



Effect of Tenthredinid Leaf Miner Invasions on Growth of Alaska White Birch in Anchorage, Alaska, USA, and the Interaction with Biological Control of Amber-Marked Birch Leaf Miner

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Effect of tenthredinid leaf miner invasions on growth of Alaska white birch in Anchorage, Alaska, USA, and the interaction with biological control of amber-marked birch leaf miner

Roy G. Van Driesche¹, Jian Duan², and Jeanne Osnas³

Abstract

The amber-marked birch leaf miner, *Profenusa thomsoni* (Konow) (Hymenoptera: Tenthredinidae), invaded the Anchorage region in southeastern Alaska, USA, about 1991 and by 1996 caused high levels of mining, resulting in browned foliage annually by Aug during the outbreak years of 1996 to 2007. A biological control program began in 2004 based on the importation of the larval parasitoid *Lathrolestes thomsoni* Reshchikov (Hymenoptera: Ichneumonidae), which previously had suppressed an outbreak of amber-marked birch leaf miner in Alberta, Canada. By 2008, this introduced parasitoid and 2 resident species (native or self-introduced) reduced damage to Alaska white birch by > 50%. In 2020, as a follow up, 100 Alaska white birch in forested parks in Anchorage were cored to see if leaf mining had reduced tree growth during the outbreak and whether biocontrol of amber-marked birch leaf miner allowed tree growth to recover. Compared to 12 yr (1984–1995) before the start of the outbreak, radial growth was suppressed by approximately 16% during the outbreak (1996–2007). During the 11 yr after suppression of damage through biocontrol (2008–2018), tree radial growth of Alaska white birch did not recover, but rather declined further. This pattern may be due to the invasion around 2008 of another birch leaf miner, *Heterarthrus nemoratus* (Fallén) (Hymenoptera: Tenthredinidae). These findings show that outbreaks of birch leaf miners caused an important drop in growth of Alaska white birch, which has implications for forest productivity and carbon sequestration by birch-dominated forest stands in southeast Alaska.

Key Words: invasive birch leaf miners; tree growth; biocontrol; parasitoid; carbon sequestration; forest pest invasion

Resumen

El minador de hojas de abedul de marcado ámbar, *Profenusa thomsoni* (Konow) (Hymenoptera: Tenthredinidae), invadió la región de Anchorage en el sureste de Alaska alrededor de 1991 y en 1996 causó altos niveles de daño, lo que resultó en un brote de follaje dorado anualmente durante agosto desde los años de 1996 hasta el 2007. En el 2004, se inició un programa de control biológico basado en la importación del parasitoide larval *Lathrolestes thomsoni* Reshchikov (Hymenoptera: Ichneumonidae), que previamente había suprimido un brote de minador de hojas de abedul marcado con ámbar en Alberta, Canadá. Para el 2008, este parasitoide introducido y 2 especies residentes (nativas o autointroducidas) redujeron el daño al abedul blanco de Alaska en > 50%. En el 2020, como seguimiento, se tomaron muestras de 100 abedules blancos de Alaska en parques boscosos en Anchorage para ver si la minería de hojas había reducido el crecimiento de los árboles durante el brote y si el biocontrol del minador de hojas de abedul de marcado ámbar permitió que el crecimiento de los árboles se recuperara. En comparación con los 12 años (1984–1995) antes del comienzo del brote, el crecimiento radial se suprimió en aproximadamente un 16% durante el brote (1996–2007). Durante los 11 años posteriores a la supresión del daño a través del control biológico (2008–2018), el crecimiento radial de los árboles del abedul blanco de Alaska no se recuperó, sino que disminuyó aún más. Este patrón puede deberse a la invasión alrededor del 2008 de otro minador de hojas de abedul, *Heterarthrus nemoratus* (Fallén) (Hymenoptera: Tenthredinidae). Estos hallazgos muestran que los brotes de minadores de hojas de abedul causaron una caída importante en el crecimiento del abedul blanco de Alaska, lo que tiene implicaciones para la productividad forestal y el secuestro de carbono por parte de los bosques dominados por abedules en el sureste de Alaska.

Palabras Clave: minadores de hojas de abedul invasivos; crecimiento de árboles; control biológico; parasitoide; secuestro de carbón; invasión de plagas forestales

Birch trees (*Betula* spp. L.; Betulaceae), especially paper birch (*Betula papyrifera* Marshall; Betulaceae) and yellow birch (*Betula alleghaniensis* Britt.; Betulaceae), are important components of forests in the northeast US, Alaska, and southern Canada (Quigley & Babcock 1969). In northern Eurasia, other species of birch such as silver birch

(*Betula pendula* Roth; Betulaceae) and downy birch (*Betula pubescens* Ehrh.; Betulaceae) also are significant parts of regional forests (Hynynen et al. 2010) but serve as hosts for various leaf miners, especially tenthredinid sawflies (Eichhorn & Pschorn-Walcher 1973). Since 1900, 5 Eurasian tenthredinid leaf miners attacking birch have invaded

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North America (Digweed et al. 2009). All 5 species have experienced regional, or wider, pest outbreaks in North America. In Alaska, 3 of these 5 species are present: *Heterarthrus nemoratus* (Fallén), *Fenusia pumila* Leach, and *Profenusia thomsoni* (Konow), while 2 others, *Fenusella nana* (Klug), and *Scolioneura vicina* Konow (all Hymenoptera: Tenthredinidae), have not yet been recorded there. In eastern North America, biological control programs have been carried out to control *F. pumila* (Van Driesche et al. 1997; Casagrande et al. 2009) and *H. nemoratus* (Dowden 1941), and in western North America for control of *P. thomsoni* (Soper 2012; Soper et al. 2015; Soper & Van Driesche 2019; Andersen et al. 2021).

Profenusia thomsoni, known as the amber-marked birch leaf miner, reached Alaska in or shortly before 1991, having spread there from eastern Canada (Digweed 1998; MacQuarrie et al. 2007; Snyder et al. 2007; Digweed et al. 2009). In southeastern Alaska (the Anchorage region), *P. thomsoni* infested Alaska white birch (*Betula neoalaskana* Sarg.; Betulaceae) (Soper 2012; Soper et al. 2015; Soper & Van Driesche 2019; Andersen et al. 2021). Populations of this leaf miner reached pest densities by 1996 (Snyder et al. 2007). In cooperation with the Canadian Forest Service and Alaskan state officials, the US Forest Service initiated a classical biological control program to control *P. thomsoni* in Alaska in 2004. This program was based on the redistribution of the larval parasitoid *Lathrolestes thomsoni* Reshchikov (Hymenoptera: Ichneumonidae) (Reshchikov et al. 2010), a species attacking *P. thomsoni* in Alberta where an outbreak of the same leaf miner had subsided due to the parasitoid (Digweed et al. 2003). The parasitoid was collected in Alberta and the Northwest Territories and then released in Alaska, primarily in the Anchorage region. The biological control project in Alaska was initiated to help property owners and the Alaskan state forest service deal with the consequences of the amber-marked birch leaf miner invasion. This invasion had caused widespread browning of Alaska white birch in both urban and forested areas in the Anchorage region and parts of the interior (Fairbanks). In urban areas, this browning led to increased use of pesticides for control of amber-marked birch leaf miner. Thus, the purpose of the biological control program was to improve the trees' appearance and reduce pesticide use in urban areas. Physiological impacts of the defoliation caused by this leaf miner on Alaska white birch were unknown, and no obvious tree mortality was associated with the outbreak.

Through 2005, the amber-marked birch leaf miner biocontrol program in Alaska was carried out by the University of Alberta (MacQuarrie 2008), and this phase included the initial releases of the imported parasitoid *L. thomsoni*. From 2006 to 2011, the program was continued by the University of Massachusetts, Amherst, Massachusetts, USA, during which time a greatly expanded set of *L. thomsoni* releases were made (Soper et al. 2015). Collectively, these efforts resulted in the parasitoid establishing and suppressing the leaf miner. The parasitoid's impact on amber-marked birch leaf miner was evaluated, together with an assessment of 2 resident (native or self-introduced) parasitoids (Soper et al. 2015; Soper & Van Driesche 2019). After an 8-yr hiatus, the status of the project was updated in 2019 (Andersen et al. 2021) by re-measuring amber-marked birch leaf miner density and levels of larval parasitism at most of the original sites established between 2006 and 2011 in the Anchorage area (Soper et al. 2015). Percentage parasitism levels were determined for *L. thomsoni* and a second, pre-existing species, *Lathrolestes soperi* Reshchikov (Hymenoptera: Ichneumonidae) that had been observed attacking the amber-marked birch leaf miner larvae in earlier research (Soper & Van Driesche 2019). After the release of *L. thomsoni* in Anchorage, the impact of amber-marked birch leaf miner declined from 70% of leaves being mined in 2006 to 19% in 2011, whereas parasitism rose from 8% to 32% (Soper et al. 2015). In an assessment in 2019, only 9% of leaves were mined by amber-

marked birch leaf miner and parasitism by the 2 *Lathrolestes* species combined was 70%; of total parasitism, 71% was caused by *L. thomsoni* and 29% by *L. soperi* (Andersen et al. 2021). In 2019, amber-marked birch leaf miner was present at below-pest densities at most sites surveyed in Anchorage.

In 2020, as a follow-up question, we asked what effect amber-marked birch leaf miner leaf mines might have had on tree radial growth before leaf miner impact was reduced by the biocontrol project. Destruction of plant leaves, either by external folivores or internal ones like leaf miners can reduce tree growth, accelerate die-back, and reduce reproductive output (e.g., Raimondo et al. 1958; Kulman 1971; Long 1988; Muzika & Liebhold 2001; Hogg et al. 2002; Thalmann et al. 2003; Nardini et al. 2004; Percival et al. 2011). Most leaf miners feed on the mesophyll, which reduces photosynthesis and may interfere with stomatal conductance (Proctor et al. 1982; Johnson et al. 1983; Whitaker 1994; Wagner et al. 2008). Mesophyll loss also can shorten leaf longevity (Pritchard & James 1984). No specific information existed on the effects on tree growth of amber-marked birch leaf miner or other invasive tenthredinid leaf miners.

Therefore, we hypothesized that the outbreak of amber-marked birch leaf miner in Alaska may have reduced the rate of birch growth compared to historical values. We also hypothesized that the reduction of amber-marked birch leaf miner mining levels from 70 to 9% from 2006 to 2019 may have returned birch growth to pre-invasion levels. To determine historical levels of growth of Alaska white birch in the Anchorage area, in 2019 Jeanne Osnas from the University of Alaska cored Alaska white birch trees in the Anchorage area at 11 of the sites used previously in the biological control project, coring 10 trees per site. Tree cores were processed and read by Patrick Sullivan of the University of Alaska in Anchorage, and the data on growth of the sampled trees are examined here.

To balance the number of yr associated with different phases of the leaf miner outbreak and suppression by biological control, we compared the 11 available yr after successful biological control for which we had tree ring data (2008–2018) to the 12 yr period between the first recorded amber-marked birch leaf miner high density population (1996) through 2007 (the yr in which the introduced parasitoid had reduced the level of leaf mining to approximately half of the peak level), and also to a control 12 yr period before high densities of amber-marked birch leaf miner were observed in Alaska (1984–1995).

The ability to evaluate the impact of amber-marked birch leaf miner on Alaska white birch growth after the successful biological control project, however, was complicated by the arrival in Anchorage in about 2003 of a second very similar invasive leaf miner, the late birch leaf edge miner, *Heterarthrus nemoratus* (Fallén) (Hymenoptera: Tenthredinidae) (Snyder et al. 2007), which by 2008 had reached substantial levels (36% leaves mined) (Lundquist et al. 2012). Therefore, as amber-marked birch leaf miner densities were declining due to the biological control programs, densities of the second invader were independently climbing (Fig. 1).

In 2021, mined birch leaves (irrespective of miner species) were collected where trees were cored to measure (1) the percentages of mines cause by amber-marked birch leaf miner versus *H. nemoratus* (as per Digweed et al. 2009), and (2) parasitism of each leaf miner species. Using the historical data on the leaf miner infestation and parasitism rates as well as tree radius growth, we tested 3 hypotheses: (1) did the outbreak of amber-marked birch leaf miner reduce growth rates of Alaska white birch, (2) did successful biological control of amber-marked birch leaf miner cause birch growth to recover, and (3) is the second invasive leaf miner's impact now similar to that of amber-marked birch leaf miner during its outbreak and is *H. nemoratus* commonly parasitized.

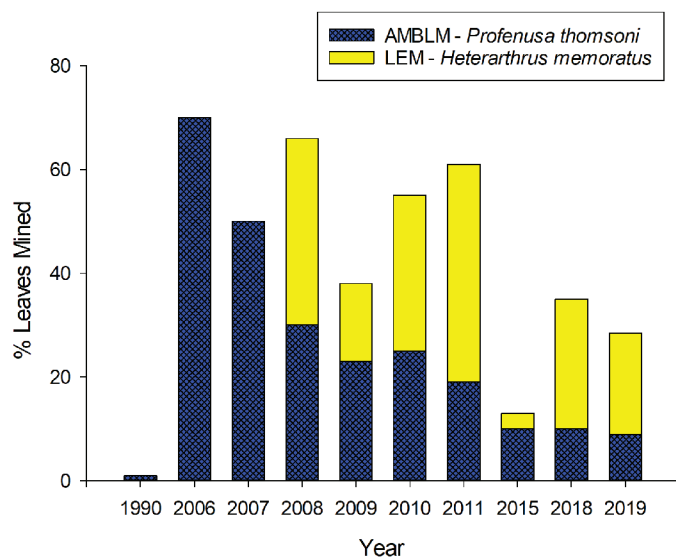


Fig. 1. Percentage of Alaska white birch (*Betula neoalaskana*) leaves in Anchorage mined by the amber-marked birch leaf miner (AMBLM on graph) (*Profenusa thomsoni*) or the late birch leaf edge miner (LEM on graph) (*Heterarthrus nemoratus*) from 1990 to 2019, from the initial invasion of amber-marked birch leaf miner (around 1991) through its suppression by classical biocontrol (2004–2015) and the invasion of a second species of leaf miner (*H. nemoratus*) (around 2008). Data on percentage of birch leaves mined by each species were taken from multiple sources: (1) *P. thomsoni*: 2006–2011 (Soper et al. 2015); 2015 and 2018 (Wenninger unpublished 2018); and 2019 (Andersen et al. 2021); and (2) *H. nemoratus*: 2008–2010 (Lundquist et al. 2012); 2011 (Mulvey & Lamb 2012, p. 15); 2015 and 2018 (Wenninger unpublished 2018); and 2019 (Andersen et al. 2021).

Materials and Methods

STUDY SITES AND COLLECTION OF CORING SAMPLES

In 2020, up to 10 Alaska white birch trees at each of 11 sites (discussed in Andersen et al. 2021) were selected randomly and cored to obtain radial growth data from 100 trees (1 core per tree) with sampled tree diameter at breast height values ranging from about 25 to 30 cm (Table 1). These cores yielded 99 usable cores, which had tree rings that defined growth for yr from 2018 backwards to a maximum of 1913, depending on the age of the tree. In general, sites were public parks with

Table 1. Locations of sites in Anchorage, Alaska, where Alaska white birch trees (up to 10 per site) were cored in 2020 to measure tree growth.

Site name	Latitude	Longitude
Earthquake Park	61.198950°N	149.991081°W
Point Woronzof	61.199356°N	150.021631°W
Balto Seppala Park	61.1907203°N	149.943576°W
Westchester Lagoon*	61.202544°N	149.918394°W
Campbell Creek (= "Jewel lake")*	61.141414°N	149.917806°W
Taku Lake Park*	61.1516705°N	149.881999°W
John's Park*	61.1053363°N	149.880044°W
Forsythe Park	61.119125°N	149.773325°W
Javier de la Vega Park	61.169071°N	149.917806°W
Kincaid Park*	61.1557466°N	150.047279°W
University of Alaska – forest edge*	61.1923860°N	149.824522°W

*Substitute sites not originally studied by Soper et al. (2015) that were nearby a Soper site, usually being forested city conservation areas (usually city parks) used in substitution for private home locations or too few birch trees.

various sized patches of natural forest, and they were spread widely over the Anchorage region. Urban yard trees were not included.

PROCESSING CORE SAMPLES FOR ANALYSIS AND MEASUREMENT OF GROWTH RINGS

The increment cores were mounted in wooden blocks and sanded successively with increasingly fine grit sandpaper. Finish sanding was performed at 1,200 grit. The cores were cross dated visually with the aid of narrow marker rings in 1970, 1977, and 2002. Ring width measurements were made to the nearest 0.001 mm using a sliding bench micrometer and digital encoder (Velmetx Inc., Bloomfield, New York, USA). In general, the increment cores were collected from healthy Alaska white birch trees with well-defined latewood boundaries. When rings were faint, measurement accuracy was improved using a variation of the "shadow technique" (DeRose & Gardner 2010). Staining of the increment cores was deemed unnecessary. After completing the ring width measurements, cross-dating accuracy was checked using the tree-ring data software COFECHA (Holmes 1983) and corrections were made as necessary. The final dataset included a tree-ring series from 99 Alaska white birch trees, with a span from 1913 to 2018 and a mean correlation with the overall chronology of 0.457.

COLLECTION OF INFORMATION ON HISTORY OF BIRCH LEAF MINERS IN SOUTHEASTERN ALASKA

The history of the invasions and outbreaks of amber-marked birch leaf miner and late birch leaf edge miner in southeastern Alaska were reconstructed from the literature (Wittwer 2003; Snyder et al. 2007; Lundquist et al. 2012; Soper et al. 2015; Wenninger 2018; Andersen et al. 2021), and data were expressed as a chronological listing of the percentage of leaves mined by either amber-marked birch leaf miner or *H. nemoratus* from the first observation in Alaska of each species through 2019. This chronology was used to divide the tree ring core series into 3 periods based on the biological events affecting leaf mine densities: (1) a 12 yr pre-amber-marked birch leaf miner outbreak period (1984–1995) before the first record of high density amber-marked birch leaf miner populations in 1996, (2) the main amber-marked birch leaf miner outbreak period from 1996 to 2007 (by which yr biological control had reduced peak leaf miner numbers by half), and (3) the post-biological control period of amber-marked birch leaf miner suppression from 2008 to 2018 (our last yr of tree ring data).

RELATIVE RATES OF LEAF MINING AND PARASITISM FOR 2 LEAF MINERS IN 2021

In 2021, samples of mined leaves were collected to determine the current relative abundance and parasitism of the 2 birch leaf miners (amber-marked birch leaf miner and late birch leaf edge miner). We did not collect leaves randomly, but rather only collected leaves with visible mines. Consequently, we did not estimate the percentage of leaves with mines, unlike in previous yr. Mined leaves were collected without regard to the species of leaf miner present. From each of the 11 sites previously investigated by Andersen et al. (2021) (Table 1), in 2021 we collected about 100 to 200 mined leaves. All locations sampled were forests, not urban yards. Samples were collected from 19 to 24 Aug in Anchorage, Alaska, USA, and sent to the University of Massachusetts, Amherst, Massachusetts, USA, where all leaves were examined, and all leaf mines were classified to species according to photo illustrations of mines by Digweed et al. (2009). Larvae from inside mines or loose in the bottom of the collection bags (both live larvae and recently dead larvae that were still adequate for dissection) were separated by spe-

cies using photos of larvae in Digweed et al. (2009) and were dissected to detect parasitoid immature stages (eggs or larvae of any species). While our primary interest was to determine levels of parasitism for *H. nemoratus*, we also dissected amber-marked birch leaf miner larvae as a positive control on the suitability for dissection of the available larvae found in samples.

ANALYSIS OF DATA

To detect any trends including cyclicity in tree growth rates (increment ring core readings), we first calculated the mean of the increment ring core readings at each yr and ran a time series analysis of the mean core readings over the period being examined (1984–2018). We then compared growth seen in tree rings for 3 periods as described above: (1) the pre-amber-marked birch leaf miner outbreak period (1984–1995), (2) the amber-marked birch leaf miner outbreak period (1996–2007), and (3) the amber-marked birch leaf miner suppression period (2008–2018, the last yr of tree ring data). We then examined the trend (slope) in the ring core readings over sampling times (yr) using a linear regression model for each of these periods. The linear regression models were fitted using the Fit Model platform of JMP[®] PRO 16 (SAS 2020), and each model's slope was tested to see if it was significantly different from zero (in each time period).

Results

LEAF MINER DENSITY IN SOUTHEASTERN ALASKA

Trends in damage by amber-marked birch leaf miner in southeastern Alaska, as presented here (Fig. 1), are found in some previously published studies (e.g., Lundquist et al. 2012; Soper et al. 2015) but are

supplemented with many yr of unpublished Forest Service or State of Alaska reports. This is the first organized summary of this pest's density during its outbreak yr. Amber-marked birch leaf miner was first reported in Alaska in 1991, in the Anchorage area (USDA Forest Service 1992), and damage from amber-marked birch leaf miner was first reported to be high in 2002 (Wittwer 2003). The first data reported on percentages of leaves mined were for 2006 to 2011 (Lundquist et al. 2012; Soper et al. 2015), both for amber-marked birch leaf miner in the Anchorage area. The highest recorded density of amber-marked birch leaf miner (70% leaf mining) occurred in 2006 (Soper et al. 2015). By 2011 (the end of the biological control project), the percent of leaves mined by amber-marked birch leaf miner had dropped to 19% (Soper et al. 2015). A separate survey carried out in 2019 found that the percentage of amber-marked birch leaf miner-mined leaves had declined further to 8.9% (Andersen et al. 2021), showing that the biological control agent (*L. thomsoni*), in conjunction with 2 pre-existing parasitoids (Soper & Van Driesche 2019) had ended the outbreak of this leaf miner. However, a second species of tenthredinid leaf miner (*H. nemoratus*) invaded the study region sometime before 2008 and became numerous (Fig. 1).

TREND IN ALASKA WHITE BIRCH GROWTH

The trend in mean annual tree growth values (Fig. 2) showed a large decline in 2002, the first yr of high amber-marked birch leaf miner densities. Thereafter, values remained low, with some variation, for the remainder of the sampled yr. Regression analyses of growth of Alaska white birch for the earliest period (1984–1994) before the invasion of amber-marked birch leaf miner (Fig. 3A) showed that annual tree radial growth rates averaged 2.12 ± 0.04 (SE) mm, and the annual growth rate (tree core reading value) ranged from 0.02 to 8.50 mm, with the slope of the linear regression being not significantly different from zero (F

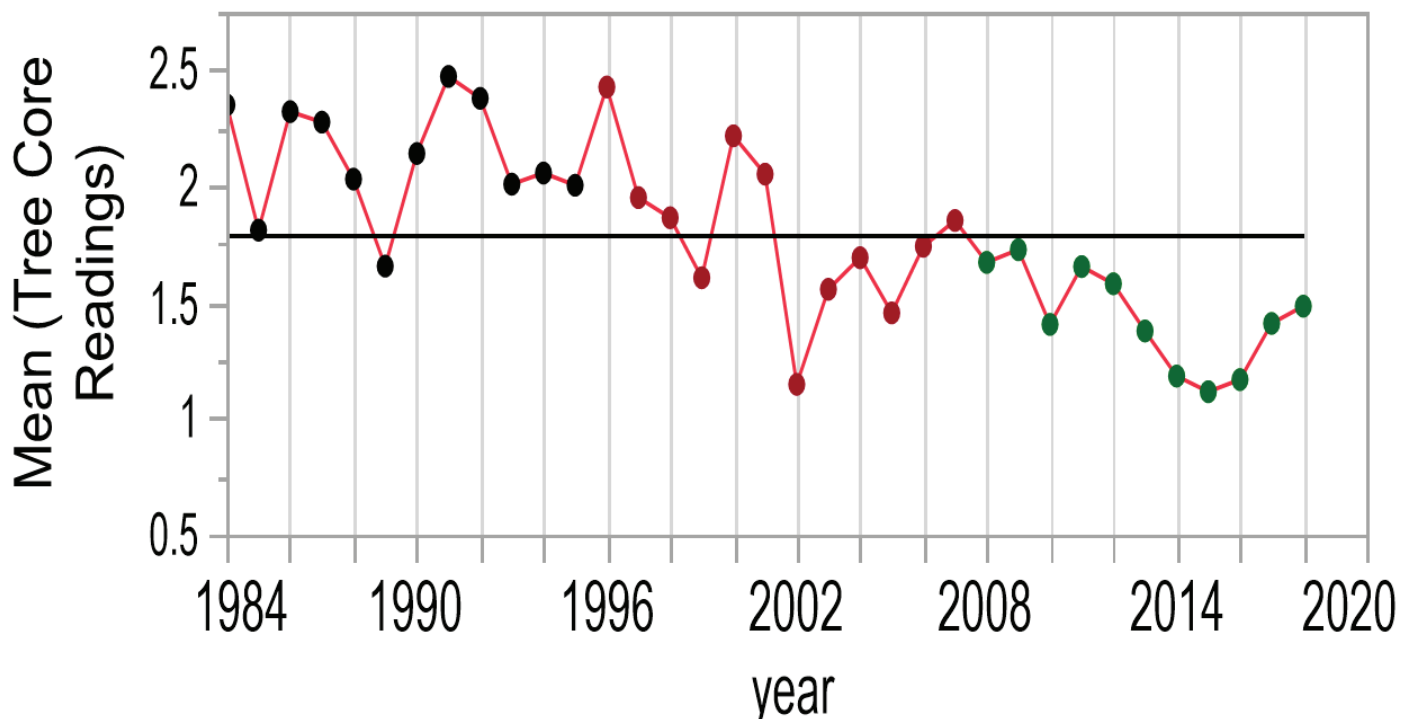


Fig. 2. Time series analysis of mean radial growth increments (mm) of Alaska white birch (*Betula neoalaskana*) in Anchorage, Alaska ($n = 99$) from 1984 to 2018: (1) pre-amber-marked birch leaf miner (*Profenusa thomsoni*) outbreak control period (1984–1995) (black dots); (2) amber-marked birch leaf miner outbreak period (1996–2007) (red dots); and (3) the amber-marked birch leaf miner suppression period due to biological control (2008–2018) (green dots). Time Series Mean = 1.7938, Std = 0.3843, $N = 35$, Zero Mean ADF (Augmented Dickey Fuller test) = -0.9887 , Single ADF = -2.8315 , Trend ADF = -4.8800 .

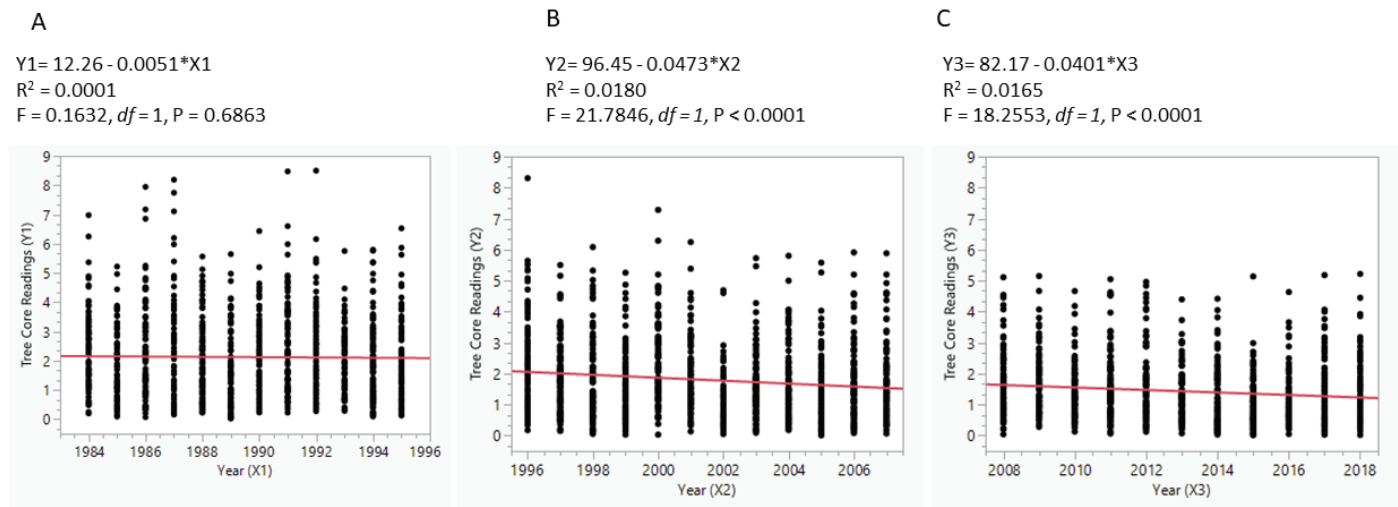


Fig. 3. Trends in annual radial growth increment (mm) from Alaska white birch (*Betula neolaskana*) in Anchorage, Alaska ($n = 99$ cores) during each of 3 periods: (A) the pre-amber-marked birch leaf miner (*Profenusa thomsoni*) outbreak period (1984–1995), (B) the amber-marked birch leaf miner outbreak period (1996–2007), and (C) the biological control amber-marked birch leaf miner suppression period (2008–2018).

$= 0.1632$; $df = 1$; $P = 0.6863$). During the period when amber-marked birch leaf miner was at high density (1996–2007), annual tree radial growth declined from the previous average value of 2.12 ± 0.04 (ranging from 0.01 to 8.30 mm), with a negative slope that was significantly different from zero (Fig. 3B) ($F = 21.7846$; $df = 1$; $P < 0.0001$). In the period after biological control suppression of amber-marked birch leaf miner (2008–2018) (2008 being when amber-marked birch leaf miner mine density dropped to half of peak levels, and 2018 being the last yr of the available tree growth data), the annual tree radial growth continued to decline to an average value of 1.43 ± 0.03 mm (ranging from 0.01 to 5.2 mm) with a negative slope that was significantly different from zero (Fig. 3C) ($F = 18.2553$; $df = 1$; $P < 0.0001$). Throughout the study period (1984–2018), the average rainfall (from Apr to Aug) in Alaska was normal (Supplementary Data – SF1), and no significant correlations were detected between birch growth rates (mean tree core readings) and summer rainfall (SF2).

RELATIVE ABUNDANCE OF LEAF MINERS AND PARASITISM IN 2021

When mined leaves from all sample locations were pooled, there were 1,338 leaves with mines. Nineteen leaves (1.4%) were attacked by both species, 156 (13%) were mined by amber-marked birch leaf miner only, and 1,163 (88.3%) leaves were mined by *H. nemoratus* only. Tallying all mines rather than leaves with mines, 1,357 mines were present in the samples, of which 175 (12.9%) were amber-marked birch leaf miner mines and 1,182 (87.1%) were *H. nemoratus* mines.

Many mines when collected were empty or had only old dead larvae in them that were not suitable for dissection. We sought to dissect approximately 40 larvae per site if available. Actual numbers of *H. nemoratus* (the abundant species) larvae that were dissected per site ranged from 26 to 61, and for amber-marked birch leaf miner, which was the uncommon species, numbers of larvae dissected per site ranged from 0 to 20, with all available larvae being dissected. Of the 96 amber-marked birch leaf miner dissected, 57 contained either parasitoid eggs or small larvae (59.4% parasitism), which was a level of parasitism similar to that reported by Andersen et al. (2021) from 2019 for the same sites. In contrast, of 460 *H. nemoratus* larvae dissected in 2021, only 4 larvae (0.9%) contained parasitoid eggs and none contained larvae. Parasitized late birch leaf edge miner larvae

each contained 1 encapsulated egg, which may have been of some unknown parasitoid species or perhaps were mistaken ovipositions by the *Lathrolestes* species associated with amber-marked birch leaf miner larvae at these sites.

Discussion

Insect damage and drought are factors that potentially can reduce annual radial growth in deciduous trees in northern latitudes such as Alaska (Cahoon et al. 2018; Boyd et al. 2019; Sullivan et al. 2021). The leaf mining moth *Phyllocnistis populiella* Chambers (Lepidoptera: Gracillariidae) has been documented to reduce radial tree growth of quaking aspen (*Populus tremuloides* Michx.; Salicaceae) in Alaska (Boyd et al. 2019). We found a significant declining trend in radial growth of Alaska white birch (Fig. 3) for the period 1996 to 2007, which corresponded with an outbreak of amber-marked birch leaf miner in Alaska. In 2008 to 2018, Alaskan white birch tree radial growth declined further (Fig. 3C) despite strong suppression of amber-marked birch leaf miner by a biological control program (Soper 2012; Soper et al. 2015; Soper & Van Driesche 2019; Andersen et al. 2021). This further decline in tree growth in the 2008 to 2018 period was concurrent with an increase in density of an additional species of invasive birch leaf miner (*H. nemoratus*) in the study area, a species causing very similar damage as amber-marked birch leaf miner (Fig. 1).

The ecological significance of this reduction in birch growth potentially is large because of the acreage of birch in Alaska that was affected by birch leaf mining, as reported in insect damage aerial surveys in Alaska that were run from 1997 to 2020 (USDA Forest Service 2021). For 1996 to 2007, birch leaf mining was essentially all due to amber-marked birch leaf miner since the first observed high level of mining by the second species, *H. nemoratus*, was in 2008 (Fig. 1). We estimated acreage of birch with leaf mining in Alaska from reports of damage in aerial surveys or by ground surveys in mid-summer (USDA Forest Service 2021). Researchers conducting these surveys indicated that the reported values for birch leaf mining were underestimates because the peak of birch leaf mining (and hence visibility of leaf mining in aerial surveys) occurred later (Aug) than surveys were run in most yr (Jul). Also, aerial detection requires high densities of leaf mining for infestations to be visible. Between 1997 and 2007 (the period when only

amber-marked birch leaf miner was in outbreak), a total of 137,391 ha (339,500 acres) were listed as being affected in Alaska by birch leaf mining. From 2008 to 2020 (when visible defoliation would be from the combination of both amber-marked birch leaf miner and the second invasive leaf miner, *H. nemoratus*), there were an additional 180,319 ha (445,580 acres) reported as affected by birch leaf mining, for a grand total of 317,710 ha (785,080 acres) for the entire period of 1997 to 2020. This figure represents a minimum number because the area surveyed each yr varied, the forest types surveyed varied (with many forest types selected for survey not including significant birch), and because surveys in general were not ideally timed to detect birch defoliation. Therefore, the estimate of 317,710 ha (785,080 acres) affected during the outbreak is highly conservative. Loss of 16 to 33% of radial growth of such a common tree as Alaska white birch has implications for reduced carbon storage and increased global warming.

The reason for the failure of Alaska white birch tree growth rates in Anchorage to return to pre-amber-marked birch leaf miner outbreak levels after successful reduction of amber-marked birch leaf miner (Andersen et al. 2021) is unknown. In other studies, growth of birch trees at high northern latitudes defoliated by outbreaks of 2 geometrid moths, *Epirrita autumnata* (Borkhausen) and *Operophtera brumata* (L.) (both Lepidoptera: Geometridae), failed to fully recover even many decades after the defoliation events (Vindstad et al. 2019). Alternatively, it is possible that the decline of birch growth in southeastern Alaska is due to the concurrent rise of very similar damage from a new invasive tenthrinid leaf miner, *H. nemoratus*. Our survey in 2021 confirmed that in the Anchorage area, about 90% of all birch leaf mining is now due to *H. nemoratus*, not amber-marked birch leaf miner. Also, in contrast to the nearly 60% parasitism found in amber-marked birch leaf miner larvae in the 2021 survey, the near zero rate of parasitism of *H. nemoratus* strongly suggests that the second leaf miner is an outbreaking species because of escape from its natural enemies. Outbreaks of other invasive tenthrinid leaf miners in North America typically have been associated with the absence of their specialized natural enemies (e.g., *F. pumila* [Cheng & LeRoux 1969]; *P. thomsoni* [Soper et al. 2019]). Given the near absence of parasitism of *H. nemoratus* in Anchorage in our 2021 survey, it appears that the parasitoids associated with *H. nemoratus* in Europe and the northeastern US (Dowden 1941) are missing in Alaska.

In conclusion, the current level of birch leaf mining in Alaska merits further attention due to the potential reduction in carbon storage caused by slower tree growth. The current lack of parasitoids associated with *H. nemoratus* in southeastern Alaska and the leaf miner's high density could potentially be corrected by introducing the species' more important parasitoids from its native range. Success in such an effort is likely, given that 2 other invasive tenthrinid sawflies that mine birch leaves (*F. pumila* and *P. thomsoni*) have been controlled through similar classical biological control introductions (*F. pumila* [Van Driesche et al. 1997; Casagrande et al. 2009] and *P. thomsoni* [Soper 2012; Soper et al. 2015; Soper & Van Driesche 2019; Andersen et al. 2021]), and earlier efforts in the eastern US for control of *H. nemoratus* (Dowden 1941) provide valuable suggestions for parasitoid species likely to be useful.

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