and subsequently burning are significant. Stands defoliated in the 1950's and burned in the 1960's exhibited major differences in amounts of both downed and standing coarse woody debris compared to

stands defoliated and burned in the 1990's. This study found a loss of 23.8 Mg/ha of C in coarse woody debris in the approximately 50 year period separating these two disturbance types.

Stands defoliated in the 1950's and burned in the 1960's had no regeneration. Stands defoliated in the 1990's, burned or unburned, were comparable in the number of seedlings found but had significantly fewer seedlings than undisturbed stands. The stands enduring only recent fire appeared to have typical boreal forest regeneration. Reversion to fir-dominated stands after a severe Siberian moth outbreak may require several centuries of successive regeneration from conifer trees along the periphery of the disturbed area.

Chapter I

Introduction

Forest succession is significantly affected by disturbance, an arresting phenomenon of landscape ecosystem processes (Palik and Pregitzer 1992, Viereck 1973, Viereck et al 1983). The type, scale of disturbance, and intervals between disturbances can have a significant effect on forest succession, species composition, and nutrient cycling (Shugart et al 1992). Repeated disturbance may affect the overall process of succession through the depletion of nutrients, reduction in the active and dormant seed banks, and influence stand composition toward more disturbance-adapted species (Aber and Melillo 1991). The shorter the interval between disturbances the more pronounced these effects might be (Pedersen 1998a).

Historically, it is theorized that a particular forested ecosystem type will predominate with a continuum of succession (Aber and Mellio 1991). For example, a mature conifer forest is disturbed and replaced by secondarily-succeeding relatively short-lived deciduous species while shade-tolerant conifer seedlings germinate in the understory and patiently await release upon necrosis of the deciduous overstory (Walker et al. 1986). Yet, there occur instances where the continuum of succession is disrupted and a particular vegetation type dominates for a longer than usual period of time. This alternative steady state typically occurs as a result of *infrequent* extreme disturbance events (Turner et al. 1998) such as volcanic eruption, catastrophic long-return interval fire, or 100-year floods. However, this type of alternative stable state appears to have occurred in the Siberian boreal forests of Russia following a *cyclical* insect outbreak in the 1950's (Kharuk et al. 2003).

While the effects of cyclical insect outbreak and fire in the North American boreal forests are well documented, little is known of this phenomena in the Siberian forests (Mattson et al. 1988, McCullough et al. 1998, Ward and Mawdsley 2000, Ward and Tithecott 1993). Because of its vast size and significant carbon stores, disturbance regimes in the Russian boreal forest may play an important role in global change effects (Kasischke and Stocks 2000, Shugart et al. 1992). The boreal forests of Siberia retain significant areas largely unscathed by human disturbance such as logging and fire suppression as compared to North

American forests. Also, the largest amount of late successional forests occurring in the Russian Federation is in Siberia (Alexeyev and Birdsey 1998).

The Siberian boreal forest ecosystems have endured many natural disturbances during the last hundred years. Native Siberian moth (Lepidoptera:Lasiocampidae, *Dendrolimus superans sibiricus* (Tschetverikov)) infestations recur every 7 to 10 years (Vorontsov 1982) while surface fires occur at intervals of 10-100 years (Conard and Ivanova 1997). These disturbances, individually, in combination, or sequentially, affect forest stand structure, composition, and function (Pedersen 1998b). This investigation focused on how the effects of Siberian moth outbreaks and fire influence 1.) overstory and understory structure and composition, 2.) coarse woody debris and implications for carbon flux, and 3.) conifer regeneration.

North American conifer forests typically have regeneration in the understory following combinations of disturbance by insects and fire (De Grande and Bergeron 1997, Frelich and Reich 1995, Witter et al. 1984, Witter and Ragenovich 1986). The spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera:Tortricidae) is the most destructive defoliator of conifers in North America. This native pest can cause significant mortality in stands of its primary hosts of balsam fir, *Abies balsamea* (L.) Mill., white spruce, *Picea glauca* (Moench) Voss, and red spruce, *Picea rubens*, Sarg (Witter et al. 1984). Mortality by the spruce budworm occurs primarily in mature conifers within the stand and does not usually have much effect on seedlings and saplings in the understory (Morin and Laprise 1997). Balsam fir is usually defoliated three or four times by the spruce budworm before significant mortality occurs.

Another serious pest of North American conifer forests is the balsam woolly adelgid, *Adelges piceae* (Ratz.) (Homoptera:Adelgidae). This non-native pest is not a defoliator but causes significant mortality with its piercing-sucking mouthparts in stems and crowns of its primary hosts Fraser fir, *Abies fraseri* (Pursh.) and balsam fir, *A. balsamea* (L.) Miller (Hain 1988, Amman and Speers 1965, Amman 1962, Balch 1952). The insertion of the adelgid's stylet inhibits water transport within the tree; large numbers will cause mortality in seven to ten years (Amman and Speers 1965). Witter and Ragenovich (1986) found significant mortality (82 to 95%) on mature Fraser fir stems in the overstory with excellent regeneration in the understory. Smith and Nicholas (2000) report good regeneration in stands decimated by the balsam woolly adelgid but at lower densities than stands not affected by this pest. Both regeneration studies were conducted at least 10 years after significant mortality caused by the balsam woolly adelgid. The native spruce budworm and the non-native balsam woolly adelgid are serious pests to fir species in North America and cause significant amounts of mortality in conifer forests.

This study was conducted in the boreal forests of Krasnoyarsk Krai, Russia where Russian investigators reported a massive outbreak of Siberian moth larvae from 1995-1997 that resulted in the loss of over 1.5 million ha of Siberian fir-dominated forest within the boundaries of Krasnoyarsk Krai (Kondakov et al. 1997, Kharuk, 1999). Initial field observations confirmed the complete defoliation of large forested stands. Historical evidence also indicated that the defoliated stands often endured fire following these cyclical moth outbreaks. Loss of large tracts of forests to this native defoliator coupled with questions on the effects on forest composition post outbreak, carbon cycling, and conifer regeneration presented an opportunity to compare and contrast relatively undisturbed Siberian fir stands with those decimated by the Siberian moth.

A stand is defined in this study as a distinct area of the forest that is relatively homogeneous in species composition or age and could be managed as a single unit. The sampling design employed simple random sampling with identical measurements in each disturbance type. Targeted stands consisted of two temporal periods of disturbance and three combinations of disturbance with ten separate undisturbed stands serving as controls. Sampling was conducted in the following stand types: (1) undisturbed fir-spruce, (2) recent fire, five or fewer years ago, (3) severe defoliation by the Siberian moth in the 1995-97 outbreak with no fire, (4) severe defoliation by the Siberian moth in the 1995-97 outbreak, with a large post-outbreak fire scar, and (5) severe defoliation in the 1954-57outbreak that burned in the 1960's.

The aforementioned stands were sampled to quantify overstory and understory structure and composition, volumes of coarse woody debris for carbon flux determination, and number and height of conifer seedlings to assess regeneration. These measurements and their subsequent analysis will suggest the potential effects of a Siberian moth invasion in North American boreal forests should it become established. The effects of this Siberian study may be viewed as conservative in contrast to potential North American effects since few, if any, natural enemies of the Siberian moth are present on this continent. Furthermore, since more coniferous genera, with more species in these genera, are present in North

American forests than in Siberia, the Siberian moth may more easily colonize these congeneric relatives (Niemela and Mattson 1996).

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Chapter II

Effects of fire and insect outbreak disturbances on the overstory and understory in the boreal forests of Krasnoyarsk Krai, Russia

Abstract

The effects of fire and Siberian moth, *Dendrolimus superans sibiricus* (Tschetverikov), (Lepidoptera:Lasiocampidae) defoliation on overstory and understory composition and structure were examined in the boreal forests of Krasnoyarsk Krai, Russia. Stands dominated by Siberian fir, *Abies sibirica* Ledeb., were subjected to disturbances in the 1950's and the 1990's. During these periods some stands experienced fire, or pest outbreaks, and some both. Stands enduring only fire exhibited typical boreal forest succession. Stands defoliated in the 1950's and burned in the 1960's exhibited minor differences in composition of both understory and overstory stems compared to stands defoliated and burned in the 1990's. Stands defoliated in the 1990's, burned or unburned, had 100% conifer mortality, including all seedlings and saplings. The older disturbed stands exhibited a dominant forb composition that included a sparse deciduous overstory of birch, *Betula spp*. No conifers were measured or observed in this area more than 50 years after the stands were defoliated and subsequently burned. A steady state of forb domination between older defoliated stands and recently defoliated stands suggests that the Siberian moth may be responsible for a disruption of succession in the boreal forest.

Introduction

Approximately 1.2 billion ha of the Earth's surface is covered by boreal forests, of which approximately 46% are located in Russia (Alexeyev and Birdsey 1998). While the effects of human and natural disturbance in the North American boreal forests are well documented, little is known of this phenomena in the Siberian forests (Mattson et al. 1988, McCullough et al. 1998, Ward and Mawdsley 2000, Ward and Tithecott 1993). Because of the Siberian boreal forests vast size and significant carbon stores, disturbance regimes in the Russian boreal forest may play an important role in global change effects (Kasischke and Stocks 2000, Shugart et al. 1992). The boreal forests of Siberia retain significant areas largely unscathed by human disturbance such as logging and fire suppression as compared to North

American forests. Also, the largest amount of late successional forests occurring in the Russian Federation is in Siberia (Alexeyev and Birdsey 1998).

The Siberian boreal forest ecosystems have endured many natural disturbances during the last hundred years. Native Siberian moth (Lepidoptera:Lasiocampidae, *Dendrolimus superans sibiricus* (Tschetverikov)) infestations recur every 7 to 10 years (Vorontsov 1982) and surface fires with a return interval of 10-100 years (Conard and Ivanova 1997). These disturbances, individually, in combination, or sequentially, affect forest stand structure, composition, and function (Pedersen 1998). This investigation focused on the effects of insects and fire on overstory and understory structure and composition.

The dominant insect responsible for disturbance in this area is the Siberian moth, *Dendrolimus superans sibiricus* (Tschetverikov), (Lepidoptera:Lasiocampidae). This destructive defoliator of conifers in Asia (Gninenko and Orlinskii 2002) prefers *Abies spp*. and *Larix spp*. but also will defoliate *Pinus spp*. and *Picea spp*. at outbreak population levels (Baranchikov et al. 1997). Siberian moth outbreaks have been recorded throughout a large area of northcentral Asia (Baranchikov et al. 1997, Grodnitsky and Palnukova 1999, Kondakov et al. 1997, Vorontsov 1982). Outbreaks occurring over the last century in Krasnoyarsk Krai, Russia are well documented by the V. N. Sukachev Institute of Forest (Pleshnikov et al. 2002).

Vorontsov (1982) reports outbreaks lasting 4-5 years and periods between outbreaks varying from 7-10 years. The magnitude of durations reportedly varies and may be related to drought (Vorontsov 1982; Grodnitsky and Palnukova 1999). The life cycle of the Siberian moth varies from two to four years depending on population density. Males usually have 5 instars while females usually have 6 instars. However, the larvae of the males may have 5 to 9 instars and the females 6 to 10 instars (Grodnitsky and Palnukova 1999). The larvae can grow up to 110 mm long and usually spend two winters coiled up in the forest litter as larvae. The insect normally overwinters in the 2nd to 3rd instars and in the 5th to 6th instars. Pupation occurs from mid-June to late July in pupal cases attached to branches or stems in tree crowns. Adult moths disperse from late June to early August and deposit egg clusters on needles or branches. Immediately preceding outbreaks, a significant segment of the increasingly dense population has a life cycle of two calendar years while the remainder has a three-year cycle. This results in the adults of two generations emerging simultaneously causing the population to reach outbreak proportions (Galkin 1993). Starvation, virus, and natural enemies cause a downward trend in population numbers. These interactions induce a portion of the population to convert to a four calendar year life cycle with three winters spent in the larval stage (Baranchikov et al. 1997, Grodnitsky and Palnukova 1999).

Larvae feed on conifer needles in May and June, causing significant tree mortality during outbreak years (Grodnitsky and Palnukova 1999). This early feeding aborts the development of cones with viable seeds and reduces the seed bank for the following years to almost zero because most conifers have seeds that are viable for only one year (Burns and Honkala 1990).

In this investigation, a landscape ecosystem was identified that was disturbed at two different temporal periods by the Siberian moth larvae. The area contained several individual large tracts over 10,000 ha that were completely defoliated during the 1954-57 moth outbreak. Adjacent to this area are stands that were defoliated during the 1995-1997 moth outbreak. Almost 100% of the area afflicted by the 1954-57 outbreak was then consumed by fire while less than 50% of the area affected by the 1995-97 infestation has endured fire. Earlier ground observation of the 1954-57 outbreak area confirmed the lack of coniferous overstory species with sparsely populated older deciduous species in a largely herbaceous species-dominated ecosystem. The more recently defoliated area was observed to contain standing dead conifer stems with small clusters of live deciduous overstory species such as *Populus tremula* L. and *Betula pubescens* Ehrh. and a vigorous shrub and herbaceous understory (Buck 1999).

The Siberian moth does not completely defoliate all stands it infests. Estimates of areal extent of defoliation varies widely due to different estimation methodologies employed by Siberian personnel. The stands in this study represented completely defoliated areas to assess forest dynamics after severe outbreak conditions. Adjacent stands were observed to have approximately 25-75% tree mortality caused by Siberian moth defoliation. Differences in understory and overstory composition were quantified in this study to determine the effects of the 1995-97 Siberian moth infestation and this pest’s contribution to the disruption of forest succession resulting from the 1954-57 infestation in severely defoliated stands.

Study Site

The study site is located along the Yenesei Transect (Pleshnikov et al. 2002) in south-central Siberia and was not glaciated during the Pleistocene; it is relatively homogeneous in ecosystem composition, structure, and function (Chlachula 2001, Velichko et al. 1997). It is located at approximately 57^0N latitude and 92^0E longitude and is a relatively flat plain with altitudes of 300 to 400 m AMSL.

The climate at the study site is strongly continental with an average January temperature of -19^0 C with a minimum of -55^0 C and an average snow depth of 65 cm. Average July temperatures are $+18^0$ C with a maximum of $+39^0$ C. Mean annual precipitation is 425 mm; eighty percent of which falls during the summer months (Kharuk et al. 2003).

The south-central Siberian dark-needled forest in this study is on discontinuous permafrost (Koropachinsky 1983). It is composed primarily of late successional dominant species of Siberian fir, *Abies sibirica* Ledeb., Siberian stone pine, *Pinus sibirica* Du Tour, and Siberian spruce, *Picea obovata* Ledeb. Siberian fir is the dominant species in this ecosystem with smaller components of Siberian spruce and Siberian stone pine, Siberian larch, *Larix sibirica* Ledeb., and Scotch pine, *Pinus sylvestris* L., interspersed throughout the study area.

Early successional species in the boreal forests of Siberia differ from North America, but generally share the same genera and have similar morphological and physiological characteristics. Dominant early successional genera include *Betula* and *Populus* with minor components of *Sorbus* and *Alnus*. The most prolific species in these genera are European white birch, *Betula pendula* Roth, downy birch, *B. pubescens* Ehrh., Eurasian aspen, *Populus tremula* L., Siberian mountain-ash, *Sorbus sibirica* Hedl., and speckled alder, *Alnus incana* (L.) Moench. (Koropachinsky 1983).

Understory vegetation consists of woody shrubs and creepers, again with genera similar to North America. Several species are not found circum-boreally and are indigenous to central Asia. These include Ural false spirea, *Sorbaria sorbifolia* (L.) A. Br. and Siberian elder, *Sambucus sibirica* Nakai. Typical boreal woody shrubs found in the study area include raspberries, *Rubus spp*., blueberries, *Vaccinium spp*., currants, *Ribes spp*., and roses, *Rosa spp*.

Understory ground cover is dominated by common herbaceous representatives of the taiga including meadow rue, *Thalictrium minus* L., northern bed straw, *Galium boreale* L., monkshood, *Aconitum septentrionale* Koelle, and the ferns, *Gymnocarpium dryopteris* (L.) Newm. and *Dryoptheris carthusiana* (Vill.) H.P. Fuchs. The graminoid community is comprised primarily of *Carex. spp*., *Calamagrostis obtusata* Trin., and *C. epigeus* (L.) Roth. Bryophytic growth is dominated by sphagnum moss, *Sphagnum spp*. L., Schreber's big red stem moss, *Pleurozium schreberi* (Brid.) Mitt., and feather moss *Hylocomium splendens*, (Hedw.) Schimp.

Methods

Targeted stands consisted of two temporal periods of disturbance and three combinations of disturbance with ten separate undisturbed stands serving as controls. Sampling was conducted in the following stand types: (1) undisturbed fir-spruce (Fig. 2.1), (2) recent fire, five or fewer years ago (Fig. 2.2), (3) severe defoliation by the Siberian moth in the 1995-97 outbreak with no fire (Fig. 2.3), (4) severe defoliation by the Siberian moth in the 1995-97 outbreak that burned post-outbreak (Fig. 2.4), and (5) severe defoliation in the 1954-57 outbreak that burned post-outbreak (Fig. 2.5).

A stand is defined in this study as a distinct area of the forest that is relatively homogeneous in species composition or age and could be managed as a single unit. Five replicate stands for each targeted disturbance type were selected to provide a more accurate estimate of the means and associated variance. Replication within disturbance cover types was accomplished by identifying five separate stands within each type of disturbance. An intensive sampling plot was randomly installed in each stand located throughout the study area. Plot selection criteria required a stand to historically be dominant *Abies* with a lesser component of *Picea* and included ease of accessibility and lack of other disturbances. Every effort was made to lessen bias of plot locations and to reduce edge effect by requiring all plot locations to be at least 50 m or more from an edge, road, or other disturbance type such as windthrow or cutting.

Selection of each sample plot was accomplished by interpreting different overstory cover types on Russian forest cover type maps and navigating to the targeted forest type for each disturbance type. Random number tables for both distance and azimuth were used to navigate to the center point of each sampling plot. Location of each sampling plot was documented using map, compass, and geographic positioning system receiver, and recorded on the plot location form. Field sampling plots were established during July and August of 2002 and 2003 (Fig. 2.6).

Field sampling methodology procedures for overstory and understory data collection were adapted from United States Department of Agriculture’s Forest Service Forest Inventory Analysis Program (USDA 2001). This sampling procedure utilized four 7.3 m radius subplots with a central subplot and three subplots emanating 30 m from the central subplot at 120, 240, and 360 degrees (Fig. 2.7). Within each subplot overstory species greater than 12.5 cm in diameter at breast height (DBH) were measured for DBH, overall tree height, status (live or dead), and identified to species.

Each subplot was sampled for individual understory species and percent cover for each species present. All understory species were identified, recorded, and quantified by percent cover. Understory species were defined as having less than 2.5 cm DBH for any woody stem and less than 2 m in height for all species. Percent cover was obtained by visually assessing what percent of each sample plot was occupied by each species while viewing all species vertically from 2 m in height. Each species was categorized into one of seven different vegetation types as defined by the USDA Plants Database (USDA 2005). Vegetation types included tree, shrub, vine, graminoid, forb, fern or fern ally, and bryophyte.

Soil samples were collected to aid in determining relative homogeneity of ecosystem physical properties. Soils data collected for this study included collection of five 10 cm deep cores extracted from each sampling plot. The five soil cores from each sampling plot were combined in the field to create a composite soil sample of each individual sampling plot. Collected soil samples were subjected in a laboratory to soil texture analysis (Gee and Bauder 1986).

Statistical analysis was conducted using SPSS version 15.0 (SPSS 2006). Overstory and understory values from individual stands were pooled by disturbance type. Analyses of variance (ANOVA) with LSD post-hoc tests were conducted to determine if disturbance had a significant effect on relative density and relative dominance of overstory values and percent of cover for understory values among disturbance types.

Results

All soils sampled were loamy with some variation from silty loam to sandy loam. Measured elevation (300-400 m AMSL) and slope were relatively constant. Percent of slope for all sampled plots was predominately level. Four plots did measure some negligible slope (<10%) and slope aspect was variable on these plots.

Overstory Results

Statistical analysis of overstory relative density and relative dominance values indicates that the type of disturbance does have an overall significant effect ($p<0.005$) on composition and structure of the overstory.

Approximately 24% of all stems sampled in the undisturbed stands were standing snags, while recently defoliated stands had no live overstory stems in the sampling plots (Table 2.1). Some relatively small patches of *Betula* and *Populus spp.* were observed in the recently defoliated stands but none occurred within the study plots. No live conifer stems were sampled or observed in the recently defoliated stands. The total number of stems and the mean DBH for both the undisturbed stands' live stems and the recently defoliated stands' dead stems is similar (Table 2.1).

Relative densities, number of stems per species divided by number of total stems sampled, for all sampled stands were dominated by *A. sibirica* with the exception of the old defoliated and burned stands (Table 2.2). A smaller component of *Picea obovata* and *Pinus sibirica* was found in the undisturbed stands while a small component of *P. obovata* was found in the recently burned stands and in the recently defoliated stands.

The recently burned stands displayed the characteristics of a severe boreal forest stand replacement fire (Chappell and Agee, 1996). In contrasting live and dead stems, composition and densities in these stands prior to burning were similar to the undisturbed stands (Table 2.1). *Betula pubescens* comprised 35% of the relative density of the recently burned stands while it was not detected in the sampling of the late successional undisturbed stands.

The relative densities for live *A. sibirica* stems differed significantly with 62% more in the undisturbed stands versus the recently defoliated stands. Relative density for only dead stems in the recently defoliated stands was 19% higher than the relative density of dead stems in the undisturbed stands.

Relative dominance (sum of individual species basal area divided by sum of all species basal area) for all sampled stands was dominated by *Abies sibirica* with the exception of the recent and older stands that were defoliated and burned (Table 2.3). The recently defoliated and burned stands were dominated by dead *A. sibirica* stems with dominant live *P. tremula* stems. The older stands that were defoliated and burned had two old *A. sibirica* snags with a sparse live dominant *B. pendula* overstory. These stands would be classified as non-stocked under USDA Forest Inventory Analysis guidelines (USDA 2001). These older (50+ yrs.) disturbed stands appeared more like a wet meadow with widely scattered birch stems.

Understory Results

Mean values for percent cover were calculated for each vegetation type in each plot and compiled by disturbance type (Table 2.4). Statistical analysis of the understory percent cover values indicate that the type of disturbance does have an overall significant effect ($p<0.005$) on the post-disturbance composition of vegetation types. The undisturbed stands had a dominant conifer overstory consisting of Siberian fir, Siberian spruce, and Siberian stone pine. All of the disturbed stands were devoid of a similar dominant conifer overstory that existed prior to stand replacement disturbance.

In the understory of undisturbed stands a significant component of bryophytic and graminoid growth (31% and 29%, respectively; Table 2.4) was measured. The presence of understory tree species declined approximately 50% from undisturbed stands to all stands with different disturbance types except the stands which endured only recent fire which only decreased approximately 25% (Table 2.4). In the undisturbed stands conifers were the dominant understory species while no conifers were present in the understory of older defoliated stands and few in the recently defoliated stands.

The stands which endured recent fire were dominated by graminoids and shrubs (34% and 22%, respectively) (Table 2.4). The understory of stands defoliated by Siberian moth in the 1995 outbreak contained a dominant forb and shrub component (39% and 31%, respectively; Table 2.4). Stands defoliated in the 1995 outbreak and burned shortly thereafter were dominated by forbs (67%) with a lesser shrub component (15%; Table 2.4). The older defoliated stands that subsequently burned were dominated by forbs (70%) with a lesser shrub component (17%; Table 2.4). The remaining 13% was comprised of graminoids and deciduous trees (6% and 7%, respectively; Table 2.4).

Shrub presence reached a peak in the recently defoliated stands and declined by approximately 50% in the recent and older stands that were defoliated and burned. Shrubs were only 8% of the undisturbed stands and increased significantly following recent fire or recent defoliation. However, the combination of recent defoliation followed by fire results in a decrease in shrubs but shrub presence still remains significantly greater than in the undisturbed stands.

Species of vines are not present in large numbers in Siberia and were not a significant factor in any of the sampled disturbance types (Table 2.4). No discernible pattern for vines is apparent across the different disturbance types.

The presence of graminoids was higher in the recent fire stands than in the undisturbed stands while decreasing by approximately 50% in the recently defoliated stands and by approximately 75% in the stands with the combination of recent defoliation and fire. Sample plots established in areas affected by recent stand replacement fires (6-8 years prior to sampling) showed a slight increase in graminoid dominance (from 29% to 34%) with a significant increase in shrub dominance (from 8% to 22%). A decrease in the presence of bryophytes from 31% to 14% also was measured in these stands.

The area where defoliation recently occurred exhibited a change to a forb and shrub-dominated understory. The only trees present in the overstory were early successional deciduous species which Siberian moth larvae do not defoliate. Graminoids and ferns were present to a lesser extent with bryophytic growth absent indicating canopy removal similar to the recent fire plots. It is interesting to note that very few conifer seedlings or saplings were present in the defoliated stands. Siberian moth larvae feed on conifers in all stratums and at outbreak population levels can cause up to 100% mortality of all conifer stems in these stands.

Forbs were the dominant cover in the stands that endured both recent defoliation and fire. The dominant forb in these stands is fireweed, *Chamerion angustifolium* (L.) Holub., an early pioneer species following fire. Forbs became more dominant with an increase in disturbance severity and time since disturbance. While only 15% of the understory consisted of forbs in the undisturbed stands, forbs in the old defoliated and burned stands increased to 70%. Contrasting recently defoliated stands and recently burned stands, forbs were 22% more abundant in the recently defoliated stands. A similarity in abundance of all vegetation types is noted when comparing stands that endured both defoliation and fire 50 years apart (Table 2.5). The greatest percent change found between individual vegetation types in these two disturbances is three percent.

Discussion

A generally accepted theory is that a particular forested ecosystem type will predominate with a continuum of succession (Aber and Mellio, 1991). For example, a mature conifer forest is disturbed and replaced by secondarily-succeeding relatively short-lived deciduous species while shade-tolerant conifer seedlings germinate in the understory and await release upon necrosis of the deciduous overstory (Walker et al. 1986).

The minor differences in dominant understory vegetation types in stands that endured both defoliation and fire approximately 50 years apart suggest that there is little change in understory composition for many years after severe defoliation by the Siberian moth larvae. This lack of succession directly contradicts the continuum theory of forest succession. The necrosis of all conifers from seedlings to dominant overstory individuals by the Siberian moth larvae directly causes the loss of the conifer seed bank and removes all conifer recruitment from the understory. This suggests that regeneration of the conifer forest will only occur around the perimeter of an outbreak and leads to a forb-dominated area that will return to coniferous forest after a slow process of regeneration by seed fall from the periphery of this disturbed area. Fire following insect outbreak in this ecosystem apparently reduces shrub presence and further reinforces the potential for forbs to dominate.

Most graminoids require fire for regeneration and an increase in their presence following fire is expected. Defoliation alone or coupled with fire appears to cause a decrease in the presence of graminoids. This may be a result of the frass and litter fall during defoliation increasing the N content of the soil allowing species of forbs to out compete the graminoids (Frost and Hunter 2004). Larval excrement and the litter generated through defoliation causes an increase in N mineralization that persists for a few years (Belovsky and Slade 2000). It is this increase in N that may be better utilized by forbs causing them to out compete other vegetation types and account for their significant increase when multiple disturbances (fire and defoliation) occur within the same area. Grodnitsky et al. (2002) cites the chemical constituents of Siberian moths' larval frass as a factor affecting the type of understory growth following outbreak populations.

Protection of the understory from the infiltration of sunlight by the coniferous overstory reduces evaporation, and coupled with the acidic soil conditions inherit in a boreal ecosystem, creates an ideal environment for bryophytic growth which further increases acidity and moisture retention in the understory (Crum 1983). Sampled soil types confirmed little difference in physical properties (Fig. 2.8).

Fire alone does not appear to be a contributing factor to the disruption of succession in the sampled stands. The Siberian moth however does appear to be the causal factor for the complete disruption of forest succession in this ecosystem. The larval stage of the Siberian moth at outbreak population levels apparently incites a disruption of the continuum of forest succession by causing significant mortality in the overstory and understory conifers causing the abortion of the future seed crop. Fire may be a contributing factor in stands that endure less defoliation through the removal of more live overstory stems and understory regeneration.

North American conifer forests typically have regeneration in the understory following combinations of disturbance by insects and fire (De Grande and Bergeron 1997, Frelich and Reich 1995, Witter et al. 1984, Witter and Ragenovich 1986). The spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera:Tortricidae) is the most destructive defoliator of conifers in North America. This native pest can cause significant mortality in stands of its primary hosts of balsam fir, *Abies balsamea* (L.) Mill., white spruce, *Picea glauca* (Moench) Voss, and red spruce, *Picea rubens*, Sarg (Witter et al. 1984). Mortality by the spruce budworm differs from that caused by the Siberian moth in that the spruce budworm mortality occurs primarily in mature conifers within the stand and does not usually have much effect on seedlings and saplings in the understory (Morin and Laprise 1997). This study, however, suggests that the Siberian moth defoliates seedlings and saplings and causes complete mortality of all conifers in some stands during outbreak conditions. Balsam fir is usually defoliated three or four times by the spruce budworm before significant mortality occurs, while some Siberian fir may succumb to the Siberian moth after a single year of defoliation. Both insects are native in their respective ranges yet the forests they inhabit are affected very differently by their infestations.

Another serious pest of North American conifer forests is the balsam woolly adelgid, *Adelges piceae* (Ratz.) (Homoptera:Adelgidae). This non-native pest is not a defoliator but causes significant mortality with its piercing-sucking mouthparts in stems and crowns of its primary hosts Fraser fir, *Abies* *fraseri* (Pursh.) and balsam fir, *A. balsamea* (L.) Miller (Hain 1988, Amman and Speers 1965, Amman 1962, Balch 1952). The insertion of the adelgid's stylet inhibits water transport within the tree; large numbers will cause mortality in seven to ten years (Amman and Speers 1965). Witter and Ragenovich (1986) found significant mortality (82 to 95%) on mature Fraser fir stems in the overstory with excellent regeneration in the understory. Smith and Nicholas (2000) report good regeneration in stands decimated by the balsam woolly adelgid but at lower densities than stands not affected by this pest. Both regeneration studies were conducted at least 10 years after significant mortality caused by the balsam woolly adelgid.

The native spruce budworm and the non-native balsam woolly adelgid are serious pests to fir species in North America and cause significant amounts of mortality in conifer forests. In comparison to the Siberian moth however, they do not cause significant mortality of seedlings or saplings in the understory. The defoliation of coniferous seedlings and saplings by the Siberian moth in the understory is unique among forest overstory pests. Coupled with the complete mortality of the overstory and loss of the seedbank, the loss of the understory regeneration prevents the return to coniferous forests for decades, possibly centuries. The lack of change temporally (50+ yrs.) in this Siberian ecosystem that experienced similar multiple disturbances suggests that forest succession may be disrupted for a significantly longer period. The results of this investigation indicate that the Siberian moth could be a much more serious pest, if it becomes established in North American conifer forests, than any of the currently known pests in these forests.

Figure 2.1. Photograph of Undisturbed Stand.

Figure 2.2. Photograph of Recent Fire Stand.

Figure 2.3. Photograph of Recently Defoliated Stand.

Figure 2.4. Photograph of Recently Defoliated and Burned Stand.

Figure 2.5. Photograph of Forb Growth in Old Defoliated and Burned Stand.

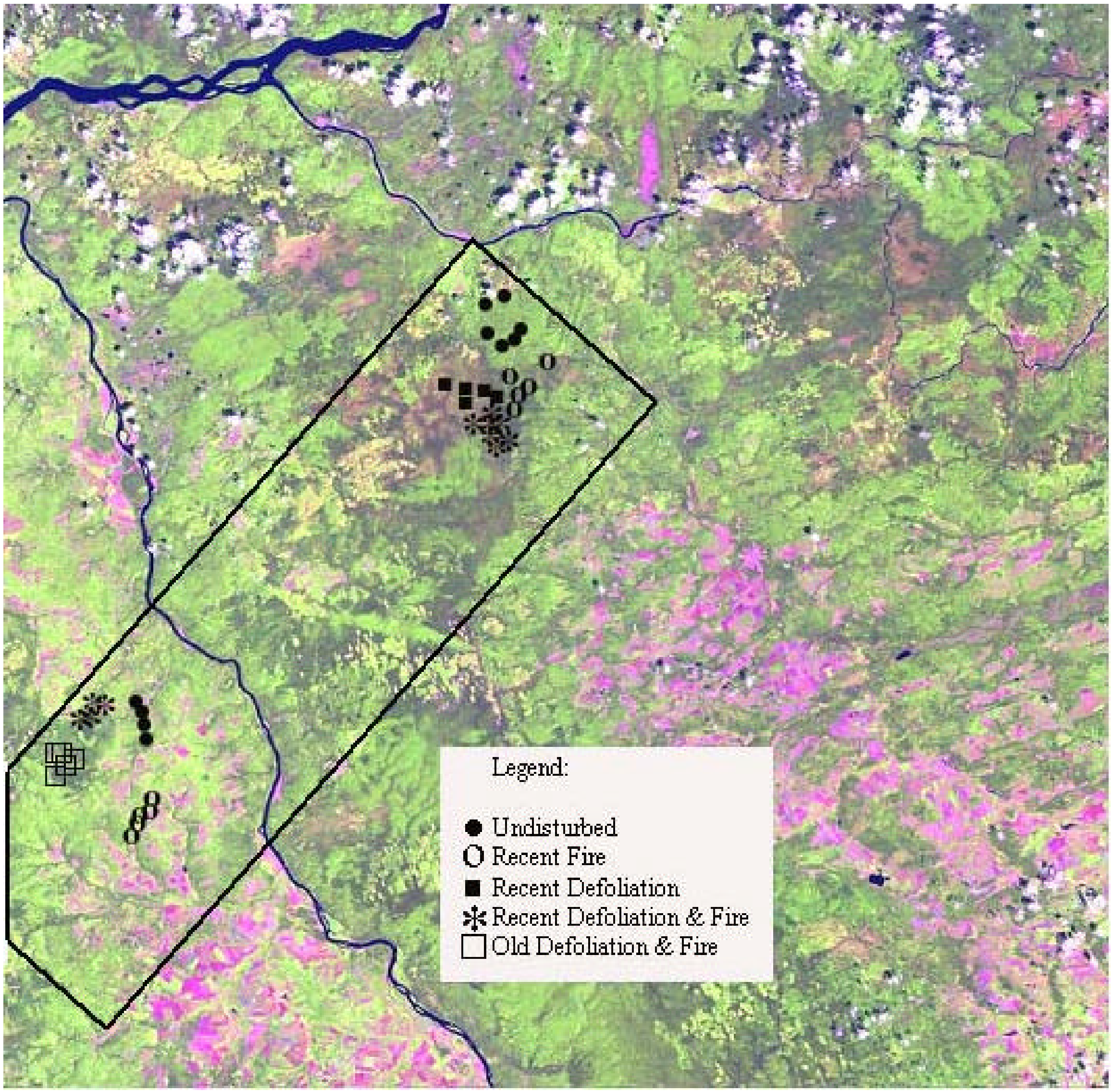

Figure 2.6. Krasnoyarsk Krai Study Area with Plot Locations

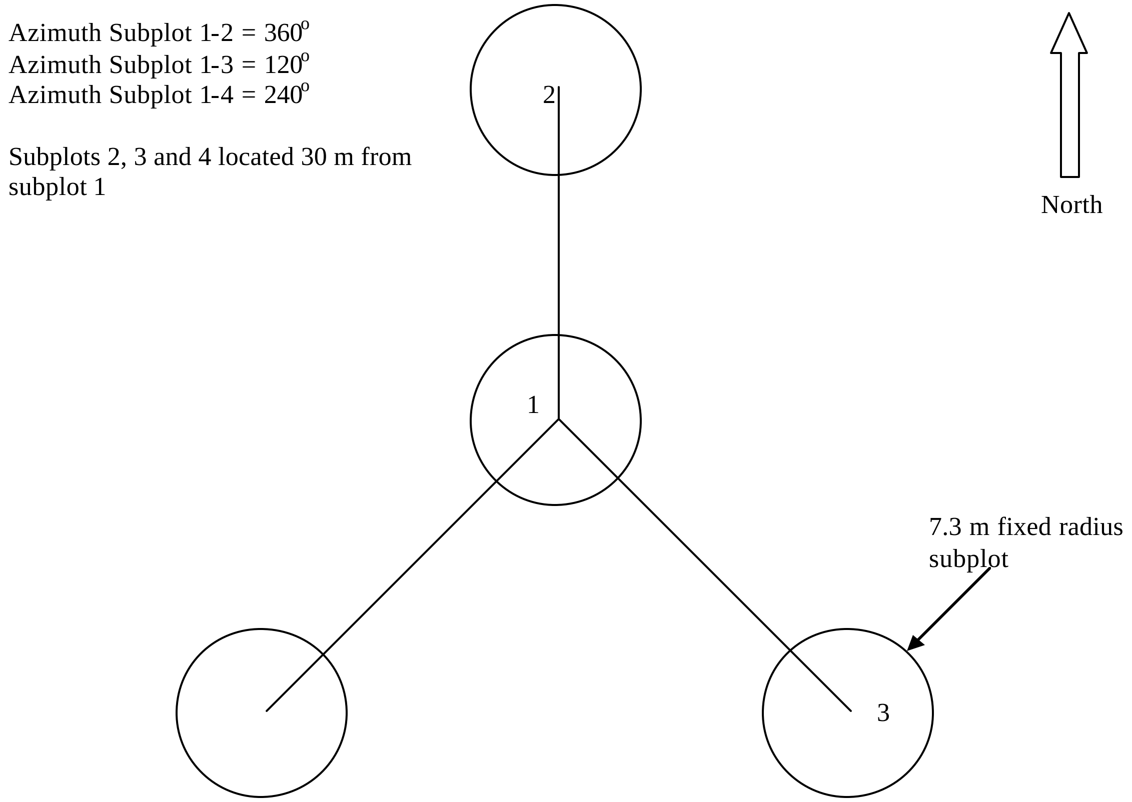

Figure 2.7. Intensive Sampling Plot Design.

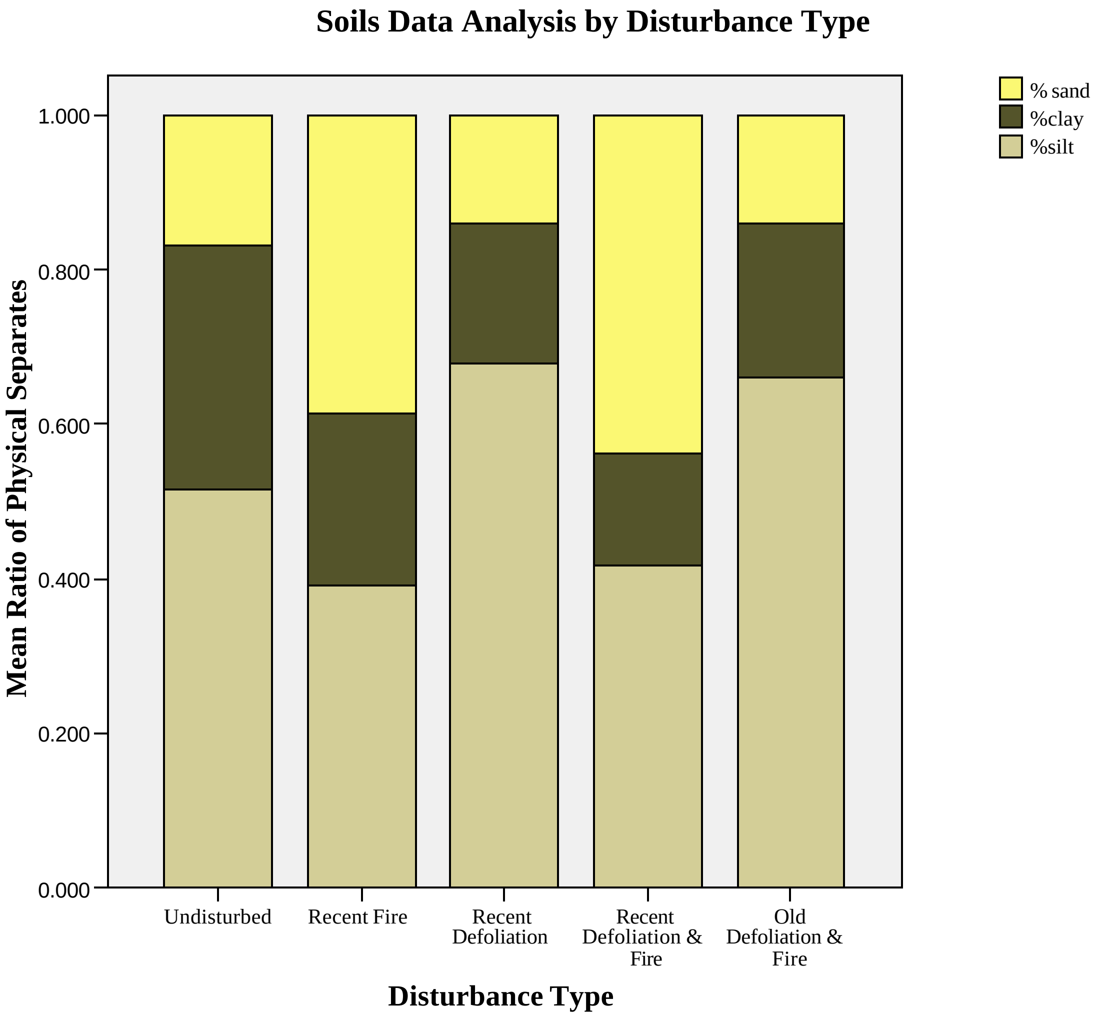

Figure 2.8. Soils Data Analysis of Physical Separates by Disturbance Type.

Table 2.1. Count, DBH, and height for live and dead conifer overstory stems by disturbance type.

Live Stems	N	Mean DBH ±SE (cm)	Minimum DBH (cm)	Maximum DBH (cm)	Mean Height ±SE (m)	Minimum Height (m)	Maximum Height (m)
Undisturbed	360	20.7±0.4	12.5	55.5	19.2±0.2	8.0	39.0
Recent Fire	17	18.7±1.1	13.5	28.7	14.7±0.6	10.5	19.5
Recent Defoliation	0	0.0±0.0	0.0	0.0	0.0±0.0	0.0	0.0
Recent Defoliation & Fire	0	0.0±0.0	0.0	0.0	0.0±0.0	0.0	0.0
Old Defoliation & Fire	0	0.0±0.0	0.0	0.0	0.0±0.0	0.0	0.0

Dead Stems							
Undisturbed	98	23.6±1.1	12.5	69.5	13.4±0.7	1.4	28.0
Recent Fire	176	19.5±0.5	12.5	41.3	13.3±0.3	2.5	29.0
Recent Defoliation	378	18.2±0.2	12.5	59.2	14.5±0.3	1.5	27.0
Recent Defoliation & Fire	47	27.2±1.4	13.0	59.1	16.2±1.2	2.0	30.0
Old Defoliation & Fire	2	22.2±0.7	21.5	22.9	5.8±4.0	1.8	9.7

Table 2.2. Percent of relative density for live and dead overstory stems by disturbance type.

Live Stems	*Abies sibirica* Ledeb.	*Betula spp.*	*Larix sibirica* Ledeb.	*Picea obovata* Ledeb.	*Pinus sibirica* Du Tour	*Populus tremula* L.
Undisturbed	62	0	2	24	12	0
Recent Fire	6	35	0	24	35	0
Recent Defoliation	0	0	0	0	0	0
Recent Defoliation & Fire	0	0	0	0	0	100
Old Defoliation & Fire	0	100	0	0	0	0
Dead Stems						
Undisturbed	67	0	1	17	15	0
Recent Fire	58	0	0	18	24	0
Recent Defoliation	86	0	1	12	1	0
Recent Defoliation & Fire	83	0	0	4	0	13
Old Defoliation & Fire	100	0	0	0	0	0

Table 2.3. Percent of relative dominance for live and dead overstory stems by disturbance type.

Live Stems	*Abies sibirica* Ledeb.	*Betula spp.*	*Larix sibirica* Ledeb.	*Picea obovata* Ledeb.	*Pinus sibirica* Du Tour	*Populus tremula* L.
Undisturbed	44	0	7	24	25	0
Recent Fire	3	36	0	26	35	0
Recent Defoliation	0	0	0	0	0	0
Recent Defoliation & Fire	0	0	0	0	0	100
Old Defoliation & Fire	0	100	0	0	0	0

Dead Stems						
Undisturbed	49	0	4	19	28	0
Recent Fire	49	0	0	19	32	0
Recent Defoliation	76	0	3	18	3	0
Recent Defoliation & Fire	69	0	0	3	0	28
Old Defoliation & Fire	100	0	0	0	0	0

Table 2.4. Mean percent cover of understory vegetation types by disturbance type with standard errors.

	Vegetation Type ±SE						
Disturbance Type	Tree	Shrub	Vine	Graminoid	Forb	Fern or Fern ally	Bryophyte
Undisturbed	13±2	8±1	1±0	29±2	15±0	3±1	31±2
Recent Fire	10±1	22±1	0±0	34±6	17±2	3±0	14±1
Recent Defoliation	5±1	31±2	2±0	16±2	39±1	7±2	0±0
Recent Defoliation & Fire	6±2	15±1	2±0	8±2	67±5	0±0	2±1
Old Defoliation & Fire	7±2	17±3	0±0	6±1	70±7	0±0	0±0

Table 2.5. Percent change of understory vegetation type for disturbed stands versus undisturbed stands.

	Vegetation Type						
Disturbance Type	Tree	Shrub	Vine	Graminoid	Forb	Fern or Fern Ally	Bryophyte
Recent Fire	-3	+14	-1	+5	+2	0	-17
Recent Defoliation	-8	+23	+1	-15	+24	+4	-31
Recent Defoliation & Fire	-7	+7	+1	-21	+52	-3	-29
Old Defoliation & Fire	-6	+9	-1	-23	+55	-3	-31

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Chapter III

Above-ground coarse woody debris volumes and implications for carbon flux following fire and insect outbreak disturbances in the boreal forests of Krasnoyarsk Krai, Russia

Abstract

The effects of fire and Siberian moth, *Dendrolimus superans sibiricus* (Tschetverikov) (Lepidoptera: Lasiocampidae), defoliation on overstory above-ground coarse woody debris volumes and implications for carbon stores transfer were examined in the boreal forests of Krasnoyarsk Krai, Russia. Selected study stands were dominated by Siberian fir, *Abies sibirica* Ledeb., of equal age at time of disturbance and consisted of two temporal periods of disturbance and three combinations of disturbance with 10 undisturbed stands serving as controls. Stands defoliated in the 1950's and burned in the 1960's exhibited major differences in amounts of both downed and standing coarse woody debris compared to stands defoliated and burned in the 1990's. Stands defoliated in the 1990's, burned or unburned, were found to have significantly more overall coarse woody debris than the other stands surveyed. The 1950's and 1960's disturbed stands exhibited almost a complete loss of the coarse woody debris quantities found in the other disturbance types. No live conifer stems were observed in the older disturbed stands more than 50 years after these stands were defoliated and subsequently burned. The implications for carbon flux based on this study's evidence of carbon stores' transfer in large areas with complete mortality by the Siberian moth and subsequently burning may provide evidence for global climate change studies. This study found a loss of standing and downed CWD in these stands of 23.8 Mg/ha of C over an approximately 50 year period.

Introduction

Accumulation of coarse woody debris (CWD) is an important result of disturbance and vital in providing substrate for invertebrates (Bouget and Duelli 2004), mammals (Rhoades 1986), and seedlings (McCullough 1948), enhancing nutrient cycling (Krankina et al. 1999, Van Cleve et al. 1983), and sequestering carbon (Krankina and Dixon 1994, Harmon et al. 1990). Carbon flux in boreal ecosystems has become an intriguing question for scientists in the search for evidence in global climate change studies.

The estimation of volumes of CWD and flux of carbon in Russian ecosystems has been the subject of several coarse-scale studies (Alexeyev and Birdsey 1998, Krankina et al. 2002, Rouvinen et al. 2002, Yatskov et al. 2003). Estimates from forest inventories, stand growth tables, and models render valuable approximations of the mean volume of CWD and the associated amount of carbon in CWD stored in boreal forests. Estimated results from previous studies of CWD mean volumes in Russian boreal forest ecosystems range from 14 m^3/ha (Krankina et al. 2002) to 80 m^3/ha (Rouvinen et al. 2002) with variation ascribed to differences in geographic location, disturbance regimes, and stand age.

Approximately 1.2 billion ha of the Earth's surface is covered by boreal forests, of which approximately 552 million ha are located in Russia (Alexeyev and Birdsey 1998). Because of the Siberian boreal forests' vast size and significant carbon stores, disturbance regimes potentially play an important role in carbon sequestration (Smith et al. 2004, Shugart et al. 1992, Harmon et al. 1990) through the creation of CWD. The Siberian boreal forest ecosystems in Russia have endured many disturbances during the last hundred years. Examples of past disturbance include Siberian moth, *Dendrolimus superans sibiricus* (Tschetverikov) (Lepidoptera: Lasiocampidae), infestations recurring every 7-10 years (Vorontsov 1982) and surface fires with a return interval of 10-140 years (Conard and Ivanova 1997, Kharuk et al. 2005). Natural disturbances such as insects and fire can individually, in combination, or sequentially affect forest stand structure, composition, and function (Pedersen 1998).

The dominant insect responsible for disturbance in Siberia is the Siberian moth. This destructive defoliator of conifers in Asia (Gninenko and Orlinskii 2002) prefers *Abies spp*. and *Larix spp*. but also will defoliate *Pinus spp*. and *Picea spp*. at outbreak population levels (Baranchikov et al. 1997). Siberian moth outbreaks have been recorded throughout a large area of north central Asia (Grodnitsky and Palnukova 1999, Baranchikov et al. 1997, Kondakov et al. 1997, Vorontsov 1982).

Fire is an important disturbance agent in Siberian boreal forests and its effect on CWD volumes may be significant. Conard and Ivanova (1997) report the annual area burned in Siberia has increased since 1983 and conclude the fire regime in Siberia has been largely unaffected by suppression activities or increased ignitions. Fire may influence insect outbreak conditions and post-outbreak woody plant regeneration. Prior to an outbreak, surface fire may consume the fuels on the forest floor and cause significant mortality of the Siberian moth's natural enemy, *Telenomus gracilis* (Mayr.), an egg parasitoid

(Vorontsov 1982). Following an outbreak, more severe fires may occur in defoliated stands consuming downed and standing coarse woody debris which results in the release of large quantities of carbon into the atmosphere.

Fire and insect defoliation, singly, or in combination, may have a significant impact on Siberian boreal forest structure, composition, and function. Quantifying CWD and its associated carbon transfer post disturbances, based on field measurements, is a specific objective of this study. This investigation will evaluate the effects of Siberian moth and post-outbreak fire disturbances on CWD volumes and carbon transfer resulting from these two major disturbances.

Study Site

The study site is located along the Yenesei Transect (Pleshnikov et al. 2002) in south-central Siberia and was not glaciated during the Pleistocene; it is relatively homogeneous in ecosystem composition, structure, and function (Chlachula 2001, Velichko et al. 1997). It is located at approximately 57^0N latitude and 92^0E longitude and is a relatively flat plain with altitudes of 300 to 400 m AMSL. The south-central Siberian dark-needled forest is on discontinuous permafrost (Koropachinsky 1983). It is composed primarily of late successional dominant species of Siberian fir, *Abies sibirica* Ledeb., Siberian stone pine, *Pinus sibirica* Du Tour, and Siberian spruce, *Picea obovata* Ledeb. Siberian fir is the dominant species in this ecosystem with smaller components of Siberian spruce and Siberian stone pine, Siberian larch, *Larix sibirica* Ledeb., and Scotch pine, *Pinus sylvestris* L., interspersed throughout the study area.

The climate at the study site is strongly continental with an average January temperature of -19^0 C with a minimum of -55^0 C and an average snow depth of 65 cm. Average July temperatures are $+18^0$ C with a maximum of $+39^0$ C. Annual precipitation ranges from 350 to 500 mm; eighty percent falls during the summer (Kharuk et al. 2003).

Early successional species in Siberia differ from North America, but generally share the same genera with species having relatively similar morphological and physiological characteristics. Typical dominant early successional genera include *Betula* and *Populus* with minor components of *Sorbus* and *Alnus*. The most prolific species of these genera are European white birch, *Betula pendula* Roth, downy birch, *B. pubescens* Ehrh., Eurasian aspen, *Populus tremula* L., Siberian mountain-ash, *Sorbus sibirica* Hedl., and speckled alder, *Alnus incana* (L.) Moench. (Koropachinsky, 1983).

In this investigation, an area was identified that was disturbed at two different temporal periods by the Siberian moth larvae. This area contained several individual large tracts greater than 10,000 ha that were completely defoliated during the 1954-57 moth outbreak and again during the 1995-1997 moth outbreak. Almost 100% of the area afflicted with the earlier outbreak was then burned by fire while less than 50% of the area affected by the more recent infestation has been burned. Ground observation of the earlier outbreak confirmed the lack of coniferous overstory species with sparsely populated late-successional deciduous trees in a largely herbaceous species-dominated ecosystem. The more recently defoliated area was observed to contain standing dead conifer stems with small clusters of live deciduous overstory species including *Populus tremula*, L. and *Betula pubescens*, Ehrh. and a vigorous shrub and herbaceous understory. The Siberian moth does not completely defoliate all stands it infests. Adjacent stands were observed to have approximately 25-75% tree mortality caused by Siberian moth defoliation. However, this study targeted stands that were completely defoliated to avoid variation due to patchiness in stands with lesser amounts of defoliation.

Methods

Targeted stands consisted of two temporal periods of disturbance and three combinations of disturbance with ten separate undisturbed stands serving as controls. Sampling was conducted in the following disturbed and undisturbed areas: (1) undisturbed fir-spruce, (2) recent fire which occurred five or fewer years ago, (3) severe defoliation by the Siberian moth in the 1995-97 outbreak with no fire, (4) severe defoliation by the Siberian moth in the 1995-97 outbreak that burned post-outbreak, and (5) severe defoliation in the 1954-57outbreak that burned post-outbreak (Fig. 3.1).

A stand is defined in this study as a distinct area of the forest that is relatively homogeneous in species composition or age and could be managed as a single unit. Five replicate stands for each targeted disturbance type were selected to provide a more accurate estimate of the means and associated variance. Replication within disturbance cover types was accomplished by identifying five separate stands within each type of disturbance. An intensive sampling plot was installed in each stand with plots randomly located throughout the study area. Plot selection criteria required a stand to historically be dominant *Abies* with a lesser component of *Picea, spp*. and included ease of accessibility and lack of other disturbances. Every effort was made to lessen bias of plot locations and to reduce edge effect by requiring all plot locations to be at least 50 m or more from an edge, road, or other disturbance type such as windthrow or cutting.

Selection of each sample plot was accomplished by interpreting different overstory cover types on Russian forest cover type maps and navigating to the targeted forest type containing each disturbance type in the field. Random number tables for both distance and azimuth were used to navigate to the center point for the first subplot of each sampling plot. Sampling plots within the same disturbance type were located in distinctly different stands. Location of each sampling plot was documented using map, compass, and geographic positioning system receiver, and recorded on the plot location form. Field sampling was conducted during July and August of 2002 and 2003.

Field sampling methodology procedures for CWD data collection were adapted from United States Department of Agriculture's Forest Service Forest Inventory Analysis Program (USDA 2001) with the exception of decay assessment. This sampling procedure utilized four subplots each 7.3 m in radius with a central subplot and three subplots emanating from the central subplot at 120, 240, and 360 degrees (Fig. 3.3). All standing dead trees greater than 45^0 from the plane of the ground were measured for diameter at breast height (DBH) and overall snag height within the fixed radius subplots. Net volumes for standing CWD were calculated using the formula for conical volume (Husch et al. 1963):

$$\text{Conic Volume} = \frac{(A_{DBH}h)}{3} \quad \textit{where } \mathrm{A_{DBH}} = \text{area at DBH and h = height of snag}$$

Snags with incomplete boles were reconstructed to original height by extrapolating mean height based on the linear trend exhibited for DBH vs. height in the undisturbed stands. The percent difference between the extrapolated original height and the actual height was then subtracted from the reconstructed bole to determine remaining gross wood volume. Percent of decay values were not applied to standing dead wood since the vast majority were recently killed (< 5 yrs.) and endured significant drying with very little decay. The actual difference in relative density due to drying and lack of decay for these snags is believed to be insignificant based on other studies (Krankina et al. 2002, Vedrova et al. 2002, Yatskov et al. 2003).

Within each subplot three transects 14.6 m in length were established from subplot center at 120, 240, and 360 degrees to assess downed CWD. Stumps were excluded in this study since none of the sampled stands were in a managed area. All downed dead woody stems intersecting a transect greater than 1 m in length of stem, less than 45^o from the plane of the ground, and greater than 2.5 cm in diameter at the large end were considered downed CWD. Each piece of downed CWD was measured for small end diameter, large end diameter, length, and identified to species. Downed CWD intersecting more than one transect in a subplot was tallied only on the first transect encountered. All diameter measurements were outside bark measurements. Percent of decay was recorded by visual and physical inspection and tallied in five percent increments from 0 to 100. The percent of decay was recorded as an assessment of the amount of wood fiber missing in each piece.

Gross wood volume calculations for each piece of downed CWD were completed using Smalian's cubic volume formula (Avery and Burkhart 1994):

$$\text{Cubic Volume} = \frac{(l+s)}{2}L$$

where l = area of the large end diameter

s = area of the small end diameter

L = length of log

Percent of decay values were applied to the gross wood volume to achieve net wood volume of downed CWD for each disturbance type. Mean bulk density values (Table 3.1) for the dominant species encountered are from Nahabtsev (1984) and were used to determine mass for each piece of standing and downed CWD. Bulk density values include bark, sapwood, and heartwood for all study species. Results from the CWD mass computation were used to calculate carbon content for each piece of CWD recorded in the field. Carbon content varies only slightly in woody plant species with a generally accepted mean value of 0.50 (Alexeyev and Birdsey 1998). Carbon content was calculated by multiplying this mean value for carbon content by the net wood volume in all CWD pieces recorded.

Soil samples were collected to aid in determining relative homogeneity of ecosystem physical properties. Soils data collected for this study included collection of five 10 cm deep cores extracted from each sampling plot. The five soil cores from each sampling plot were combined in the field to create a composite soil sample of each individual sampling plot. Collected soil samples were subjected in the laboratory to soil texture analysis (Gee and Bauder 1986).

Statistical analysis was conducted using SPSS version 15.0 (SPSS 2006). Downed and standing CWD values from individual stands were pooled by disturbance type. Analyses of variance (ANOVA) were conducted to test for significant effects ($p<0.05$) on disturbance type and volumes of CWD among disturbance types.

Results

All soils sampled were loamy with some variation from silty loam to sandy loam. Measured elevation (300-400 m AMSL) and slope were relatively constant. Percent of slope for all sampled plots was predominately level. Four plots did measure some negligible slope (<10%) and slope aspect was variable on these plots.

Coarse Woody Debris Volumes

Approximately 1,500 pieces of downed and standing CWD, equally divided between the two types were sampled in 30 stands of five different disturbance types. Standing dead wood volumes for each disturbance type were determined from DBH and actual or reconstructed height (Table 3.2). Standing and downed CWD volume ANOVA tests revealed a significance difference ($p<0.05$) among disturbance types.

The recently defoliated stands retained the greatest amount of downed woody debris with a mean net volume of 141.0 m^3/ha. All conifers, with the exception of 17 seedlings on two sampling plots, in these stands were dead as a result of the Siberian moth infestation five years prior to sampling. Mean standing CWD volume for this disturbance type was 135.4 m^3/ha and it was dominated by Siberian fir.

In the recently defoliated stands where fire also occurred, the net volume of downed CWD decreased to 106.4 m^3/ha. Standing CWD volume in this disturbance type decreased to 48.1 m^3/ha as compared to standing CWD volume in the recently defoliated stands. The undisturbed control stands were found to contain 86.1 m^3/ha of downed wood and 30.8 m^3/ha of standing dead wood which is slightly less than the volumes found in recently defoliated and burned stands. The stands which burned recently were found to contain 76.5 m^3/ha of downed CWD and 79.2 m^3/ha of standing CWD while the stands that were both defoliated and burned over 50 years ago retained the least amount of CWD at 16.7 m^3/ha of downed wood and 0.5 m^3/ha of standing dead wood. Total volumes for both downed and standing CWD were summed by disturbance type (Table 3.2). Composition of downed CWD and standing CWD (Table 3.3) were determined for the six dominant species by disturbance type and then calculated for overall species composition by disturbance type (Table 3.3).

Carbon Transfer

Bulk density values (Nahabtsev 1984) for the six dominant overstory species were applied to the downed CWD volume results in order to calculate carbon content in the five different disturbance types (Table 3.4). Downed CWD C stores in undisturbed stands is similar to that sequestered in recently defoliated stands and stands that were recently defoliated and burned: 26.0 Mg/ha, 28.9 Mg/ha, and 24.4 Mg/ha, respectively. Downed CWD in recently burned stands contained approximately 10 Mg/ha of C less than recently defoliated stands. The older stands with defoliation followed by fire had the least amount of C sequestered in downed CWD (7.6 Mg/ha).

C content in standing CWD volumes is lower in all disturbance types compared to downed CWD (Table 3.4). The old defoliated stands that burned contained the least amount of C at 0.1 Mg/ha. The greatest amount of C in standing CWD was found in recently defoliated stands which approximated more than four times the amount of C sequestered in standing CWD in the undisturbed stands. Over twice as much C was found in snags in the recently burned stands as compared to the undisturbed stands. The standing C content in recently defoliated and burned stands is almost three times lower than in stands which were only recently defoliated.

Total C content including snags and downed CWD was comparable across three disturbance types: 1) undisturbed, 2) recent fire, and 3) recent defoliation and fire. The greatest variation occurred in the recently defoliated stands with approximately 20 Mg/ha of C more than the three disturbance types with comparable quantities. The older defoliated and burned stands contained significantly less total C (7.7 Mg/ha) than any of the other disturbance types.

Downed CWD carbon transfer (Table 3.5) was determined by comparing downed CWD in the different combinations of disturbance to the undisturbed stands to ascertain whether downed CWD increased or decreased by disturbance type. C content of downed CWD in recently defoliated stands (+2.9 Mg/ha) increased while recently defoliated and burned stands (-1.6 Mg/ha), recent fire stands (-7.0 Mg/ha), and old defoliation and fire stands (-18.4 Mg/ha) decreased in comparison to undisturbed stands. Comparing the recently defoliated and burned stands to the stands that endured the same disturbances over 50 years earlier revealed that 23.0 Mg/ha of carbon was lost due to decomposition and emission of downed CWD.

Discussion

The recently defoliated stands were almost equal in the amount of downed CWD compared to standing CWD. The undisturbed stands, not unexpectedly, contained less than half of this amount of overall CWD and less than a quarter of the snags found in the recently defoliated stands. The total amount of CWD found in the recently defoliated stands is more than three times the amounts reported in other studies (Alexeyev and Birdsey 1998, Krankina et al. 2002, Rouvinen et al. 2002, Yatskov et al. 2003).

The stands that endured only fire had less downed wood volume but twice as much standing dead wood volume. This is not atypical for burned stands as even surface fires will consume downed woody debris with the associated emissions of fire to the atmosphere and eluviations of residual chemical elements into the soil (Heinselman 1981, Kasischke et al. 1995). Depending on the severity of the fire some mortality may occur in the overstory. The relatively thin bark of the dominant *A. sibirica* in these stands indicates that the fires caused mortality as standing dead wood volume was more than twice that of undisturbed stands.

In a direct comparison of similar multiple disturbances that occurred approximately 50 years apart, this study found CWD volumes diminishing significantly over time. The recently defoliated plots that subsequently burned retained an overall mean volume equivalent to the stands that were only recently burned. However after 50 years this volume declines to 11% of the volume found in the recently defoliated and burned stands. This is a direct result of the Siberian moths' ability to cause 100% mortality of the overstory. The Siberian moth larvae also indirectly cause the loss of the seed bank since tree mortality occurs prior to cone maturation. CWD inputs from conifers in this moth-disturbed ecosystem are halted shortly after the outbreak. The stands that were defoliated and burned approximately 50 years ago resembled a wet meadow of dominant forbs with a small population of birch species and no live conifer stems.

The total amount of CWD in the recently defoliated stands approximates what is typically found in an undisturbed stand in this area (Kharuk et al. 2004) after subtracting the undisturbed downed CWD from the recently defoliated total CWD. Stands that were recently burned contained more total CWD than undisturbed stands but less downed CWD. Effects on CWD in recently burned stands are typical of fire as it probably caused an increase in overstory mortality while consuming some downed CWD. The effects of fire in recently defoliated stands and burned stands show a significant decrease in the amount of standing CWD compared to the stands where only recent fire had occurred. This decrease is offset by the increase in downed CWD in the recently defoliated stands that subsequently burned. Fire in these stands caused more felling of already dead boles increasing the amount of downed CWD while reducing the standing amount of CWD and consuming some overall CWD.

Computation of the carbon content of CWD within these various combinations of disturbance refines the effects of disturbance still further. Undisturbed stands, recently burned stands, and stands recently defoliated and burned were approximately equal in total CWD C content. While fewer live stems were observed in the recently burned stands and in the recently defoliated stands that burned, the effects of fire have contributed to an increase in C content in standing CWD and a decrease in downed CWD as compared to the undisturbed stands.

The recently defoliated stands exhibited the greatest increase (+19.6 Mg/ha) in the amount of carbon in CWD compared to the undisturbed stands. After fire and approximately 50 years these stands then decline in storage of overall CWD to -23.8 Mg/ha. No live conifer stems were observed in these older defoliated and burned stands confirming the loss of the seed bank and all regeneration.

The impact the Siberian moth has on fir stands during outbreak years can have a significant impact on the stores of carbon in CWD. The most recent Siberian moth outbreak defoliated approximately 700,000 ha at various levels of defoliation. It is estimated that of the 700,000 ha affected, 300,000 ha suffered 100% mortality (Kharuk et al. 2004). Using values for C content derived from this study, this most recent outbreak would cause the accumulation of 1.53×10^{-7} Mg/ha within the dead stands. Over the course of 50 years one would expect the eventual, and almost complete loss of this quantity of carbon stored in CWD through fire and decomposition based on the findings of this study in the older defoliated and burned stands.

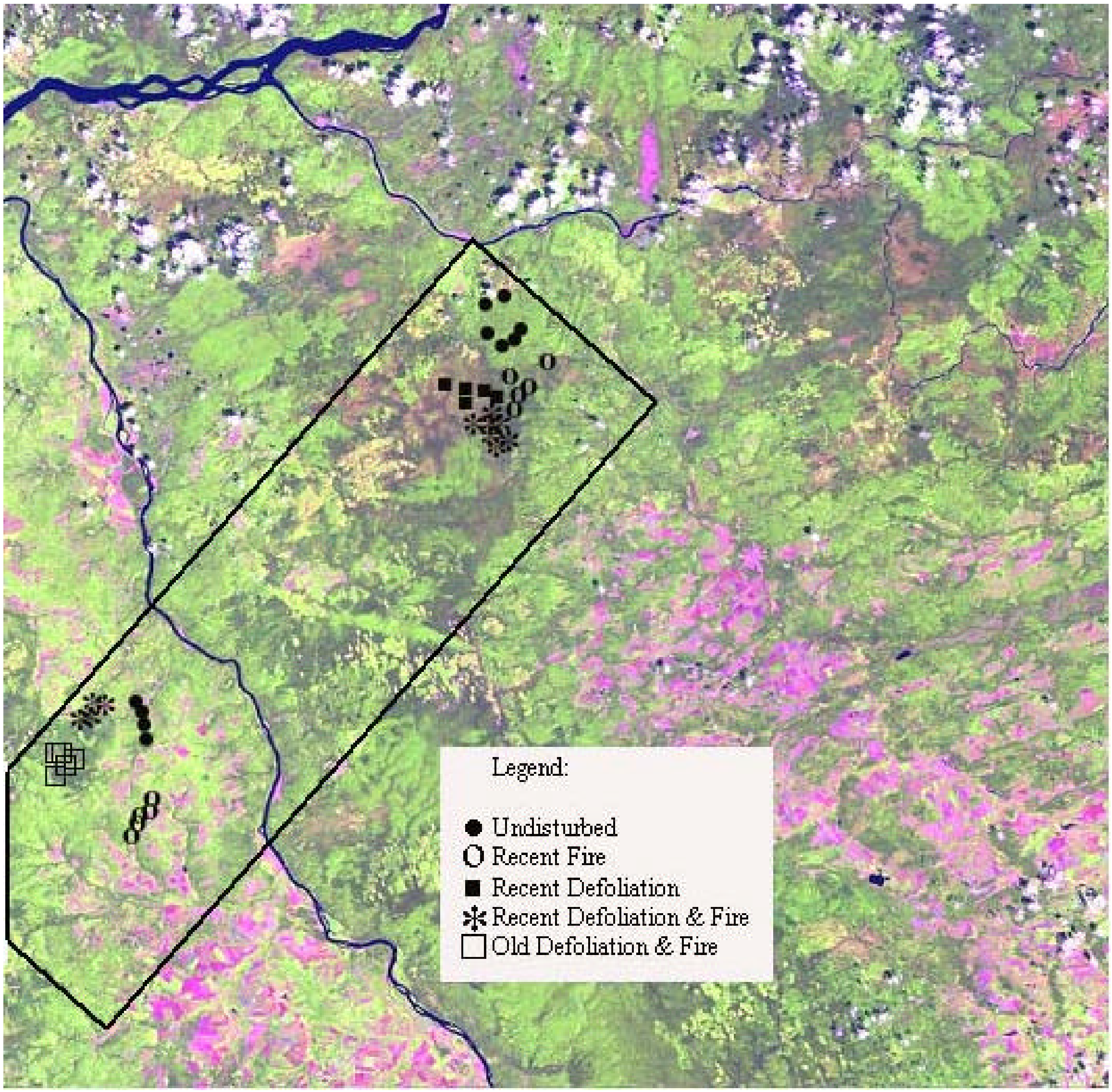
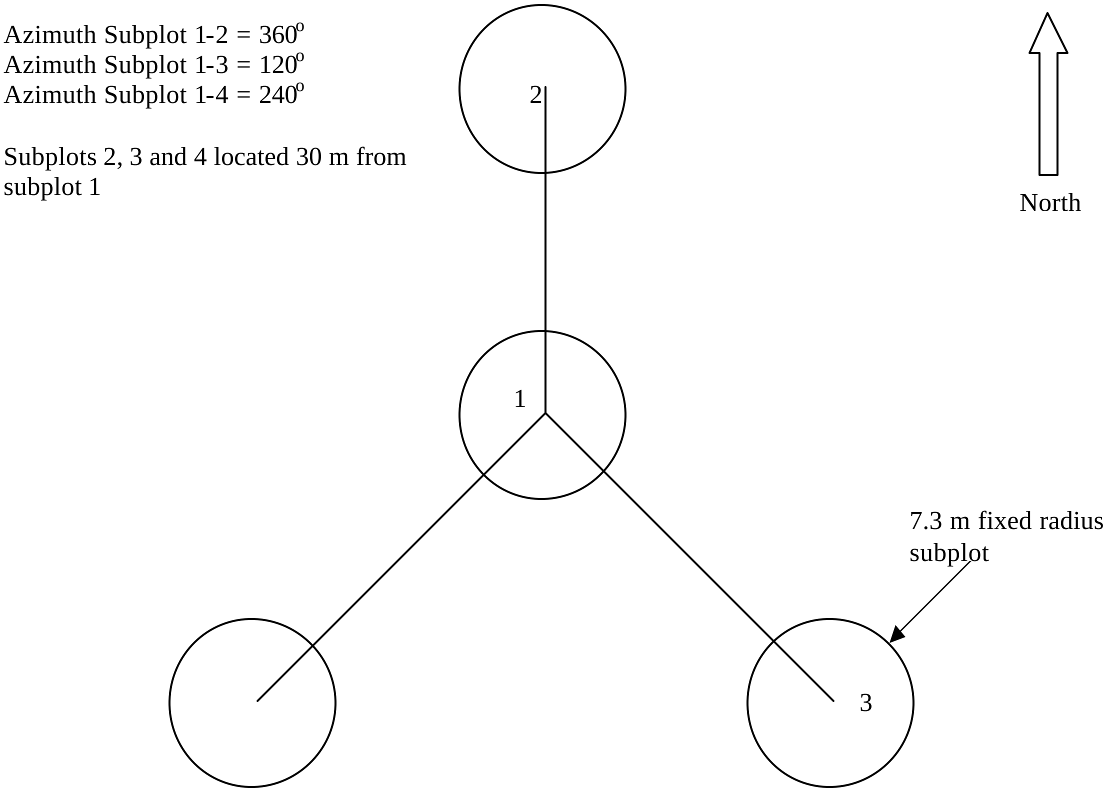


Figure 3.1. Krasnoyarsk Krai Study Area with Plot Locations



Azimuth Subplot 1-2 = 360°
Azimuth Subplot 1-3 = 120°
Azimuth Subplot 1-4 = 240°

Subplots 2, 3 and 4 located 30 m from subplot 1

Figure 3.2. Intensive Sampling Plot Design.

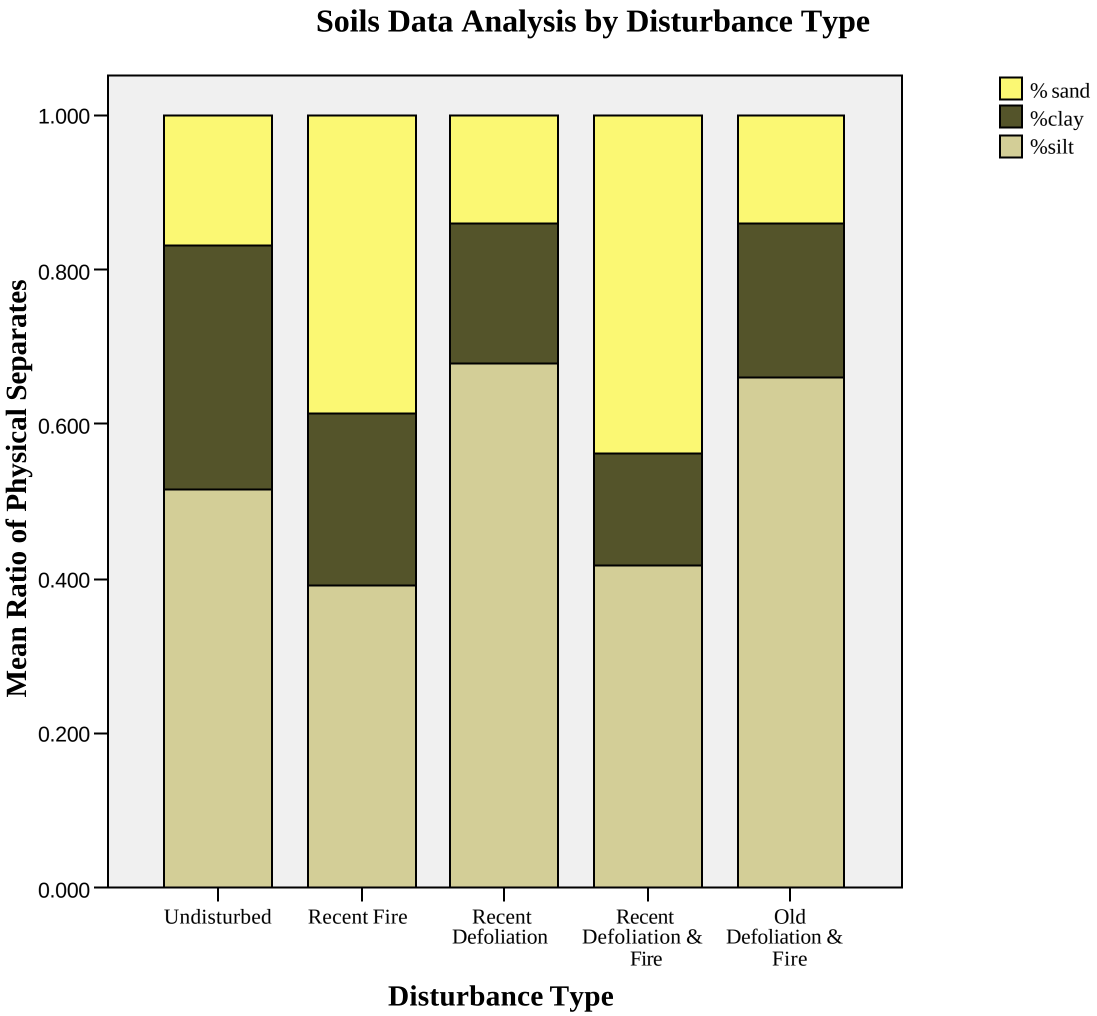


Figure 3.3. Soils Data Analysis of Physical Separates by Disturbance Type.

Table 3.1. Bulk density values for dominant Siberian overstory species (from Nahabtsev, 1984).

Species	Bulk Density (kg/m^3)
Abies sibirica	310
Betula pendula	485
Larix sibirica	488
Picea obovata	396
Pinus sibirica	378
Populus tremula	370

Table 3.2. Downed, standing, and total coarse woody debris (CWD) volumes by disturbance type.

Disturbance Type	Downed CWD Mean Volume m^3/ha (± SE)		Standing CWD Mean Volume m^3/ha (± SE)	Total CWD Mean Volume m^3/ha		N
	Gross	Net	Net	Gross	Net	
Undisturbed	145.6	86.1(±2.56)	30.8(±1.92)	176.4	116.9	282
Recent Fire	111.3	76.5(±0.82)	79.2(±0.72)	190.5	155.7	366
Recent Defoliation	170.3	141.0(±0.65)	135.4(±0.48)	305.7	276.4	781
Recent Defoliation and Fire	153.1	106.4(±5.10)	48.1(±3.52)	201.2	154.5	46
Old Defoliation and Fire	41.5	16.7(±9.59)	0.5(±3.33)	42.0	17.2	16

Table 3.3. Percent of downed, standing, and total coarse woody debris (CWD) of species by disturbance type.

	Species																	
	Abies sibirica Ledeb.			*Betula spp.*			*Larix sibirica* Ledeb.			*Picea obovata* Ledeb.			*Pinus sibirica* Du Tour			*Populus tremula* L.		
Disturbance Type	Downed	Standing	Total	Downed	Standing	Total	Downed	Standing	Total	Downed	Standing	Total	Downed	Standing	Total	Downed	Standing	Total
Undisturbed	62	48	55	7	0	4	9	6	7	21	15	18	1	31	16	0	0	0
Recent Fire	67	49	58	7	0	4	0	0	0	6	16	11	17	35	26	3	0	1
Recent Defoliation	72	84	77	3	0	2	0	3	2	24	7	15	0	6	3	1	0	1
Recent Defoliation and Fire	92	70	81	3	0	2	0	0	0	0	4	2	0	0	0	5	26	15
Old Defoliation and Fire	27	100	64	0	0	0	0	0	0	48	0	24	25	0	12	0	0	0

Table 3.4. Coarse woody debris (CWD) C content by disturbance type.

Disturbance Type	Downed CWD (Mg/ha)	Standing CWD (Mg/ha)	Total CWD(± SE) (Mg/ha)
Undisturbed	26.0	5.5	31.5(±0.45)
Recent Fire	19.0	13.8	32.8(±0.16)
Recent Defoliation	28.9	22.2	51.1(±0.11)
Recent Defoliation and Fire	24.4	7.9	32.3(±0.87)
Old Defoliation and Fire	7.6	0.1	7.7(±1.31)

Table 3.5. Coarse woody debris (CWD) net changes in carbon stores by disturbance type versus undisturbed stands.

Disturbance Type	Downed CWD ± C (Mg/ha)	Standing CWD ± C (Mg/ha)	Net flux ± C (Mg/ha)
Recent Fire	-7.0	+8.3	+1.3
Recent Defoliation	+2.9	+16.7	+19.6
Recent Defoliation and Fire	-1.6	+2.4	+0.8
Old Defoliation and Fire	-18.4	-5.4	-23.8

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Chapter IV

Assessing conifer regeneration following insect outbreak and fire in the boreal forests of Krasnoyarsk Krai, Russia

Abstract

The effects of fire and Siberian moth, *Dendrolimus superans sibiricus* (Tschetverikov), (Lepidoptera:Lasiocampidae) defoliation on conifer regeneration were examined in the boreal forests of Krasnoyarsk Krai, Russia. Stands dominated by Siberian fir, *Abies sibirica* Ledeb., were subjected to disturbances in the 1950's and the 1990's. During these periods some stands experienced fire, or pest outbreaks, and some both.

Stands defoliated in the 1950's and burned in the 1960's had no regeneration. Stands defoliated in the 1990's, burned or unburned, were comparable in the number of seedlings found but had significantly fewer seedlings than undisturbed stands. The stands enduring only recent fire appeared to have random patches of regeneration typical of post-fire boreal forest regeneration.

The old defoliated and burned stands were dominated by forbs and shrubs. The aggressive and persistent nature of the shrubs and forbs shaded out the few seedlings that were left following both disturbances. Severe Siberian moth outbreaks may create large areas almost devoid of conifers. Reversion to fir-dominated stands may require five or more centuries of successive regeneration from conifer trees along the periphery of the disturbed area.

Introduction

The process of boreal forest succession is a continuum that normally proceeds in complement with endemic population levels of native insect pests and disturbance by wild fire (McCullough et al. 1998, Johnstone et al. 2004). There occur instances when endemic insect populations periodically reach outbreak levels such that even healthy individual trees cannot repel or sustain severe defoliation (Hermes and Mattson 1992). Heavily defoliated stands endure a significant change in stand structure, composition, and function (Bouchard et al. 2004, Rydgren et al. 2004). With the increased fuel load of dead standing stems and windfall following a severe pest outbreak, fire may occur in defoliated stands consuming snags and coarse woody debris and perhaps altering the seed bank and nutrient cycle (Turkington et al. 1993, Schimmel and Granstrom 1996). The effects on forest composition and structure during secondary succession may be significant.

From 1995-1997 an outbreak of the Siberian moth, *Dendrolimus superans sibiricus* (Tschetverikov) (Lepidoptera: Lasiocampidae), in Krasnoyarsk Krai, Russia defoliated approximately 1.5 million ha of coniferous forest (Kondakov et al. 1997, Kharuk 1999). Populations of up to 20,000 damaging larvae per tree were reported (Grodnitsky 1999) with nearly 100 percent defoliation of host trees in the afflicted area. Ground observations two years after the end of the outbreak (personal observation 1999) indicated there was close to 100 percent mortality of all coniferous species including seedlings and saplings in the outbreak area.

Data from previous moth outbreaks (Pleshnikov et al. 2002) revealed that wildfire commonly followed due to the significant increase in fuel loads resulting from windfall of dead conifer boles. An area adjacent to the 1995-1997 outbreak was identified that was severely defoliated in 1955-1957 and subsequently burned in the 1960's. Field observation (Grodnitsky 1999) prior to this investigation indicated a lack of coniferous species more than 50 years after the initial outbreak.

Fire may influence insect outbreak conditions and post outbreak woody plant regeneration. In this Siberian fir-dominated ecosystem, prior to an outbreak, surface fire may consume the fuels on the forest floor and cause significant mortality of a Siberian moth's natural enemy, *Telenomus gracilis* (Mayr), an egg parasitoid (Vorontsov 1982). Subsequent attacks by bark beetles and pathogens associated with windfall commonly occur in stands where high tree mortality occurred due to insect infestation. Windfall and deterioration of snags add to the fuel load on the forest floor, and with the proper weather conditions can lead to fire. Fire can consume the organic soil layer and expose bare mineral soil. This aids in the establishment of early successional species such as aspen, *Populus spp*., or birch, *Betula spp*. (Aber and Melillo 1991).

Regeneration studies of boreal species following a disturbance have been conducted for several forest pests and disturbances (Tappeiner and Helms 1971, Witter and Ragenovich 1986, Schimmel and Granstrom 1996). Richter et al. (1989) studied the balsam woolly adelgid, *Adelges piceae* (Ratz.) a sap-sucking insect, in the coniferous forest of Appalachia. They cite the dynamics of soil organic matter as a major factor in controlling soil moisture and nutrient availability and ultimately, long-term return to pre-disturbance ecosystem conditions. Chambers et al. (1990) investigated seedling establishment in alpine sites and suggests disturbance characteristics and species life history and physiological traits impact seedling establishment. Hulme (1996) reviewed a survey of studies that suggest herbivory is more important than competition in understory communities. Chappell and Agee (1996) found that fire severity had a major influence on seedling establishment and eventual structure and composition of forested stands. Gap size in forest canopies caused by disturbance affected seedling establishment (Gray and Spies 1996) in the Pacific Northwest. Gray and Spies (1996) also indicated seedlings appear in greater quantities in gaps than under closed canopy, but larger gaps with increased solar insolation decreased seedlings' ability to establish. Kinnaird (1974) noted the establishment of pioneer species were dependent on site conditions and suggested seedling survival is dependent on disturbance and canopy cover. In a study of a conifer/hardwood stand, Maguire and Forman (1983) suggested that seedling density or number of seedlings present were not related to abiotic factors, but to herbaceous cover present and canopy structure. Conversely, Sirois and Payette (1991) conclude fire is responsible for decreased regeneration and patchy composition in a boreal forest zone of northern Quebec. Arseneault (2001) investigated the long-term effects of fire behavior in a boreal forest and suggests fire severity is an important factor in determining specific species regeneration.

These regeneration studies used a variety of sampling designs and associated sample sizes. Although these disturbances have been studied independently, very few studies have examined the cumulative effects of insect outbreak and fire. The study presented herein is an effort to determine Siberian boreal forest regeneration patterns following fire and Siberian moth outbreak, both singly and in combination by quantifying regeneration on the variously disturbed areas.

Study Site

The study site is located along the Yenesei Transect (Pleshnikov et al. 2002) in south-central Siberia and was not glaciated during the Pleistocene; it is relatively homogeneous in ecosystem composition, structure, and function (Chlachula 2001, Velichko et al. 1997). It is located at approximately 57^0N latitude and 92^0E longitude and is a relatively flat plain with altitudes of 300 to 400 m AMSL. The south-central Siberian dark-needled forest is on discontinuous permafrost (Koropachinsky 1983) and is composed primarily of late successional dominant species of Siberian fir, *Abies sibirica* Ledeb., Siberian stone pine, *Pinus sibirica* Du Tour, and Siberian spruce, *Picea obovata* Ledeb. Siberian fir is the dominant species in this ecosystem with smaller components of Siberian spruce, Siberian stone pine, Siberian larch, *Larix sibirica* Ledeb., and Scotch pine, *Pinus sylvestris* L., interspersed throughout the study area.

The climate at the study site is strongly continental with an average January temperature of -19^0 C with a minimum of -55^0 C and an average snow depth of 65 cm. Average July temperatures are $+18^0$ C with a maximum of $+39^0$ C. Mean annual precipitation is 425 mm; eighty percent of which falls during the summer (Kharuk et al. 2003).

Early successional species in the boreal forests of Siberia differ from North America, but generally share the same genera and have similar morphological and physiological characteristics. Dominant early successional genera include *Betula* and *Populus* with minor components of *Sorbus* and *Alnus*. The most prolific species of these genera are European white birch, *Betula pendula* Roth, downy birch, *B. pubescens* Ehrh., Eurasian aspen, *Populus tremula* L., Siberian mountain-ash, *Sorbus sibirica* Hedl., and speckled alder, *Alnus incana* (L.) Moench. (Koropachinsky 1983).

Understory vegetation consists of woody shrubs and creepers, again with genera similar to North America. Several species are not found circum-boreally and are indigenous to central Asia. These include Ural false spirea, *Sorbaria sorbifolia* (L.) A. Br. and Siberian elder, *Sambucus sibirica* Nakai. Typical boreal woody shrubs found in the study area include raspberries, *Rubus spp*., blueberries, *Vaccinium spp*., currants, *Ribes spp*., and roses, *Rosa spp*.

Understory ground cover is dominated by common herbaceous representatives of the taiga including meadow rue, *Thalictrium minus* L., northern bed straw, *Galium boreale* L., monkshood, *Aconitum septentrionale* Koelle, and the ferns, *Gymnocarpium dryopteris* (L.) Newm. and *Dryoptheris carthusiana* (Vill.) H.P. Fuchs. The graminoid community is comprised primarily of *Carex. spp*., *Calamagrostis obtusata* Trin., and *C. epigeus* (L.) Roth. Bryophytic growth is dominated by sphagnum moss, *Sphagnum spp*. L., Schreber's big red stem moss, *Pleurozium schreberi* (Brid.) Mitt., and feather moss *Hylocomium splendens*, (Hedw.) Schimp.

Methods

The sampling design employed simple random sampling with identical measurements for each disturbance type. Targeted stands consisted of two temporal periods of disturbance and three combinations of disturbance with ten separate undisturbed stands serving as controls. Sampling was conducted in the following undisturbed and disturbed stands: (1) undisturbed fir-spruce, (2) recent fire which occurred five or fewer years ago, (3) severe defoliation by the Siberian moth in the 1995-97 outbreak without fire, (4) severe defoliation by the Siberian moth in the 1995-97 outbreak with a large post-outbreak fire scar, and (5) severe defoliation in the 1955-57 outbreak that burned in the 1960's (Fig. 4.1).

A stand is defined in this study as a distinct area of the forest that is relatively homogeneous in species composition or age and could be managed as a single unit. Five replicate stands for each targeted disturbance type were selected to provide a more accurate estimate of the means and associated variance. Replication within disturbance cover types was accomplished by identifying five separate stands within each type of disturbance. An intensive sampling plot was installed in each stand with plots randomly located throughout the study area. Plot selection criteria required a stand to historically be dominant *Abies* with a lesser component of *Picea* and included ease of accessibility and lack of other disturbances. Every effort was made to lessen bias of plot locations and to reduce edge effect by requiring all plot locations to be at least 50 m or more from an edge, road, or other disturbance type such as windthrow or cutting.

Selection of each sample plot was accomplished by interpreting different overstory cover types on Russian forest cover type maps and navigating to the targeted forest type containing each disturbance type in the field. Random number tables for both distance and azimuth were used to navigate to the center point for the first subplot of each sampling plot. Sampling plots within the same disturbance type were located in distinctly different stands. Location of each sampling plot was documented using map, compass, and geographic positioning system receiver, and recorded on the plot location form. Field sampling was conducted during July and August of 2002 and 2003.

The regeneration plot design in this study utilized eight 30 m transects emanating from the initial center point of a typical USDA Forest Inventory Analysis sample plot (USDA 2001). Each transect consisted of 2 one-m radius regeneration subplots 15 m apart (Fig. 4.2). A regeneration subplot also was established at the center point of the transects' origination point to provide a total of 17 regeneration subplots on each sample plot. In each of the regeneration subplots, all coniferous species less than 2.5 cm in diameter at breast height were recorded for species, number of seedlings, and height.

Soil samples were collected to aid in determining relative homogeneity of ecosystem physical properties. Soils data collected for this study included collection of five 10 cm deep cores extracted from each sampling plot. The five soil cores from each sampling plot were combined in the field to create a composite soil sample of each individual sampling plot. Collected soil samples were subjected to soil texture analysis (Gee and Bauder 1986).

Statistical analysis was conducted using SPSS version 15.0 (SPSS 2006). Regeneration quantity values from individual stands were pooled by disturbance type. ANOVA and LSD post-hoc tests were conducted to determine if disturbance has a significant effect on quantity of regeneration among disturbance types. Height measurements were subjected to identical statistical analysis.

Results

All soils sampled were loamy with some variation from silty loam to sandy loam. Measured elevation (300-400 m AMSL) and slope were relatively constant. Percent of slope for all sampled plots was predominately level. Four plots did measure some negligible slope (<10%) and slope aspect was variable on these plots. SPSS (SPSS 2006) was used to determine if there exists a significant difference between the eastern plots sampled and the western plots sampled through analysis of the soil physical separates (sand, silt, and clay). ANOVA results indicate significant differences within the sampled areas between separates but no significant differences between the eastern and western areas. The image depicting sample plots is a Landsat scene which is skewed on the north-south axis, hence labeling of east-west areas (Fig. 4.1).

Seedling quantity analysis revealed a significance difference among disturbance types ($p<0.005$). The undisturbed stands had a total of 1,101 seedlings in the regeneration subplots ($n = 170$) approximating 20,626 seedlings/ha. In contrast to the undisturbed subplots, the subplots that endured defoliation in the 50's and subsequently burned in the 60's ($n = 85$) had no conifer seedlings (Table 4.1).

Recently defoliated plots had 14 total seedlings/saplings in the regeneration subplots ($n = 85$) equivalent to 525 seedlings/ha. The 14 seedlings were interspersed across three different stands. The area that was burned recently had 58 total seedlings/saplings in the regeneration subplots (n = 170) or approximately 1,087 seedlings/ha. The area defoliated in the 1995-1997 outbreak and consumed by wildfire shortly thereafter had 17 total seedlings in the subplots (n = 170) accounting for 318 seedlings/ha. These recently defoliated stands were without regeneration except for one stand where seedlings were found on six regeneration subplots (Table 4.1).

Species composition of seedlings in the undisturbed stands was primarily Siberian fir (79.6%) followed by lesser components of Siberian spruce (12.6%), Siberian stone pine (7.3%), and Scotch pine (0.5%). In the recently burned stands Siberian spruce seedlings were dominant (55.2%) followed by Siberian fir (27.6%), Siberian larch (10.3%), Siberian stone pine (5.2%), and Scotch pine (1.7%). Stands defoliated in 1995-1997 had only eight Siberian fir seedlings and three each of Siberian spruce and Siberian stone pine. Only one Siberian fir seedling was observed in the stands recently defoliated and burned. Of the 16 remaining seedlings in this disturbance type, seven were Siberian stone pine, six Scotch pine, and three Siberian spruce (Table 4.2).

Seedling height analysis revealed a significance difference among disturbance types ($p<0.005$). Mean overall seedling height was greatest (75 cm) in the plots which endured recent defoliation and fire where few seedlings (n = 17) were found (Table 4.3). The undisturbed plots where the greatest amount of regeneration was recorded (n = 1,101) had seedlings with a mean height of 69 cm. The mean tree height for overstory Siberian fir in undisturbed stands was 18.8(±0.4) m with minimum and maximum heights of 8.5 and 33.0 m, respectively. The seedlings in the fire only plots had a mean height of 34 cm while seedlings measured in the recently defoliated plots had a mean height of 35 cm.

Discussion

It appears that the plot groups represent simple segregation which would violate rules preventing pseudoreplication (Hurlbert 1984). However, they do represent randomized blocks. While each plot was chosen based on, first, accessibility, and secondly, disturbance type, once these criteria were met, random azimuth and random distance from the road were applied to determine plot location. It was not possible to select these plots any differently given the difficulties encountered with Siberia logistics. All plots were less than ten degrees slope negating effects of aspect and at relatively the same altitude.

Analysis of data from the regeneration plots suggests specific trends in boreal forest regeneration following Siberian moth infestation and/or fire. Seedlings were abundant and well dispersed across all plots in the undisturbed stands. The species composition found in these stands is typical of late-successional Siberian boreal forest composition. Siberian fir is the dominant species in both the understory and the overstory.

Stands that experienced recent fire but were not defoliated by the Siberian moth larvae exhibited significantly less regeneration than the undisturbed stands. Stands which endured defoliation from the recent outbreak contained approximately half the number of seedlings per hectare than the stands where only fire occurred recently. This suggests that the Siberian moth is more damaging to regeneration than a crown fire due to incomplete combustion at ground level and the typical patchiness created by fire.

Seedling height showed little variation in the undisturbed stands while the greatest variation occurred in the recently defoliated stands where fire followed. The small amount of regeneration measured in the recently defoliated and burned stands likely contributed to this variation. The recently defoliated and burned stands, not unexpectedly, did have the greatest seedling height likely due to greater exposure to solar radiation and lack of competition since the overstory was removed. Inexplicably, the few seedlings in the recently defoliated stands where no live conifer trees survived were less than half the height of the seedlings measured in the recently defoliated and burned stands. The height of regeneration in recently defoliated stands was comparable to that found in the recently burned stands. However, the number of seedlings in the recently burned stands was more than four times that of the recently defoliated stands.

The biology of the Siberian moth may be a causal factor in the lack of regeneration found on these sites. Siberian moth larvae can cause mortality in conifers prior to cone maturation (Grodnitsky and Palnukova 1999). During outbreak years this would cause a loss of the following year’s seed crop. Conifer seeds naturally dispersed in a forest ecosystem are typically viable for only the current year (Burns and Honkala 1990). During outbreaks Siberian moth larvae defoliate overstory and understory conifers, including seedlings, which in effect removes immediate and potential regeneration. Many dead seedlings were observed in the defoliated stands confirming the moths’ larvae propensity to consume all sizes of conifers.

In the 1955-1957 outbreak area mature birches were observed but no mature conifers were observed in any of these stands. Very few seedlings were detected in any of the regeneration subplots which were predominately populated by forbs and shrubs. Persistent aggressive forb and shrub species appear to out-compete the few surviving shade tolerant conifer species' seedlings.

The more recently defoliated and burned plots contained approximately 318 seedlings/ha which is fewer than any of the other disturbance types with the exception of the older defoliated and burned stands. If observed forb and shrub species continue to dominate in these stands, the few remaining conifer seedlings may succumb to competition as appears to have occurred in the older defoliated and burned stands. Areas where severe Siberian moth outbreaks occur will require seeding in from conifer trees on the periphery of the disturbed area over many decades to return to a fir-dominated stand.

Abies spp. usually attain cone-bearing maturity at the age of 20-30 years. The average distance of effective seed dispersal for non-mountainous locations of *Abies spp.* in North America ranges from 1.5 to 2.5 times the tree height in the windward direction (Burns and Honkala 1990). Average tree height for sampled Siberian fir in undisturbed areas was 18.8 m. This suggests that average effective seed dispersal distance should be 28.2 – 47 m. Of course, some seeds can be spread as far as 300 m by seeds blown over snow or movement by rodents.

The 1955-1957 outbreak included an area west of Bolshaya Murta of approximately 20,000 ha that was completely defoliated (Kharuk et al 2003). Given a completely defoliated square area with a volume of 20,000 sq. ha, approximately every 20-30 years this forb and shrub dominated area would revert along the edge to fir-dominated forest by approximately 30-300 m. With 100 linear m on each side of a square ha, this conservatively equates to approximately three ha from the forest edge returning to fir-dominated status every 20-30 years. The linear distance to the center of this example square area from the imaginary forest edge would be approximately 7,000 m which would require, minimally, 450 years to return to a completely stocked fir-dominated boreal forest stand.

North American pests such as the non-native balsam woolly adelgid, *Adelges piceae* (Ratz.) (Homoptera:Adelgidae), and native spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera:Tortricidae), cause mortality in the overstory yet cause little damage to regeneration (Smith and Nicholas 2000, Witter and Ragenovich 1986). However, in contrast to the Siberian moth, they cause little mortality of seedlings or saplings in the understory. The defoliation of coniferous seedlings and saplings by Siberian moth larvae in the understory is unique among forest overstory pests. Coupled with the complete mortality of the overstory and loss of the seedbank, the loss of the understory regeneration prevents the return to coniferous forests for perhaps as long as five centuries. The results of this investigation indicate that the Siberian moth could be a much more serious pest, if it becomes established in North American conifer forests, than any of the currently known pests in these forests.

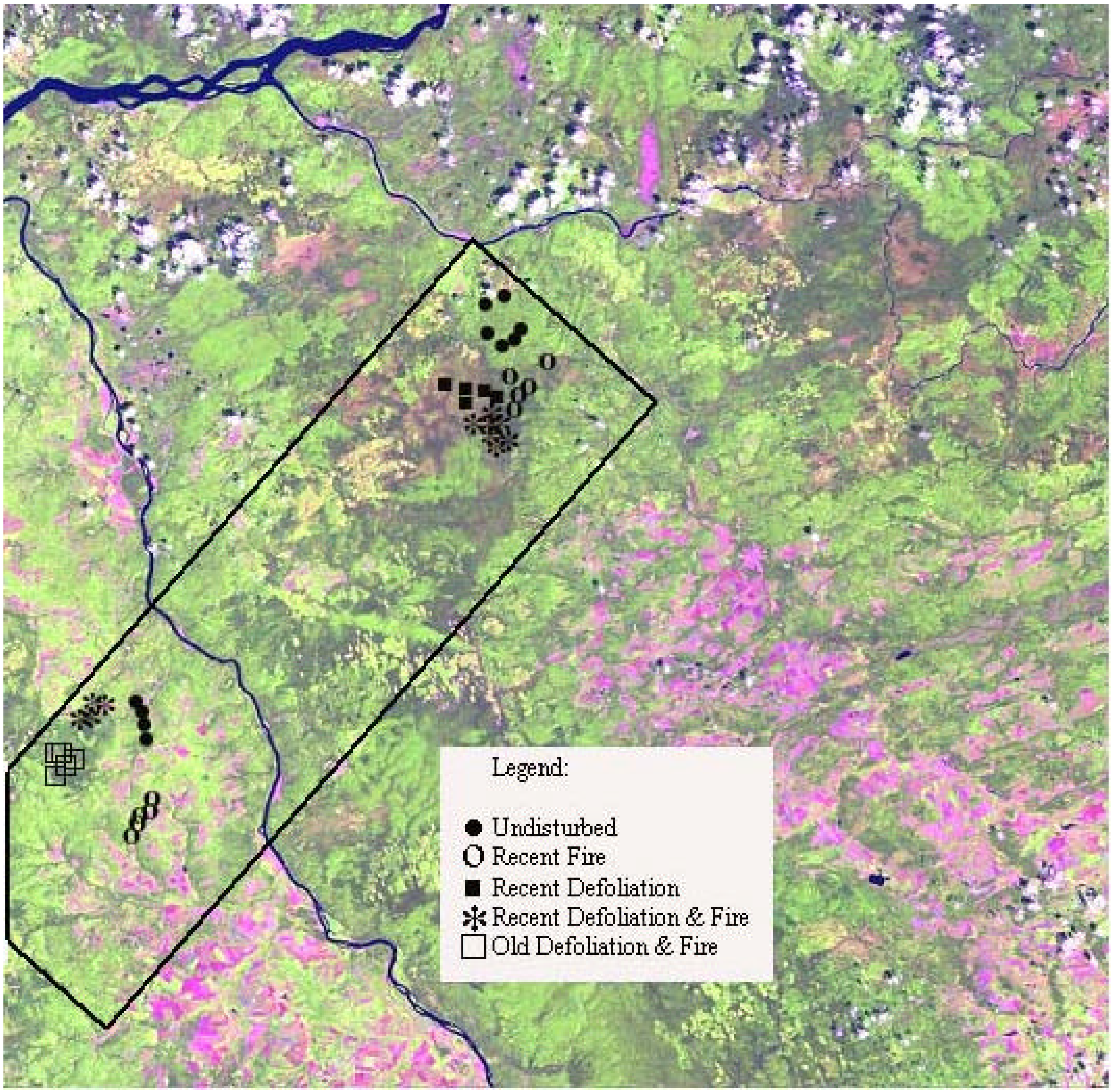

Figure 4.1. Krasnoyarsk Krai Study Area with Plot Locations

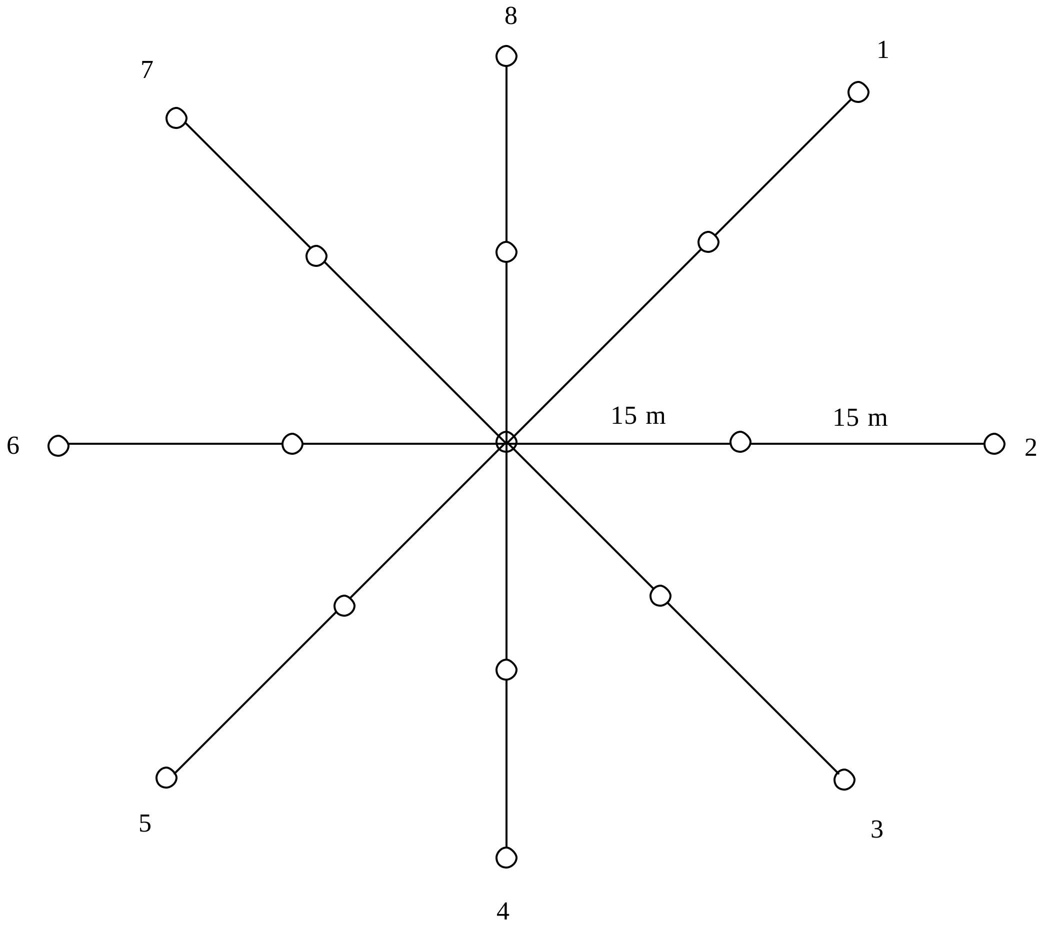

Figure 4.2. Regeneration plot schematic showing locations of transects. There are 17 subplots/sampling plot.

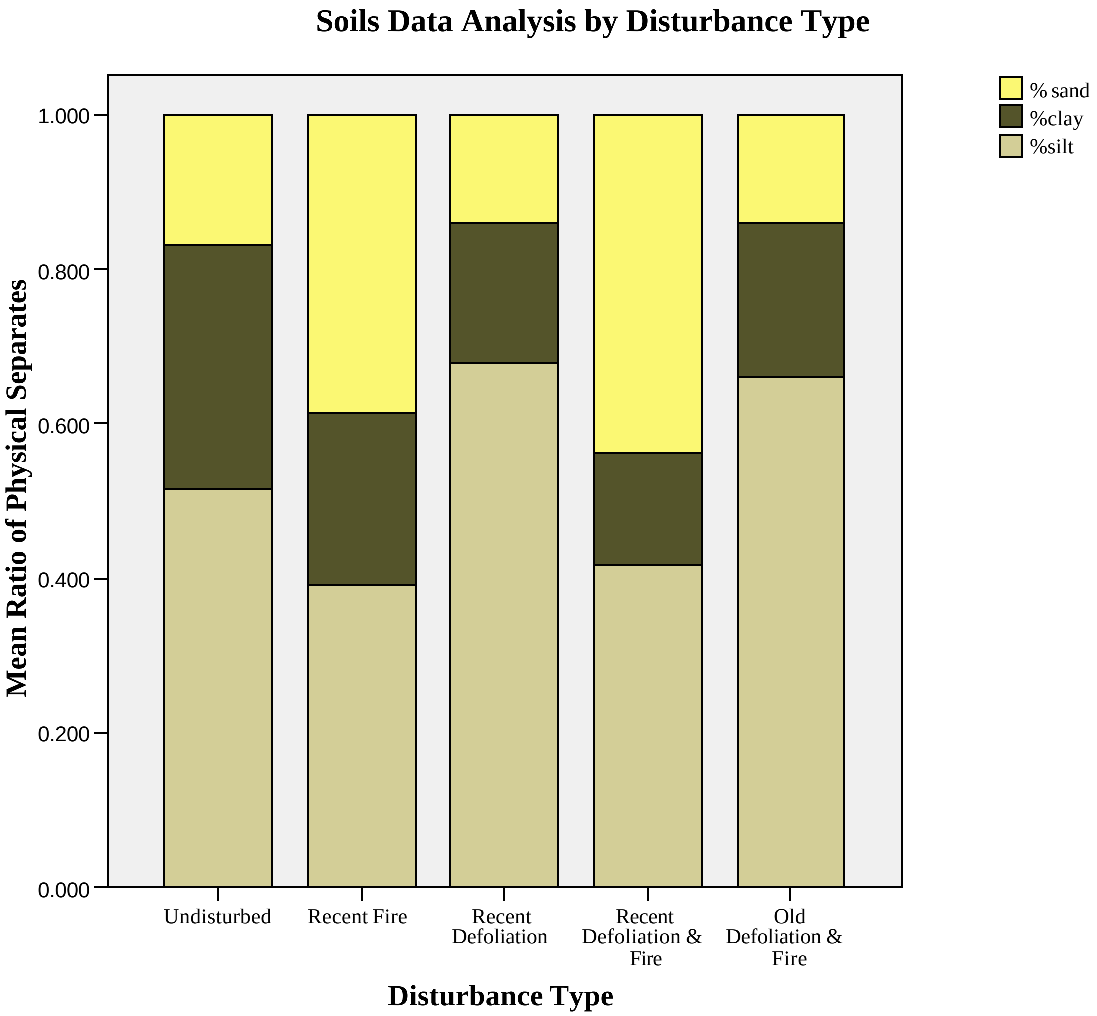

Figure 4.3. Soils Data Analysis of Physical Separates by Disturbance Type. e.

Table 4.1. Number of conifer seedlings by disturbance type.

Disturbance Type	Total No. Seedlings	No. Regeneration Subplots	Mean No. Seedlings/ha (SE)
Old Defoliation & Fire	0	85	0(±0.0)
Recent Defoliation & Fire	17	170	318(±78.6)
Recent Defoliation	14	85	525(±383.4)
Recent Fire	62	170	1087(±93.5)
Undisturbed	1102	170	20626(±20.2)

Table 4.2. Percent seedlings' species composition by disturbance type.

Disturbance Type	*Abies sibirica* Ledeb.	*Larix sibirica* Ledeb.	*Picea sibirica* Ledeb.	*Pinus sibirica* Du Tour	*Pinus sylvestris* L.	N
Old Defoliation & Fire	0.0	0.0	0.0	0.0	0.0	0
Recent Defoliation & Fire	5.9	0.0	17.6	41.2	35.3	17
Recent Defoliation	57.2	0.0	21.4	21.4	0.0	14
Recent Fire	27.6	10.3	55.2	5.2	1.7	58
Undisturbed	79.6	0.0	12.6	7.3	0.5	1,101

Table 4.3. Mean seedling height by disturbance type.

Disturbance Type	Mean Height ±SE (cm)
Old Defoliation & Fire	0±0.0
Recent Defoliation & Fire	13.2±3.2
Recent Defoliation	5.4±1.4
Recent Fire	10.2±1.8
Undisturbed	66.9±1.4

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Chapter V

Conclusions

The preceding chapters provide compelling evidence of the long term effects the Siberian moth inflicts in its native habitat and suggests potential effects it may have as an invasive species elsewhere. At outbreak population levels this pest is capable of causing complete mortality of coniferous overstory species and, significantly, removing current and future regeneration. Russian literature cites the Siberian moth's propensity for all overstory coniferous species as preferred hosts (Grodnitsky and Palnukova 1999, Baranchikov et al. 1997, Kondakov et al. 1997, Vorontsov 1982). Since North America retains more species in more genera than found in the native range of this Lepidopteran, it appears that an invasion of this pest could have catastrophic effects in this Western Hemispheric continent's conifer forests (Niemela and Mattson 1996). Summarizing the evidence of these effects presented by this study follows.

Stands dominated by Siberian fir, *Abies sibirica* Ledeb., were subjected to disturbances in the 1950's and the 1990's. During these periods some stands experienced fire, or pest outbreaks, and some both. Stands defoliated in the 1950's and burned in the 1960's exhibited minor differences in composition of both understory and overstory stems compared to stands defoliated and burned in the 1990's. Stands defoliated in the 1990's, burned or unburned, had 100% conifer mortality, including all seedlings and saplings. The older disturbed stands exhibited a dominant forb composition that included a sparse deciduous overstory of birch, *Betula spp*. No conifers were measured or observed in this area more than 50 years after the stands were defoliated and subsequently burned. A steady state of forb domination between older and recently defoliated stands suggests that the Siberian moth may be responsible for a disruption of succession in the boreal forest. Stands enduring only fire exhibited typical boreal forest succession.

Stands defoliated in the 1950's and burned in the 1960's exhibited major differences in amounts of both downed and standing coarse woody debris compared to stands defoliated and burned in the 1990's. Stands defoliated in the 1990's, burned or unburned, were found to have significantly more overall coarse woody debris than the other stands surveyed. The older disturbed stands exhibited almost a complete loss of the coarse woody debris quantities found in the other disturbance types. No live conifer stems were observed in the older disturbed stands more than 50 years after these stands were defoliated and subsequently burned. The implications for carbon flux in large areas suffering complete mortality by the Siberian moth and subsequently burning are significant. This study found a loss of 23.8 Mg/ha of C over an approximately 50 year period.

Stands defoliated in the 1950's and burned in the 1960's had no regeneration. Stands defoliated in the 1990's, burned or unburned, were comparable in the number of seedlings found but had significantly fewer seedlings than undisturbed stands. The stands enduring only recent fire appeared to have typical boreal forest regeneration (Aber and Melillo 1991, Sirois and Payette 1991).

The old defoliated and burned stands were dominated by forbs and shrubs. The aggressive and persistent nature of which shaded out the few seedlings that were left following both disturbances. Severe Siberian moth outbreaks may create large areas almost devoid of conifers. Reversion to fir-dominated stands may require centuries of successive regeneration from conifer trees along the periphery of the disturbed area.

The evidence presented herein suggests that the Siberian moth may be an even more insidious pest than any existing phytophagous insect in North American boreal forests. North American pests such as the non-native balsam woolly adelgid, *Adelges piceae* (Ratz.) (Homoptera:Adelgidae), and native spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera:Tortricidae), cause mortality in the overstory yet cause little damage to regeneration (Smith and Nicholas 2000, Witter and Ragenovich 1986). However, in contrast to the Siberian moth, they cause little mortality of seedlings or saplings in the understory. The defoliation of coniferous seedlings and saplings by Siberian moth larvae in the understory is unique among forest overstory pests. Coupled with the complete mortality of the overstory and loss of the seedbank, the loss of the understory regeneration prevents the return of large high mortality areas (>20,000 ha) to coniferous forests for perhaps as long as five centuries. The results of this investigation indicate that the Siberian moth could be a much more serious pest, if it becomes established in North American conifer forests, than any of the currently known pests in these forests.

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