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Seed cone traits and insect damage in *Tsuga canadensis* (Pinaceae)

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Abstract: We measured seed cones of *Tsuga canadensis* (L.) Carrière, assessed seed potential (number of fertile scales × 2) and seed efficiency (number of filled seeds/seed potential), and estimated the impact of *Eupithecia mutata* Pearsall (Lepidoptera: Geometridae) and *Megastigmus hoffmeyeri* Walley (Hymenoptera: Torymidae) on seed production. Mean length, width, and volume of healthy cones varied little among sites from Ontario. Cones had about 28 scales; 13 were sterile. Seed potential and seed efficiency differed among sites, ranging from 25 to 31 ovules and 24% to 72%, respectively. The number of scales (both sterile and fertile) increased with cone volume, but the proportion of fertile scales was independent of cone size. The maximum proportion of cones infested by *E. mutata* was 21%. On average, each larva destroyed >90% of the filled seeds from each cone, thus from a practical perspective, the proportion of *T. canadensis* seeds destroyed per site was equivalent to the proportion of seed cones infested. The proportion of cones infested by *M. hoffmeyeri* ranged from 9% to 40%, but the proportion of seeds destroyed per site (range: 1.1%–6.1%) was much lower than that of *E. mutata*. The maximum number of *M. hoffmeyeri*-infested seeds per cone was seven. To our knowledge, this is the first report documenting cone traits of *T. canadensis* and the impact of *E. mutata* and *M. hoffmeyeri*.

Résumé : Nous avons mesuré des cônes de *Tsuga canadensis* (L.) Carrière, calculé la production potentielle de semences (nombre d'écailles fertiles × 2) et le rendement des semences (nombre de semences pleines/production potentielle de semences) et estimé l'impact de *Eupithecia mutata* Pearsall (Lépidoptères : Géométridés) et de *Megastigmus hoffmeyeri* Walley (Hyménoptères : Torymidés) sur la production de semences. En Ontario, la longueur, la largeur et le volume des cônes sains variaient peu selon le site. Les cônes portaient environ 28 écailles dont 13 étaient stériles. La production potentielle de semences et le rendement des semences différaient d'un site à l'autre, variant respectivement de 25 à 31 ovules et de 24 à 72 %. Tant le nombre d'écailles stériles que le nombre d'écailles fertiles augmentaient avec le volume des cônes, mais la proportion d'écailles fertiles était indépendante de la dimension des cônes. La proportion maximum de cônes infestés par *E. mutata* atteignait 21 %. En moyenne, chaque larve avait détruit >90 % des semences pleines de chaque cône; ainsi, d'un point de vue pratique, la proportion de semences de *T. canadensis* détruites par site correspondait à la proportion de cônes infestés. La proportion de cônes infestés par *M. hoffmeyeri* variait de 9 à 40 %, mais la proportion de semences détruites par site (intervalle de variation : 1,1 à 6,1 %) était beaucoup moindre beaucoup moindre que celle de *E. mutata*. Un maximum de sept semences par cône étaient infestées par *M. hoffmeyeri*. À notre connaissance, ceci constitue le premier rapport faisant état des caractéristiques des cônes de *T. canadensis* et de l'impact de *E. mutata* et de *M. hoffmeyeri*.

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Introduction

Most conifer seed cones consist of a main axis bearing spirally arranged bract–ovuliferous scale complexes (Beck 1988). The base and tip of each seed cone contain rudimentary or sterile ovuliferous scales, whereas the central region contains the fertile ovuliferous scales (Owens et al. 1991). Performance of seed cones under a variety of growing conditions can be assessed by evaluating seed potential (number of fertile ovuliferous scales × 2), which measures the maximum number of seeds a cone can produce, and seed efficiency (number of filled seeds per cone/seed potential). These cone traits have been evaluated on species of *Pinus* L. (Bramlett 1974; Todhunter and Polk 1981; Lopez-Upton and

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Table 1. Geographic location of sampling sites and description of cone collections of *Tsuga canadensis*.

Year of collection	Site	UTM	Cone collection
1999	Mount Mitchell, N.C., U.S.A.	17 385618 3958388	312 cones from six trees growing along Blue Ridge Parkway within 8 km east of Mount Mitchell
	Mount Pisgah, N.C., U.S.A.	17 338125 3917290	180 cones from three trees growing along Blue Ridge Parkway within 8 km east of Mount Pisgah
2000	Papineau Lake, Ont., Canada	18 281093 5026040	638 cones from two trees
	Bon Echo Park, Ont., Canada	18 325395 4973862	1255 cones from a bulk collection of cones from an undetermined number of trees being processed by the Ontario Tree Seed Plant
2002	East Mills Township, Ont., Canada	17 589969 5085255	About 200 cones from each of five trees
	Gould Township, Ont., Canada	17 313568 5155391	About 200 cones from each of five trees

Donahue 1995; de Groot and Schnekenburger 1996), *Picea* L. (Caron and Powell 1989; de Groot and Schnekenburger 1996), *Abies* Mill. (Scurlock 1978; Owens and Morris 1998), *Juniperus* L. (Ortiz et al. 1998), *Taxus* L. (DiFazio et al. 1998), and *Pseudotsuga* Carrière (Owens et al. 1991). They have also been determined for *Tsuga heterophylla* (Raf.) Sarg. (Colangeli and Owens 1990) but not for *Tsuga canadensis* (L.) Carrière.

In 1994, we initiated a study aimed at establishing the species richness of insects infesting cones of conifers of limited economic importance in eastern North America (e.g., *T. canadensis*). At that time, the only insects known to exploit *T. canadensis* seed cones were *Leptoglossus occidentalis* Heidemann (Hemiptera: Coreidae), *Megastigmus hoffmeyeri* Walley (Hymenoptera: Torymidae), and *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae) (Milliron 1949; de Groot et al. 1994). The discovery in 2000 of lepidopteran larvae identified by K. Nystrom (Natural Resources Canada, Canadian Forest Service, Sault Ste Marie, Ont.) as *Eupithecia mutata* Pearsall (Lepidoptera: Geometridae) in samples from Ontario provided an opportunity to assess seed loss by this insect and by *M. hoffmeyeri*, whose impact had never been assessed.

Reported here, although not part of our primary objective for that study, is information on cone traits (including seed potential and seed efficiency) of *T. canadensis* for six sites in eastern North America and the proportion of cones infested and seeds destroyed by *E. mutata* and *M. hoffmeyeri*.

Materials and methods

Cone traits

Mature seed cones of *T. canadensis* were collected prior to seed dispersal in late August or early September from mature trees at six sites with heavy cone crops (many cones on more than 75% of the trees) across its native range (Table 1). The Ontario sites were near the northern limit of the *T. canadensis* range, whereas those in North Carolina were near the southern limit (Godman and Lancaster 1990). At each site, the seed potential and seed efficiency were determined for randomly selected cones with no external evidence of damage. The length and width of cones collected in 2000 were measured prior to dissection, and cone volume was estimated using the equation for an ellipsoid ($4/3\pi r_1 r_2 r_3$, where r_1 = cone length/2 and $r_2 = r_3$ = cone width/2). Dissection consisted of systematically removing each scale with forceps, starting at the base, and determining whether it was sterile or fertile. Scales were considered fertile if one or two fully developed ovules or seeds that resembled a mature seed were present. Fully developed seeds were detached from each scale and placed in the order they had been removed on the sticky side of mailing labels (10.2 cm × 3.7 cm) for seed analysis, which consisted of irradiating the labels with a Faxitron Specimen Radiography System (Model Mx-20) for 120 s at 10 kV. The exposed paper (Industrex 620) was processed using a model P-1 Kodak Industrex Instant Processor. A hand lens (× 10 magnification) was used to examine the radiographic images and determine for each cone the numbers of filled, empty, and chalcid-infested seeds. In 2002, the number of sterile scales from the base (proximal end) and tip (distal end) of each cone were recorded separately.

Insect damage

The impact of *E. mutata* was assessed for each Ontario site by calculating the number of infested cones in each of five handfuls (range: 40–105 cones per handful) taken blindly among all cones collected (cones from 1999 and 2002 showed no external evidence of damage). A cone was considered infested if coarse frass and ragged holes were present on its surface (Turgeon and de Groot 1992). The number of seeds eaten by *E. mutata* could not be determined directly, because in most instances, larval feeding resulted in the complete destruction of the ovules from each scale, which made it impossible to distinguish sterile from fertile scales (i.e., whether ovules were fully developed). Thus, the seed-destroying capacity was assessed indirectly by taking apart scale by scale a random subsample of *Eupithecia*-infested cones. All fully developed ovules from each cone were removed; a seed analysis was performed as above; and all filled, empty, and chalcid-infested seeds were counted. The impact of larval feeding on filled seeds per cone was calculated for each site as follows: (mean number of filled seeds per healthy cone – mean number of filled seeds per *Eupithecia*-infested cone)/(mean number of filled seeds per healthy cone).

The impact of *M. hoffmeyeri* was assessed by calculating the proportion of cones (among those used to assess cone traits) that contained infested seeds. The number of seeds destroyed per cone was assessed using the traditional formula for calculating chalcid attack (infested/(infested + filled); Lessman 1974), because it is currently unknown whether *M. hoffmeyeri* can infest unfertilized seeds (i.e., that would not have produced filled seeds), as is the case for *Megastigmus spermotrophus* Wachtl. (Niwa and Overhulser 1992). Furthermore, the number of cones infested in most sites was too low (<10) to obtain accurate estimates of the number of filled seeds per chalcid-infested cone, a requirement for the revised formula for calculating chalcid attack (Rappaport et al. 1993). This revised formula takes into account that some of the chalcid-infested seeds might not have been fertilized.

Voucher specimens of *E. mutata* larvae, pupae, and adults and of *M. hoffmeyeri* adults found in cones from Ontario have been deposited in J.J.T.'s collection at the Great Lakes Forestry Centre.

Data analysis

The mean values of each cone trait were compared using t test or one-way ANOVA. When data were heteroscedastic even after transformation, the t test for unequal variances or the Kruskal–Wallis test (adjusted for ties when required) was performed. The relationships among the number of scales per cone, scales eaten per cone, the proportion of fertile scales per cone, and cone volume were examined by regression. The log-likelihood ratio goodness-of-fit test (G test) was performed to test the null hypothesis of equal infestation rates in all localities. All values are given as mean ± SE. All statistical analyses were performed using Minitab (version 13).

Results

Cone traits

Cones collected in 2000 from Papineau Lake and Bon Echo Park had similar dimensions; there was no difference in mean cone length (t = 0.356, $P > 0.7$), width (t = 1.661, $P > 0.1$), or volume (t = 0.404, $P > 0.6$) between these sites (Table 2). In contrast, cones collected in 2002 from Gould were smaller than those from East Mills (length: t = 5.834, $P < 0.001$; width: t = 4.375, $P < 0.001$; volume: t = 4.978, $P < 0.001$) (Table 2).

Cones of *T. canadensis* contained 26–30 scales, 13 of which were sterile (Table 2). The number of sterile scales at the base (Gould, 10.4 ± 0.2; East Mills, 9.3 ± 0.2) was slightly more than twice that at the tip (Gould, 3.6 ± 0.1; East Mills, 3.8 ± 0.1). Values of seed potential varied from 25 to 31 ovules per cone, depending on the site. Seed efficiency varied greatly among sites (Table 2).

The proportion of the variation in the total number of scales per cone that was explained by cone volume was 70.3% ($P < 0.001$, n = 50) at Bon Echo Park, 46.4% ($P < 0.001$, n = 50) at Gould, 42.6% ($P < 0.001$, n = 25) at Papineau Lake, and 3.5% (P = 0.102, n = 50) at East Mills. The proportion of fertile scales in a cone, however, was independent of cone volume at three of the four sites (Bon Echo Park: r^2 = 0.307, $P < 0.001$, n = 50; Papineau Lake:

Table 2. Traits (mean ± SE) of *Tsuga canadensis* seed cones at six sites in North America.

Site	No. of cones	Cone: Length (mm) (range)	Cone: Width (mm) (range)	Cone: Volume (mm^3) (range)	No. of sterile scales/cone	No. of fertile scales/cone	No. of filled seeds/cone	Seed potential*	Seed efficiency†
Mount Mitchell	30‡	—	—	—	13.17±0.49	14.83±0.46	7.93±0.95	29.67±0.91	26.48±3.12
Mount Pisgah	15‡	—	—	—	13.67±0.81	15.40±0.57	16.80±1.74	30.80±1.13	54.03±5.00
Papineau Lake	100	17.76±0.15 (12.85–21.65)	8.44±0.05 (7.48–9.64)	669±12 (416–1053)	13.76±0.58	13.27±0.14	6.29±0.31	26.54±0.29	23.87±1.19
Bon Echo Park	50	18.05±0.25 (14.48–22.49)	8.27±0.10 (6.97–9.61)	659±24 (384–991)	13.08±0.15	13.14±0.33	14.40±0.82	26.28±0.65	54.44±2.71
East Mills	50	18.11±0.21 (15.46–22.09)	8.47±0.09 (7.33–10.14)	692±23 (446–1189)	13.10±0.20	14.46±0.24	20.66±0.59	28.92±0.48	71.65±1.80
Gould	50	16.11±0.27 (11.02–20.37)	7.85±0.11 (5.91–9.23)	534±21 (201–871)	14.02±0.25	15.42±0.29	15.50±0.91	30.84±0.58	49.95±2.77

*Number of fertile scales per cone × 2.
†(Number of filled seeds per cone/seed potential) × 100.
‡Five cones from each sampled tree.

Table 3. Impact of *Eupithecia mutata* and *Megastigmus hoffmeyeri* on seed cones of *Tsuga canadensis* at six sites in North America.

Site	% cones infested/site (*n*)*		% seed destroyed/site	
	E. mutata	*M. hoffmeyeri*	*E. mutata*†	*M. hoffmeyeri*‡
Mount Mitchell	—	23.3 (30)	—	4.5±2.2 (29)
Mount Pisgah	—	20.0 (15)	—	1.1±0.6 (15)
Papineau Lake	4.5 (306)	9.4 (96)	4.1	1.6±0.6 (93)
Bon Echo Park	21.0 (358)	14.0 (50)	20.3	3.5±1.6 (50)
East Mills	—	10.0 (50)	—	0.9±0.4 (50)
Gould	—	40.0 (50)	—	6.0±1.5 (50)

*Number of cones examined at each site in parentheses.

†% seed destroyed per site = (% filled seed destroyed per infested cone × % cones infested per site) × 100; % filled seed destroyed per infested cone were 90.1% and 96.7% at Papineau Lake and Bon Echo Park, respectively.

‡Mean ± SE % of seed infested per cone. Value in parentheses represents the number of cones dissected per site.

$r^2 = 0.029$, $P = 0.204$, $n = 25$; East Mills: $r^2 = 0.043$, $P = 0.081$, $n = 50$; Gould: $r^2 = -0.0001$, $P = 0.325$, $n = 50$). Cone volume also explained 49.3% ($P < 0.001$, $n = 50$) of the variation in the number of filled seeds per cone at Bon Echo Park, 31.2% ($P < 0.001$, $n = 50$) at Gould, 27.7% ($P < 0.001$, $n = 50$) at East Mills, and 3.9% ($P < 0.029$, $n = 96$) at Papineau Lake.

Insect damage

The proportion of cones infested by *E. mutata* at Bon Echo Park was higher than at Papineau Lake ($G = 11.585$, $P < 0.001$; Table 3). At the time of dissection, most infested cones were without larvae (Bon Echo Park: 78%, $n = 50$; Papineau Lake: 73%, $n = 29$); the remainder contained a single larva, most of which were still alive. Dissection of infested cones revealed that larvae of *E. mutata* moved from seed to seed, spiralling around the cone axis by burrowing through scale tissues. At Bon Echo Park, the average number of scales eaten per infested cone was 15.08 ± 0.22 (range: 12–18), which is greater than the number of fertile scales produced by healthy, uninfested cones at that site (Table 2). The log number of scales eaten increased with cone volume ($r^2 = 0.283$, $P < 0.001$, $n = 50$). Fully developed seeds were found in some of the cones infested by *E. mutata*; however, filled seeds (<5 per cone) were found in less than a third of the infested cones (Bon Echo Park: 25%; Papineau Lake: 31%). The proportion of seeds destroyed per infested cone was 90.1% ($n = 29$ cones) at Papineau Lake and 96.7% ($n = 50$ cones) at Bon Echo Park. At the time of dissection, the average number of filled seeds in cones from Bon Echo Park that contained a larva was 1.33 ± 0.62 compared with 0.28 ± 0.11 in cones without larvae. At Papineau Lake, the number of filled seeds were 0.75 ± 0.41 and 0.57 ± 0.24, respectively. None of the seeds recovered from infested cones contained a seed chalcid larva.

The proportion of cones containing seeds infested by *M. hoffmeyeri* varied between 9% and 40% (Table 3). The proportion of infested seeds per site was much lower (range: 1.1%–6.1%). The maximum number of infested seed in a cone was seven.

Discussion

The overall range of *T. canadensis* cone length (11–22 mm) examined during our study was slightly larger than that provided by Godman and Lancaster (1990) (13–19 mm). Our estimates of seed potential and seed efficiency for *T. canadensis* are within the range reported by Colangeli and Owens (1990) for *T. heterophylla* but whether our values are typical for *T. canadensis* is unknown. Variation in attack rates by *M. hoffmeyeri* is too small to explain the large differences in seed efficiency among sites (Table 2). Detailed studies on the factors affecting seed cone development in *T. canadensis* are required to identify the causes responsible for these differences.

This appears to be the first report of *E. mutata* infesting *T. canadensis* seed cones. Our observations that the number of scales eaten by *E. mutata* at Bon Echo Park was greater than the number of fertile scales suggest that this species consumes tissues from sterile and fertile scales. Feeding by *E. mutata* resulted in the destruction of most (>90%) filled seeds produced by infested cones. The presence of larvae in cones at the time of dissection and the consistently higher (not significant because of high standard errors) number of filled seeds in cones with larvae than of that in those infested but without larvae imply that feeding was not completed at the time of impact assessment and suggest that the seed-destroying capacity of this species may be slightly higher than estimated. Furthermore, the resin present between cone scales at the time of dissection may prevent the shedding of filled seeds remaining in damaged cones. Thus, from a practical standpoint, seed loss of *T. canadensis* by *E. mutata* should be considered equivalent to the proportion of cones infested. This impact appears more important than that reported for the species of *Eupithecia* infesting other species of conifers (Hedlin et al. 1980). For example, *Eupithecia spermaphaga* (Dyar) can infest about 20% of fir cones, but destroys a maximum of 10% of the seeds in infested cones (Hedlin et al. 1980).

The feeding pattern of *E. mutata* is consistent with that of conospermatophagous species, as defined by Turgeon et al. (1994). Its absence from most cones at the time of dissection suggests that this species has an exoconophytic life cycle. Of the three live pupae found during this study, one adult emerged in 2001. The other specimens were kept in an insectary and emerged in 2002. This demonstrates that this species is capable of extended diapause, a mechanism used by several conophytes to survive in years when cones are absent or scarce.

Our values of seed infestation rate by *M. hoffmeyeri* suggest that this insect had little impact on seed production of *T. canadensis*. The absence of chalcid-infested seeds in cones infested by *E. mutata* could indicate that *E. mutata* larvae might have fed upon chalcid-infested seeds and thus obscured the impact of *M. hoffmeyeri*. Conversely, this absence could indicate a possible avoidance of cones infested by the other species and would result in additive impacts. Blatt and Borden (1998) demonstrated under controlled conditions that *Leptoglossus occidentalis* Heidemann (Hemiptera: Coreidae) avoided feeding upon seeds infested by *M. spermotrophus* Wachtl. Whether such interactions also exist between *M. hoffmeyeri* and *E. mutata* remains to be substantiated experimentally. For many insects exploiting coniferous seed cones, the impact is negatively correlated with seed cone abundance (Turgeon et al. 1994). Thus, until impact data under different levels of cone production are available, the real impact of this insect remains uncertain.

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