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Abstract

A tamarack [*Larix laricina* (Du Roi) K. Koch] provenance plantation, consisting of 33 seed sources from the United States and Canada, was established in 1969 in southern Michigan (Kalamazoo County). About half of the trees were removed in fall 1984 when the stand was thinned, with the cut trees piled on the edge of the stand. The stand then experienced a severe ice storm in January 1985. The eastern larch beetle, *Dendroctonus simplex* LeConte, colonized the cut logs in 1985 and also infested many of the standing trees. By the end of 1986, over half the remaining trees had been killed by *D. simplex*, with six seed sources suffering no beetle-related tree mortality, twenty having 20–61% tree mortality, and seven having 67–100% mortality. Mean tree height and DBH were negatively related to the latitude of the seed source origin. However, no significant linear relationships were found between percent tree mortality in 1986 with either mean tree DBH or latitude of the seed-source origin, but there was a significant negative relationship with increasing ice-storm damage.

Keywords: Eastern larch beetle, eastern larch, bark beetle, environmental stress

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The eastern larch beetle, *Dendroctonus simplex* LeConte (Coleoptera: Curculionidae: Scolytinae), is a native bark beetle, occurring throughout the range of its primary host tamarack or eastern larch [*Larix laricina* (Du Roi) K. Koch, Pinaceae] (Bright 1976, Wood 1982). Tamarack is the most widespread North American conifer, growing from Newfoundland and Labrador to Alaska and south to the Great Lakes region and West Virginia (Johnston 1990, Shearer 2008; Fig. 1).

Aspects of the life history and chemical ecology of *D. simplex* have been studied by several researchers in both Canada and the United States for over a century (Hopkins 1909; Swaine 1911; Simpson 1929; Prebble 1933; Werner 1986; Langor and Raske 1987a,1987b, 1988; Graham and Storer 2011; McKee and Aukema 2015a, 2015b, 2016; Durand et al. 2019; McKee et al. 2022). Briefly, *D. simplex* is generally univoltine throughout its range, with most parent females producing two or three separate broods during summer. Adults overwinter under bark in their pupal chambers or at the base of infested trees. Adults take flight in late spring, usually in May or June, with females initiating attack and gallery construction. A male soon joins each female with mating occurring in the gallery. The galleries are constructed in the inner bark (phloem) and are mostly vertical in orientation, following the wood grain. Eggs are laid in niches along the gallery walls, usually 1–4 eggs per niche. After eclosion, larvae construct individual feeding galleries in the phloem, and eventually pupate and transform to adults at the end of the gallery. Progeny adults from the first brood generally emerge through the bark, walk down the trunk, and bore into the bark near groundline to overwinter. Progeny adults from the second and third broods tend to remain in their pupal cells to overwinter. Although *D. simplex* is considered univoltine, it has the potential to become multivoltine (McKee and Aukema 2015b, McKee et al. 2022).

Historically, *D. simplex* was reported to attack primarily trees weakened by environmental stress such as drought, defoliation, fire, flooding, and storm damage (Langor and Raske 1989, Seybold et al. 2002). However, since the 1970s, widespread multiyear outbreaks of *D. simplex* have occurred throughout the beetle's range, and in many cases no predisposing factors were obvious (Aukema et al. 2016). In Michigan, the first report of *D. simplex* killing tamarack trees in both the Lower and Upper Peninsulas of

Michigan occurred in the 1880s (Schwarz 1888). More recently, dozens of *D. simplex* outbreaks have occurred in Michigan's Upper Peninsula, beginning in 2002 and ending around 2015 (MIDNR 2002, 2015). In many cases, but not all, drought, and heavy defoliation by the non-native larch casebearer, *Coleophora laricella* (Hübner) (Lepidoptera: Coleophoridae), predisposed the trees to *D. simplex* attack (Ward and Aukema 2019).

For over a century, foresters have grown many species of trees from seed collected in specific geographic areas (provenances) of a tree's natural range with the objective of finding superior seed sources for particular traits, such as growth rate or wood quality (Zobel and Talbert 1984). The "North Central Cooperative Regional Project NC-51: Forest Tree Improvement through Selection and Breeding" began in 1960 and involved the USDA Forest Service, industry, and over a dozen state agricultural experiment stations (Wright 1963, Jeffers 1971). Members of Regional Project NC-51 (which later became NC-99) initiated dozens of provenances trials, including both conifers and hardwood tree species (Wright 1965, Rudolf 1966).

Tamarack was one of the conifers selected for provenance testing during the 1960s, with seed collected rangewide, but mostly in the Great Lakes region (Pauley 1965, Fig. 1). Two of the main objectives were to (1) obtain information on the pattern of genetic diversity for various traits throughout the geographic range of tamarack, and (2) identify the best adapted seed sources for plantation culture of tamarack in different parts of the United States (Pauley 1965).

One of the five test plantings in Michigan was at the W. K. Kellogg Forest Experiment Station (Kalamazoo County, 42.4° N, 85.4° W), managed by the Michigan State University, Department of Forestry (Mohn et al. 1985). Of the 125 distinct tamarack seed lots collected in the 1960s, 33 were planted at Kellogg Forest, and represented collection sites that ranged in latitude from 39.7° (Maryland) to 59.0° N (Alberta) and longitude from 65.0° (Nova Scotia) to 123.4° W (British Columbia) (Fig. 1, Table 1). There were nine Canadian seed sources (Alberta—2, British Columbia—1, Manitoba—2, Ontario—3, and Nova Scotia—1), and 24 US seed sources (Maine—1, Maryland—2, Michigan—10, Minnesota—5, Pennsylvania—1, Vermont—1, and Wisconsin—4) (Fig. 1, Table 1). The tamarack planting at Kellogg Forest was established in 1969, using 2-1 nursery stock (= grown 2 years in the seedbed, and 1 year in a transplant bed). Seedlings were planted at an 8 x 8 foot (2.4 x 2.4 m) spacing, using a randomized complete-block design with four trees per plot (Mohn et al. 1985). The number of 4-tree plots per seed source varied from one plot for four seed sources (105-MD, 119-WI, 126-PA, and 132-ON) to 10 plots for nine seed sources (102-MN, 109-MB, 110-AB, 117-MB, 118-AB, 127-ME, 157-WI, 158-MN, 159-MN), and one seed source (153-MI) having 11 plots. A 1-tree-wide border was planted around the test trees, using extra seedlings from three seed sources (101-MN, 120-MI and 122-MI). The original 1969 tamarack planting map indicated that the provenance test at Kellogg Forest consisted of 1203 seedlings.

In autumn 1984, the tamarack planting was thinned, leaving no more than two of the original four trees per plot. The trunks of the thinned trees were cut to various lengths and piled along the edge of the stand. In January 1985, a severe ice storm impacted the stand (Ross 2014), causing the trunks of many tamarack trees to bend, and some to break. During summer 1985, unbeknownst to the Kellogg Forest staff, *D. simplex* colonized the cut logs and many of the standing tamarack trees. By late summer 1985, foliage of several tamarack trees had prematurely turned yellow with many trees dying. Upon later inspection in 1985 and 1986, it was found that *D. simplex* had successfully infested and developed in all the trees that had died.

One of the other tamarack plantings in Michigan was at the Fred Russ Forest Experiment Station (Cass County, 42.0° N, 86.0° W), which is also managed by the Michigan State University, Department of Forestry (Mohn et al. 1985). This rangewide provenance planting, located about 64 km southwest of Kellogg Forest, was established in 1967 and consisted of 39 seed sources. The age of the tamarack seedlings and planting design used at Russ Forest were the same as those described above for the Kellogg Forest (Mohn et al. 1985). The Russ Forest tamarack planting was also thinned in late 1984, with the logging slash left within the stand. The January 1985 ice storm had little impact on the trees at Russ Forest. Still, high tree mortality occurred at Russ Forest as a result of *D. simplex* in 1985 and 1986.

The *D. simplex* outbreaks at Kellogg and Russ Forest were both listed by Langor and Raske (1989) in their historical report on this bark beetle, crediting author RAH for unpublished data. However, given that few details were provided in Langor and Raske (1989) about these two Michigan outbreaks, the focus of this paper will be on the outbreak at Kellogg Forest, where the most detailed data were recorded. The main objective of the present study was to determine if there was any pattern in how *D. simplex* colonized the tamarack trees at Kellogg Forest with respect to seed source in terms of the latitude of the seed collection sites, as well as average tree height and DBH (diameter at breast height: ca. 1.4 m above ground), and degree of ice-storm damage.

Methods and Materials

On 18 October 1985, we visited the tamarack stand and noted that *D. simplex* had infested, developed, and emerged from both the cut logs that were in various piles along the perimeter of the tamarack stand as well as from several of the trees throughout the stand. Given that natural needle drop had already begun at that time it was not possible to determine which tamarack trees had already been killed by *D. simplex* and therefore no formal measurements were taken.

On 11 April 1986, we recorded DBH on all tamarack trees and rated each for residual trunk damage from the January 1985 ice storm. The following rating scale was used: 1—trunk straight with no apparent damage; 2—upper trunk bent from vertical but less than 45°; 3—upper trunk bent from vertical 46–90°; and 4—upper trunk bent more than 90°, including stem breakage.

On 23 April 1986, three trees that had died from *D. simplex* attack in 1985 were cut with about 1 m of the lower trunk from each tree transported to Dansville, Ingham County, Michigan, and placed in a mostly shaded, outdoor rearing cage and monitored for insect emergence at regular intervals through July 1986; see details on rearing methods in Haack (2020). When bark- and wood-boring insects and their likely parasitoids (Hymenoptera) were found in the cage, they were placed in labeled vials, frozen, and later sent to specialists for identification (see Results and Acknowledgments). All parasitoids were identified by staff at the US Department of Agriculture, Systematic Entomology Laboratory in Beltsville, MD. Specimens of each species were retained by the identifiers in their personal or institutional collections.

In mid-May 1986, all trees were classified as being either alive (as evidenced by the buds expanding and producing current-year foliage) or dead (as evidenced by the lack of any new foliage). We looked for evidence of *D. simplex* infestation on all trees classified as dead, such as adult beetle entrance holes and exit holes on the bark surface as well as characteristic *D. simplex* egg galleries and larval galleries under the bark along lower trunk. The trees classified as dead in spring 1986 with signs of *D. simplex* infestation will be referred to as having died in 1985, although some likely did not die until early months of 1986.

During site visits in July and August 1986, we flagged the trunk of any tamarack tree in the stand that showed premature yellowing of the foliage and noted if there was evidence of *D. simplex* attack along the lower trunk, i.e., adult entrance and exit holes on the bark surface. On 8 September 1986, all trees that had shown premature yellowing of the foliage, various degrees of early needle drop, and signs of *D. simplex* infestation were recorded and were classified as having died in 1986.

Analyses. The percent of tamarack trees that were alive in spring 1985, after the fall 1984 thinning and January 1985 ice storm, and subsequently died in late summer 1985 or 1986 following *D. simplex* infestation was calculated by seed source. Using Excel's statistical "toolpak," simple linear regression was used to explore the relationships between (1) tree mortality by year and (a) latitude of the seed-source collection site, (b) mean tree height and DBH by seed source, and (c) mean ice-storm rating, as well as (2) seed source latitude and (a) mean tree height and DBH and (b) mean ice-storm damage rating. The tree height data had been collected in 1982 by the Kellogg Forest staff, measuring the two tallest trees in each four-tree plot through the first three replications, which included trees from all 33 seed sources. Relationships between mean tree DBH, tree height, and seed-source latitude were also explored with linear regression. A *t*-test was used to compare means of some tree variables (DBH and height) between various groups of trees or seed sources. An alpha level of 0.05 was used for significance in all tests.

Results

Survival of the tamarack test trees at Kellogg Forest was 87.6% as of 1982, based on trees in plots from the first three replicates (N = 356 trees), which represented all 33 seed sources (Mohn et al. 1985). However, as of spring 1985, there were only 502 of the original 1203 tamarack trees still alive in the stand (including the border trees), with the others having been cut during the 50% thinning operation in fall 1984 or having suffered stem breakage during the January 1985 ice storm. These 502 trees represented 32 of the seed sources given that no trees from seed source 132-ON remained. Note that seed source 132-ON had only four original trees (one 4-tree plot), and only two were left after thinning, both of which suffered stem breakage during the 1985 ice storm (Table 1).

Of the 502 living trees as of spring 1985, 223 died later that same summer from

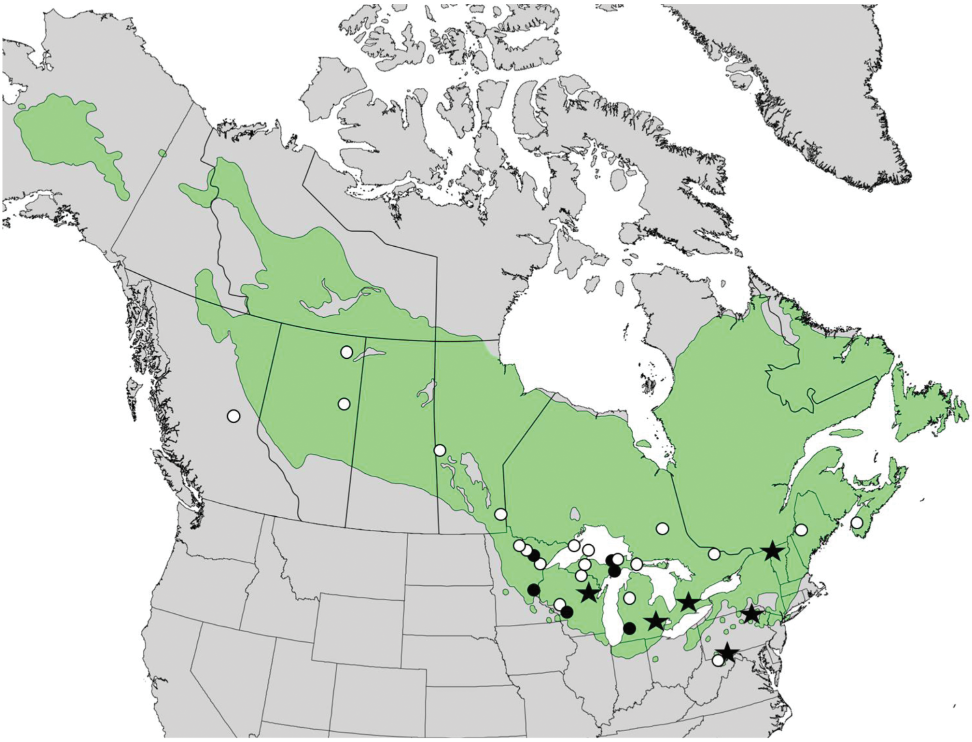

Figure 1. Map of the native range of tamarack (*Larix laricina*) in North America in green based on Johnston (1990) with circles and stars indicating the approximate location of the 33 seed sources treated in this paper: closed circles = seed sources with high (67–100%) tree mortality caused by *Dendroctonus simplex* in the provenance stand at Kellogg Forest (Kalamazoo County, MI) in 1985 and 1986; closed stars = seed sources that suffered no tree mortality from *D. simplex*; and open circles = seed sources that suffered some mortality from *D. simplex,* but less than 67% (see data in Table 1).

D. simplex infestation (44.4% stand mortality), with an additional 33 trees dying from *D. simplex* in 1986 (6.6% of the original 502 trees). For both years combined, *D. simplex* was responsible for killing 256 of the 502 trees or 51%. Tree mortality varied greatly among the tamarack seed sources, with six suffering no tree mortality from *D. simplex* (106-MD, 113-MI, 119-WI, 125-VT, 126-PA and 129-ON; Fig. 1, Table 1), whereas seven had mortality rates as high as 67 to 100% (100-MN, 115-MI, 152-WI, 153-MI, 154-MI, 157-WI and 159-MN; Fig. 1, Table 1).

There was a significant negative relationship between latitude of the seed-source origin and both mean tree DBH and mean tree height (Table 2). In fact, the smallest trees were from the most northerly latitudes where collections were made, i.e., in Alberta (sources: 110 and 118) and British Columbia (source: 161) (Table 1). However, no significant linear relationships were found between latitude and the mean ice-storm damage rating or percent tree mortality in 1985 or 1986 (Table 2). As expected, there was a highly positive significant linear relationship between mean tree DBH and tree height (Table 2). However, no significant relationships were found between mean tree DBH and either the mean ice-storm damage rating or percent tree mortality in 1985 or 1986 (Table 2). Yet, based on only the trees planted in the test plots in the interior of the stand, mean (± SE) DBH was significantly, but only slightly, greater for the trees that had died by the end of 1986 (12.9 ± 0.14 cm, range 3.6–17.8 cm, N = 219) compared to those still alive at the end of 1986 (11.4 ± 0.17 cm, range 4.3–16.8 cm, N = 187) (*t*-test: $t = -6.51$; df = 404; $P = 0.0001$). In addition, significant negative relationships were found between the mean ice-storm damage rating by seed source and subsequent percent tree mortality in 1985 and 1986 (Table 2), suggesting that seed sources that suffered greater ice-storm damage were less often attacked and killed by *D. simplex*. In fact, when considering the six seed sources that suffered no tree mortality vs. the seven with

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Table 1. Summary data for the 33 tamarack seed sources used in a provenance test planting at the Kellogg Forest Experiment Station in Kalamazoo County, MI, including the official seed source number used in other publications, latitude and longitude of the seed source location, mean ice-storm damage rating (1-4 scale, see methods), mean tree DBH and height, number of live trees in the stand as of spring 1985, and percent cumulative tree mortality after one and two years of *D. simplex* infestation (1985 and 1986).

Source Location	Source number	Latitude °N	Longitude °W	Mean ice storm damage rating in 1986	Mean height in 1982 (m)	Mean DBH in 1986 (cm)	Number of live trees in spring 1985 after stand thinning and ice storm	Percent of trees alive in spring 1985 that died by late 1985 (%)	Percent of trees alive in spring 1985 that died by late 1986 (%)
Canada									
AB	110	56.6	111.2	1.8	7.2	8.1	12	25.0	41.7
AB	118	59.0	111.7	1.5	6.4	6.5	11	0	27.3
BC	161	53.8	123.4	1.6	6.5	7.6	7	28.6	28.6
MB	109	53.9	101.2	1.5	8.4	10.3	14	21.5	35.7
MB	117	50.1	95.4	1.7	9.1	11.0	16	62.5	62.5
ON	124	46.0	77.4	2.1	10.4	14.1	12	50	50
ON	129	43.2	80.6	1.8	11.2	12.6	2	0	0
ON	132	49.5	82.2	4.0	10.1	12.4	0	—	—
NS	131	44.8	65.0	2.1	10.4	13.4	9	33.3	33.3
United States									
MD	105	39.7	78.9	2.0	10.3	13.0	2	0	50
MD	106	39.7	78.9	2.2	9.0	11.5	7	0	0
ME	127	45.6	70.3	1.8	10.4	13.5	17	23.5	35.3
MI	113	42.5	83.5	3.2	10.4	12.4	1	0	0
MI	115	42.2	85.4	1.7	10.0	13.2	15	60	66.7
MI	116	48.1	88.7	2.0	8.2	11.1	5	20	20.0
MI	120	46.3	86.3	1.4	10.4	13.5	99	44.4	53.5
MI	122	46.3	84.2	1.2	10.5	13.2	76	50	55.3
MI	128	47.0	88.4	1.8	9.4	12.6	12	50	58.3
MI	153	46.3	86.0	1.6	9.6	11.7	18	61.1	66.7
MI	154	46.3	86.0	1.4	8.6	11.5	13	61.5	76.9
MI	155	44.2	85.5	1.6	9.9	12.4	6	16. 7	33.3
MI	160	46.2	89.2	1.9	9.8	12.2	13	46.2	46.2
MN	100	45.2	93.1	1.6	10.2	12.5	11	72.7	81.8
MN	101	47.5	93.0	1.65	8.8	11.6	32	31.4	34.4
MN	102	46.7	92.5	1.9	8.9	11.5	13	30.8	38.5
MN	158	47.5	94.1	1.45	9.6	11.4	18	55. 6	61.1
MN	159	47.4	93.6	1.7	9.6	11.9	16	81.4	81.3
PA	126	41.3	75.7	3.0	11.0	13.7	1	0	0
VT	125	45.6	70.3	2.3	9.5	12.2	3	0	0
WI	111	44.1	91.5	2.29	10.4	13.5	10	60.0	60
WI	119	44.6	88.5	2.5	10.5	14.1	2	0	0
WI	152	45.8	89.2	1.86	10.0	12.7	12	83.3	91.7
WI	157	43.8	91.1	1.55	10.4	13.4	17	100	100

*Location abbreviations: AB = Alberta, BC = British Columbia, MB = Manitoba, MD = Maryland, ME = Maine, MI = Michigan, MN = Minnesota, PA = Pennsylvania, ON = Ontario, NS = Nova Scotia, VT = Vermont, and WI = Wisconsin.

Table 2. Simple linear regression summary data for analyses between various seed source, tree, and insect variables related to a tamarack provenance plantation that was established in 1969 in Michigan with seedlings grown from seed collected in 33 locations in the United States and Canada, that was infested by *Dendroctonus simplex* in 1985 and 1986, which resulted in the death of about half the trees.

Variables*	Number of seed sources**	df	F	*P*	r
Latitude vs Mean DBH in 1985	33	1,31	62.37	<0.0001†	-0.79
Latitude vs Mean height in 1982	33	1,31	52.71	<0.0001†	–0.82
Latitude vs Mean ice damage rating	33	1,31	1.85	0.18	–0.24
Latitude vs % Mean tree mortality in 1985	32	1,30	0.01	0.92	+0.02
Latitude vs Mean % tree mortality in 1986	32	1,30	0.143	0.71	+0.07
Mean DBH in 1985 vs Mean height in 1982	33	1,30	222.3	<0.0001†	+0.94
DBH vs Mean % tree mortality in 1985	32	1,30	1.10	0.30	+0.19
DBH vs Mean % tree mortality in 1986	32	1,30	0.307	0.58	+0.10
DBH vs Mean ice damage rating	33	1,31	2.15	0.15	+0.25
Mean ice damage rating vs Mean % tree mortality in 1985	32	1,30	9.18	<0.01	–0.48
Mean ice damage rating vs Mean % tree mortality in 1986	32	1,30	15.6	<0.001	–0.58

* Values used in the analyses were the seed source means from Table 1. See Methods for details.
** There were 33 tamarack seed sources in the original planting, but one Ontario seed source (132, see Table 1) had no surviving trees as of spring 1985 and therefore some analyses only had 32 seed sources in the dataset.
† Linear regression equations: DBH_{cm} = 27.6–0.33 LAT; HT_{dm} = 195.7–2.15 LAT; HT_{dm} = 21.0 + 6.2 DBH_{cm}.

the highest tree mortality (Table 1), there were no significant differences in mean tree height ($P = 0.237$) or DBH ($P = 0.486$); however, the mean ice-storm damage rating was significantly greater ($P = 0.002$) for the seed sources that suffered no tree mortality (mean 2.49, range 1.8–3.2, N = 6; scale 1–4, see Methods) compared to those sources that suffered 67–100% mortality (mean 1.64, range 1.4-1.9, N = 7).

One species of bark beetle and six species of parasitoids were reared from the tamarack logs collected at Kellogg Forest in April 1986. *Dendroctonus simplex* was the only bark- or wood-boring insect reared during the summer months of 1986, although other borers could have been present but needed more time to complete development. Specimens of *D. simplex* were confirmed by Stephen L. Wood. The six parasitoids represented four hymenopteran families, three of which were identified to species and three only to genus. They included the Braconidae (determined by Paul M. Marsh)—*Coeloides pissodis* (Ashmead), *Eubazus* sp. and *Spathius* sp.; Eurytomidae (determined by Robert W. Carlson)—*Eurytoma* sp.; Ichneumonidae (determined by Robert W. Carlson)—*Dolichomitus pygmaeus* (Walsh); and Pteromalidae (determined by Eric E. Grissell)—*Dinotiscus dendroctoni* (Ashmead).

Discussion

The *D. simplex* outbreak at Kellogg Forest occurred in 1985 and 1986. The predisposing factors that led to the outbreak were likely a combination of the fall 1984 thinning operation in which the cut trees were left in piles on the edge of the stand and the January 1985 ice storm. Others have reported *D. simplex* breeding in recently cut logs and storm damaged trees (Langor and Raske 1987a, 1989; Aukema et al. 2016), which is also a common behavior among many other species of conifer-infesting bark beetle (Ryall et al. 2006, Gandhi et al. 2007).

It appears that *D. simplex* colonized both the log piles and some standing trees at Kellogg Forest in spring 1985 and then had subsequent broods in summer 1985 primarily in the standing trees. It is not known how many sister broods occurred in 1985. However, given that about 44% of the trees were killed by *D. simplex* in 1985, at least two sister broods seem likely, or if not, there was a large *D. simplex* population nearby that allowed for rapid colonization of the cut and standing trees in 1985. Nevertheless, three *D. simplex* broods per year is likely at Kellogg Forest given its more southerly latitude (42.4° N) compared with the Canadian studies by Simpson (1929), who recorded three broods per year near Fredericton, New Brunswick (45.9° N), and Langor and Raske (1987b), who reported two broods at field sites near St. John's, Newfoundland (47.5° N).

All sizes of tamarack trees available in the stand at Kellogg Forest were infested by *D. simplex*, from the smallest (DBH 3.6 cm) to the largest tree (DBH 17.8 cm). At other locations where *D. simplex* outbreaks followed defoliation events (Langor and Raske 1989), tamarack trees as small as 6 cm DBH were killed in New Brunswick (Magasi 1984) as well as trees under 2 cm DBH in Alaska (Werner 1986). In more recent outbreaks, often where no predisposing factor was obvious, *D. simplex* initially attacked the largest trees first (Aukema et al. 2016), and when multiple infestations occurred in the same area, usually more trees were killed in tamarack stands with greater average DBH (Crocker et al. 2016).

In general, the shortest and smallest diameter tamarack trees at Kellogg Forest originated from the more northern-latitude seed sources in Alberta, British Columbia, and Manitoba (Table 1). For many north temperate tree genera, including *Larix*, slower growth is well documented when trees from more northern latitudes are grown at more southern latitudes (Vaartaja 1959, Kozlowski 1964). This growth pattern indicates a strong genetic response to photoperiod where the more northern-latitude trees cease shoot elongation and set bud earlier than those that originated from more southern latitudes. Similar growth patterns in tree height were noted at many other provenance test sites in Michigan, Minnesota, and Wisconsin that tested similar tamarack seed sources (Cech et al. 1977, Riemenschneider and Jeffers 1980, Mohn et al. 1985).

Of the 33 tamarack seed sources planted at Kellogg Forest, the six that suffered no tree mortality originated more from the southeastern part of tamarack's range, whereas the seven sources that suffered the highest rates of tree mortality originated nearby but more in the southwestern portion of the tree's range (Fig. 1). For the six seed sources that suffered no tree mortality, note that they were represented by only 1 to 7 trees each (Table 1). Therefore, it is unclear if these trees were simply escapes or if they were avoided for some particular reason, but in all cases, they were surrounded by many heavily infested trees. As noted above, the trees from these six seed sources all suffered much higher levels of ice-storm damage (i.e., the trunks were mostly bent 46-90° from vertical) than the trees in the seed sources with the highest levels of tree mortality (trunks bent 0–45°). Although *D. simplex* will colonize both standing and fallen trees (Langor and Raske 1989, Aukema et al. 2016), perhaps when offered a choice, *D. simplex* initially prefers trees with a more vertical silhouette than trees that are leaning. In studies of other bark beetles, *Dendroctonus frontalis* Zimm. showed a preference for vertical trunks (Gara et al. 1965), *Ips pini* (Say) for horizontal logs (Seybert and Gara 1970), and *Tomicus piniperda* (L.) for leaning trees (Schlyter and Löfqvist 1990).

Another possible reason for the observed variation in the attack pattern among tamarack seed sources could relate to differences in the monoterpene composition of their phloem, making some trees more susceptible and others more resistant. For example, Althoff et al. (2023), working in Minnesota and Wisconsin, showed that alpha pinene and delta-3-carene were the two major monoterpenes in tamarack phloem, but they varied widely from tree to tree, e.g., alpha pinene varied from 12.8% to 75.5% of the terpenoid blend while delta-3-carene varied from 1.5% to 67.4%. These and other monoterpenes can serve as attractants or repellents to bark beetles (Raffa et al. 2015). It would be interesting to compare the monoterpene composition of trees from those seed sources that had high survival with those suffering high mortality. Unfortunately, the tamarack stands at Kellogg Forest and Russ Forest no longer exist, but perhaps some of the other tamarack test sites described by Rudolf (1966) and Mohn et al. (1985) still exist and trees from the various seed sources could be located and analyzed.

Tamarack is the main host of *D. simplex* throughout its North American range, but *D. simplex* has been reported to infest and kill some exotic larch species as well, including exotic larches planted as both ornamentals or forest trees within its range (Seybold et al. 2002). For example, at Kellogg Forest, there was a provenance plantation of Japanese larch [*Larix kaempferi* (Lamb.) Carrière] next to the tamarack stand monitored in the present study. This stand of Japanese larch was planted in 1961 and contained 22 seed sources from Japan. Although we did not take detailed notes on these trees, we did record that *D. simplex* infested and killed several Japanese larch trees in 1986, with most of the beetle-killed trees located along the border of the stand nearest the infested tamarack stand.

As for the parasitoids reared in the present study, the braconids, eurytomid, and pteromalid were likely all parasitoids of *D. simplex*, given that the same species or species in the same genera have been reared by others from *D. simplex* (Blackman and Stage 1918, Mason 1978, Langor 1991). However, the ichneumonid *D. pygmaeus* was probably associated with a different and larger bark- or wood-boring beetle given that it has been reared from *Plectrura spinicauda* Mannerheim (Cerambycidea) in western Canada (Townes and Townes 1960) as well as from Douglas-fir [*Pseudotsuga menziesii* (Mirbel) Franco] bolts infested with both *Melanophila drummondi* (Kirby) (Buprestidae) and *Pissodes fasciatus* LeConte (Curculionidae) in Washington State (Deyrup 1975). In Michigan and the Great Lakes region there are several species of Buprestidae (Wellso et al. 1976, Hallinen et al. 2021) and Cerambycidae (Gosling 1973, 1984) that infest tamarack and have 1- or 2-year life cycles. It is likely that the *D. pygmaeus* reared in the present study used one of the borers with a 2-year life cycle given that we reared the tamarack bolts for only one season following tree death and *D. simplex* was the only borer reared during that time.

It is unclear if the *D. simplex* outbreak at Kellogg Forest would have been as severe as it was if the logging slash from the 1984 thinning operation had not been left in piles along the stand perimeter. Or even if the slash had been moved or chipped, perhaps the stress from the January 1985 ice storm would have been sufficient to initiate an outbreak. Interestingly, the *D. simplex* outbreak at the nearby Russ Forest, which was not impacted by the January 1985 ice storm, still resulted in about 90% tree mortality by the end of 1986 (Langor and Raske 1989), compared with 51% at Kellogg Forest in 1986. These differences in mortality rates may reflect how the cut trees were handled after thinning in autumn 1984. Recall, that at Kellogg Forest, cut trees were moved to the edge of the planting and bucked into short lengths, whereas at Russ Forest the cut trees were left within the stand near where each had grown. Thus, if *D. simplex* first colonized the cut trees before infesting the standing trees, adult beetles would initially have been concentrated along the stand perimeter at Kellogg Forest, but evenly dispersed throughout the planting at Russ Forest. Unfortunately, the seed sources of the trees that were alive at Russ Forest in late 1986 were not recorded, thus it is not possible to determine if any seed sources had 100% survival. Nonetheless, given that *D. simplex* caused high stand mortality at these two rangewide provenance plantings in Michigan within a 2-year period, along with dozens of other reports of *D. simplex* outbreaks throughout the beetle's entire North American range (Langor and Raske 1989, Aukema et al. 2016, McKee et al. 2022), suggest that nearly all tamarack trees are susceptible to *D. simplex.*

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