Effects of structural retention harvesting on seed production and seed characteristics of old-growth eastern white pine (*Pinus strobus* L.) stands in northern Ontario

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ABSTRACT

Seed production and seed characteristics were examined during a mast seeding year in unmanaged, old-growth eastern white pine (*Pinus strobus* L.) stands located in northeastern Ontario and compared with those in adjacent stands partially harvested 16 years earlier using a structural retention system. Seed yields from old-growth stands were comparable to those of mature, second growth white pine stands but seed production assessed relative to unit area ($\# \text{ ha}^{-1}$) and pine basal area ($\# \text{ m}^{-2}$) was lower in partially harvested stands. In both unmanaged and harvested stands, seed production rate of trees growing in localized areas of lower pine basal area was higher. Seed characteristics and seed viability did not differ between harvest treatments. Although structural retention harvesting reduced seed production, results suggest that supply and viability of seed are unlikely to limit seedling recruitment in managed or protected old-growth white pine forests.

Key words: germination, old-growth forest, partial harvest, seed mass, seed production

RÉSUMÉ

La production de semence et les caractéristiques des graines ont été étudiées au cours d'une année semencière dans de vieux peuplements non aménagés de pin blanc de l'est (*Pinus strobus* L.) situés dans le nord-est de l'Ontario et ont été comparées avec celles de peuplements adjacents partiellement récoltés 16 années auparavant faisant partie d'un système de rétention de la structure. Les quantités de graines des vieux peuplements étaient comparables à celles des pinèdes blanches à maturité issues de seconde venue, mais la production de semence évaluée en fonction de l'unité de superficie ($\# \text{ ha}^{-1}$) et de la surface terrière des pins ($\# \text{ m}^{-2}$) était inférieure dans les peuplements partiellement exploités. Tant pour les peuplements non aménagés que pour les peuplements exploités, le taux de production de semence des arbres croissants dans des zones localisées de surface terrière inférieure était plus important. Même si la récolte avec rétention de la structure a réduit la production de semence, les résultats laissent entendre que l'approvisionnement et la viabilité des graines ne devraient pas limiter l'émergence de semis ni dans les pinèdes blanches aménagées ni dans les vieilles pinèdes protégées.

Mots clés : germination, vieille forêt, récolte partielle, année semencière, production de semence

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Introduction

Over the past 30 years, recognition of the biological and cultural importance of old-growth forests for biodiversity, ecosystem function, recreation, and more recently carbon storage (Whitney 1987, Barnes 1989, Luyssaert *et al.* 2008) has resulted in heightened emphasis on the creation, protection, and management of Ontario's old-growth forests (OMNR 2003, Latremouille *et al.* 2008). However, for white pine (*Pinus strobus* L.) and other fire-dependent forest ecosystems, protection alone is unlikely to ensure their persistence on the landscape (Barnes 1989, Frelich 2002). Most old-growth white pine stands in Ontario support minimal pine regeneration and are threatened by successional replacement to more mesophytic, shade-tolerant mixedwood forest types (Day and Carter 1990, Quinby 1991, Bebbler *et al.* 2005). In the absence of periodic natural disturbance by recurrent, low-intensity surface fires that create understory conditions suitable for seedling recruitment, management intervention is needed to secure adequate regeneration for perpetuation of old-growth white pine forests (Day and Carter 1990, Dovčiak *et al.* 2003, Bebbler *et al.* 2005, Latremouille *et al.* 2008). In Ontario and elsewhere, interest in management and conservation of old-growth forests has resulted in the development and use of novel silvicultural systems that seek to balance partial harvesting for fibre production with maintenance of stand structural complexity and ecological values (Kohn and Franklin 1997, Beese *et al.* 2003, Pinto 2003).

The 6000-ha Ranger North Conservation Reserve contains the largest identified old-growth white and red pine (*Pinus resinosa* Ait.) forest in northeastern Ontario. The adjacent west Galloway Lake area includes 1800 ha of old-growth white and red pine that was designated for harvest in 1991 with the objectives of managing for old-growth values, regenerating pine, and producing timber to support the local forest industry. Pine-dominated stands were managed using a structural retention (SR) partial harvest system aimed at retaining some of the structural attributes and biological legacy of old-growth forests. This approach differed from the traditional uniform shelterwood system approved for use on Crown lands in Ontario (OMNR 1998), which involves retention centred on tree health, size, and seed-bearing potential, in that a significant number of dead and dying overstory trees were retained for wildlife and other ecological values. These stands represent an early documented example of modified harvest of managed old-growth white pine stands in Ontario. The effects of SR harvest on genetic diversity, understory and overstory growth response, and stand structural characteristics in these stands were examined earlier (Buchert *et al.* 1997; Rajora *et al.* 2000; Bebbler *et al.* 2004, 2005).

Like many forest tree species, white pine exhibits synchronized, periodic production of very large seed crops, or *mast seeding* (Puritch 1977, Kelly and Sork 2002). In mast seeding years, second-growth white pine stands can produce up to 2.5 million viable seed per hectare, but little is known about the effects of partial harvest on seed production (Graber 1970, Heckman *et al.* 1986, OMNR 1998, Raymond *et al.* 2003). Although observations of seedling density suggest that white pine as old as 350 years can produce viable seed (e.g., Mayall 1941, Zenner and Peck 2009), to our knowledge seed production has not been formally quantified in old-growth white pine stands. Therefore, whether old-growth white pine trees

provide an adequate supply of viable seed for regeneration is unknown. The occurrence of a mast seed crop in the west Galloway Lakes area in 2008 provided an opportunity to examine seed production, seed characteristics, and germination performance of undisturbed old-growth white pine stands to compare with stands that had been SR harvested 16 years earlier.

Materials and Methods

Study area

This study was conducted in white pine-dominated, old-growth stands within and adjacent to the 6000-ha Ranger North Conservation Reserve located 80 km northeast of Sault Ste. Marie, Ontario (47°13'N, 83°55'W). In 2008, field reconnaissance was used to identify three uncut (UC) and three SR stands located within 1 km of one another. These stands were visually assessed and found to have heavy cone crops typical of mast years, with almost all trees producing cones and many canopy dominants having well over 300 cones. The six stands were regionally representative of a central Ontario ecosite 21, i.e., white cedar (*Thuja occidentalis* L.)–white pine–white birch (*Betula papyrifera* Marsh.)–white spruce (*Picea glauca* [Moench] Voss) (Chambers *et al.* 1997). Overstory species associated with this ecosite include balsam fir (*Abies balsamea* L.), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and yellow birch (*Betula alleghaniensis* Britt.). The large, old white pine trees in these stands form a supercanopy 25 m to 35 m in height, with a subordinate canopy of other tree species at about 15 m (Buchert *et al.* 1997, Bebbler *et al.* 2004). The average age of white pine in these stands was estimated to be in excess of 200 years, with some trees as old as 350 years (Buchert *et al.* 1997, Rajora *et al.* 2000). Soils are deep, fresh to very fresh, very fine silty sand of moderate stoniness with a few scattered boulders.

The SR harvest system was applied in stands with white and red pine representing $\geq 50\%$ of total basal area and with ≥ 70 pine trees per hectare. The three SR study stands had a pre-harvest density of 80 to 85 pine per hectare, representing about 62% of total stand basal area. Tree marking focused on achieving a 15-m spacing of residual trees to create stands with a mixture of about 50% healthy seed producers and 50% with old-growth attributes, i.e., large size, dead or dying tops, and wildlife cavities.

Stand characteristics

Stand structural characteristics were determined using 14-m radius (615.7 m²) circular plots centred on seed trap locations 1, 7, and 15 (see below for details). In each of the six study stands, all living trees ≥ 10 cm in diameter at breast height (DBH at 1.3 m) in the plots were measured to estimate mean DBH, basal area, and density by species. Five dominant white pine trees closest to the three seed trap locations were used to assess crown condition, i.e., the incidence and proportional extent of dead stem in the upper crown. Percent live crown length was visually estimated as the percentage of the main bole from the base of the crown that was occupied by living stem and branches (i.e., trees without dead tops had a live crown length of 100%). Individual tree height was measured on every third tree used for crown measurements ($n = 5$). Basal area by species was also measured at each trap location with a 2 basal area factor (BAF 2) prism.

Age of dominant seed-producing trees was estimated from individual tree DBH (14 cm to 78 cm) and age (30 to 221 years) determined using complete increment cores collected from 118 trees during original timber cruises of 25 old-growth stands in this area. The linear relationship of age with DBH was quantified using simple regression and current age estimated from individual tree DBH (SR: $n = 26$, UC: $n = 62$) using the equation: $y = 73.87 + 1.62(x)$, $r^2 = 0.49$.

Seed production

A few weeks (August 28, 2008) prior to cone opening, 15 seed traps were placed in the understory of all six stands. Seed traps were suspended (1.5 m above ground) from metal posts positioned about 5 m apart along a central linear transect established at least 50 m from the edge of the stands. Seed traps were constructed of flexible, vinyl fabric with a circular opening (0.28 m²) that was covered by a metal grid frame to prevent seed and cone predation by birds and small mammals. Seed falling through this grid were deposited in a screen-lined collection jar fastened to the base of the trap.

Seed were removed from traps every six to 12 days between September 18 and November 13, 2008, for a total of seven seed collection dates over a 98-day period. (The September 18 collection contained seed that fell over the previous 21 days). Individual seed trap contents from each collection were placed in separate plastic bags, returned to the laboratory, and stored at 2°C. Within four weeks of collection, intact white pine seed were separated from leaf litter, seed fragments, and other canopy debris and counted. Seed traps were removed November 13 to avoid snow damage. In the northern portion of its range, seed rain in white pine occurs from early September to late November, with most seed disseminated within a month of cone maturity (Hocker 1968, Graber 1970, Wendel and Smith 1990). Although some seed may have fallen after trap removal, we assumed it was less than 5% of the total collected.

Prior to the period of fertilization, unpollinated ovules of *Pinus* species gradually collapse, abort, and form small, rudimentary seed most commonly located in the proximal and distal region of cones (Sarvas 1962, Owens 1995). These structures accounted for about 2% of the total seed collected, typical of white pine and other gymnosperm species (Owens and Blake 1985, Noland *et al.* 2006), and were not included in further analysis. Occasionally, entire cones ($n = 75$) were found on the grilled tops of seed traps and attributed to squirrel cone harvest activity observed in the canopy. Cones were retrieved, dried, and seeds manually removed, counted, and stored separately. Seed extracted from cones was not included in analysis to avoid significant overestimation of seed production. However, it is likely that some seed from these fallen cones was released into traps between sampling dates.

The number of seed collected in individual traps on a given sampling date was scaled to a per-hectare basis to provide estimates of seed production (# ha⁻¹) at each trap location. Seed production per hectare for a given stand and sampling date was estimated using the mean of the 15 seed traps. Total seed production per hectare for each stand over the study period was estimated as the mean of the total amount of seed collected in each trap. To normalize data for differences in numbers and sizes of residual pine in each stand, total seed production was also expressed relative to pine basal area by dividing mean seed production per hectare by mean

pine basal area. This provides a stand-level estimate of the seed production rate (# m⁻² basal area) of the overstory pine. The seed production rate at each trap location was also estimated using paired observations ($n = 45$, $N = 90$) for total seed production (# ha⁻¹) and pine basal area (m² ha⁻¹) measured by point sampling with a BAF 2 prism.

Seed characteristics

To estimate the percentage of empty, partially filled, and completely filled, sound seeds (Noland *et al.* 2006), seed were bulked by stand and x-rayed at 11 kV for two minutes with a Model Mx-20 Faxitron Specimen Radiograph System (Faxitron X-Ray LLC, Lincolnshire, IL) (Simak 1980). Exposure to this low level of radiation does not affect germination performance (Simak 1980). Partially filled seeds were defined as resulting from successful fertilization but incomplete morphological maturation, with female gametophyte and embryo tissues typically occupying <80% of the seed cavity (in longitudinal section) (Edwards 1980). Empty seeds were defined as fully formed, normal-appearing seeds either (1) devoid of tissues or (2) containing evidence of small, abnormally developed female gametophytes or aborted embryos. Empty seeds were assumed to be the result of self-fertilization, which initiates the continuous degeneration of embryo and gametophyte tissues until the original contents of the seed are barely or no longer visible (Smith *et al.* 1988, Rajora *et al.* 2002, Williams 2009). Mean fresh individual seed mass was determined for each stand by bulk measurement of three replicates of 25 sound seed.

Seed germination performance

Sound seed was soaked in aerated, deionized water for 24 hours, drained, transferred to plastic bags, and stored at 2°C for 60 days. After stratification, four 100-seed samples were sealed in plastic Petri dishes containing filter paper moistened with deionized water. For the SR stands seed traps did not provide sufficient seed for germination tests, so seed extracted from cones collected in traps and x-rayed using the method described above, provided about half of the 400 sound seed required for two of the three SR stands. In a separate trial, laboratory germination performance of 400 seed extracted from cones was very similar to that of individual seeds gathered from traps in the same stand (data not shown). Insufficient seed from traps for one SR stand necessitated the use of four 60-seed samples for the germination test.

Germination tests were performed in a controlled environment chamber that provided 75% relative humidity, a 16/8 hour light/dark photoperiod, and 8/16 hour, 30°C/20°C air temperature regime (Farmer 1997). Lighting was provided by both cool, white fluorescent and incandescent bulbs. Germination, defined as radicle protrusion and geotropic curvature, was assessed every three to four days for 64 days. On the final day of assessment, all ungerminated seed were cut open and examined. The number of empty and partially filled seeds in each replicate was subtracted from the initial number of seeds so that germination performance was based only on sound, full seed.

Assessment of laboratory germination performance of each replicate was confined to the first 28 days of incubation, since very few seeds germinated thereafter. Final percent germination (G28), a measure of seed viability, was calculated from cumulative number of seeds germinated on day 28. The

speed of germination was estimated using the peak value (PV), the maximum quotient of cumulative percent germination, and day during a germination test (Czabator 1962). Germination value (GV), a measure of germination vigour, was estimated by the product of PV and the mean number of germinants observed per day (Czabator 1962). To account for differences in number of sound seeds per replicate among stands, the value for the number of germinants observed per day used to calculate GV was first normalized to reflect the equivalent for replicates of 100 seeds.

Cone predation

During periodic seed trap collections, high rates of cone harvesting by red squirrels (*Tamiasciurus hudsonicus* Erxleben) were observed. To calculate a rough estimate of seed predation by these animals in each stand, the number of current year (intact and feeding damaged) cones on the forest floor were counted within a series of 1-m radius circular plots ($n = 15$) established at the midpoint between the seed traps. This assessment was performed on October 28, shortly after the period of maximum seed dispersal. Since natural cone abscission in white pine does not occur until a few months to a year after seed dispersal, we assumed the forest floor survey provided a cursory measure of squirrel cone harvest (Schopmeyer 1974). This survey likely underestimated pre-dispersal cone predation, since cones already cached at the time of our survey were not accounted for. Infestation by the white pine cone beetle (*Conophthorus coniperda* [Schwarz]) also causes cone abortion but occurs primarily in the late spring and early summer months (Godwin and Odell 1965).

Statistical analysis

Harvest treatment effects on stand structural features, seed production, cone predation, seed characteristics, and germination performance were determined using one-way analysis of variance (ANOVA) and the General Linear Model (GLM) procedure of SAS (SAS Institute, v. 8.0, Cary, NC, USA). In all cases, stand means were used as primary data for ANOVA ($n = 3$ stands per treatment, $N = 6$ total stands). Where ANOVA indicated harvest treatment effects were significant ($p < 0.05$),

mean comparisons were performed using a Tukey-Kramer test and type III sums of squares. Model residuals were examined to verify that the assumptions of homogeneity of variance and normality were met. Data transformations were not necessary.

The relationship of seed production rate with pine basal area for the SR and UC treatments was quantified using individual seed trap data and point sampling basal area measurements ($n = 45$), and a combination of correlation analysis, Pearson product-moment correlation coefficients (r), and nonlinear regression (SAS Institute, v. 8.0, Cary, NC, USA). Dispersal curves relating seed density to distance from a source typically show an initial exponential decline with most seed deposited within a comparatively short distance, and an extended tail of longer distance dispersal of relatively few seed (Greene *et al.* 1999, Nathan and Mueller-Landau 2000). The shape of these curves depends on factors such as speed of descent, height of release, wind speed and turbulence, and morphological adaptations for dispersal (Greene *et al.* 1999, Nathan and Mueller-Landau 2000). In second-growth and old-growth stands, most white pine seed falls within 30 m of parent trees, with mean dispersal distances of 15 m to 22 m (Ribbens *et al.* 1994, Marquardt and Epperson 2004, Dovčiak *et al.* 2005, Marquardt *et al.* 2007). Using a BAF 2 prism, the sight-limiting distance for the largest tree (93 cm DBH) measured was 32.9 m, while for trees with mean DBH (60 cm) this distance was 21.2 m (Hayden *et al.* 1999), which are both within the range of reported dispersal distances. Spatial variation in pine density within UC and SR stands will result in localized differences in wind speed, the distance of seed dispersal, and therefore the number of trees contributing seed to individual seed traps (Greene *et al.* 1999). As a result, we assume that trees counted in the trap-centred prism point sampling contributed most but not all of the seed deposited in a given trap.

Results

Harvesting affected residual stand structure, with SR stands having lower total basal area ($p = 0.039$), pine basal area ($p = 0.011$), and overstory density ($p = 0.009$) than UC stands

Table 1. Variation in stand structural characteristics and tree age of old-growth white pine stands (a) harvested by the structural retention system (SR) and (b) unharvested (UC). Least squares (LS) means ($n = 3$), standard error (SE) of least square means, and the $p > F$ values for treatment comparisons are presented.

Treatment	Stand No.	Total basal area ($\text{m}^2 \text{ ha}^{-1}$)	Pine basal area ($\text{m}^2 \text{ ha}^{-1}$)	Pine density (trees ha^{-1})	DBH (cm)	Height (m)	Live crown length (%)	Age (years)	Range in age (years)
(a) SR	1	20.1	14.2	48.7	61.6	31.8	94.3	173	150–209
	2	26.3	18.8	54.1	70.1	31.7	99.5	186	166–216
	3	24.5	12.7	37.9	65.1	26.7	94.3	179	156–191
	LS Mean	23.7	15.2	46.9	65.6	30.1	96.1	179	–
	SE	6.3	2.7	9.5	2.2	2.0	1.2	3.2	–
(b) UC	1	65.3	38.9	124.5	62.0	32.1	98.0	174	171–176
	2	50.8	31.2	124.5	56.7	24.8	98.0	166	158–174
	3	35.4	27.3	86.6	62.0	31.0	97.7	174	158–184
	LS Mean	50.5	32.5	111.9	60.2	29.3	97.9	171	–
	SE	6.3	2.7	9.5	2.2	2.0	1.2	3.2	–
$p > F$		0.039	0.011	0.009	0.15	0.79	0.35	0.15	–

(Table 1). White pine was the predominant species in the SR and UC stands, representing an average of 64% of total basal area in both treatments (Table 1). Dominant white pine did not differ in mean DBH ($p = 0.15$), height ($p = 0.79$), percent live crown length ($p = 0.35$), or age ($p = 0.15$) between treatments (Table 1). The age of dominant seed-bearing white pine trees ranged from 150 to 216 years, averaging about 174 (Table 1).

Seed rain in all stands began in mid-September, increased to a seasonal maximum rate in mid-October, and declined gradually thereafter (Fig. 1). The fairly high standard deviation for total seed production on individual sampling dates was likely due in part to differences in the number of pine in the vicinity of seed traps. The temporal pattern of seed rain differed slightly among stands, but 85% to 95% of total seed collected occurred between October 7 and November 7. Less than 2% of total seed rain occurred in the final sampling interval in mid-November. The UC stands had higher total seed production ($\# \text{ ha}^{-1}$) ($p = 0.0008$) and seed production rate ($\# \text{ m}^{-2}$) ($p = 0.069$) than SR stands (Table 2).

Within treatments, seed production rate of white pine was affected by spatial variation in pine basal area (SR: $r = -0.70$, $p < 0.0001$; UC: $r = -0.65$, $p < 0.0001$) and less so by total stand basal area (SR: $r = -0.16$, $p = 0.31$; UC: $r = -0.44$, $p = 0.002$). For both treatments, a significant negative exponential relationship was evident between seed production per unit pine

basal area and total pine basal area, indicating more open-grown pine formed larger numbers of seed (Fig. 2).

The density of cones found on the forest floor and attributed to red squirrel harvest varied widely among sampling locations, averaging about 4900 and 18 000 per hectare in the SR and UC stands, respectively, and did not differ ($p = 0.12$) with harvest treatment (Table 2).

The percentage of partially filled ($p = 0.22$) and empty seed ($p = 0.13$) did not differ between harvest treatments, but percent sound seed produced was somewhat higher ($p = 0.08$) in the UC stands. Harvest treatment had little effect on seed mass ($p = 0.46$), PV ($p = 0.29$), GV ($p = 0.20$), or G28 ($p = 0.47$) (Table 3).

Discussion

Seed production

The SR and UC old-growth white pine stands produced an average of about 640 000 and 2 500 000 seeds per hectare, respectively, in 2008. This is comparable to rates reported for second-growth stands in years of above average to heavy seed crops (Graber 1970, Heckman *et al.* 1986, Raymond *et al.* 2003). Conifer seed are a preferred food source of red squirrels that may harvest from 20% to more than 80% of annual cone crops (Horton and Bedell 1960, Halvorson 1986, Hurley and Robertson 1990). Assuming an average of 50 seeds per cone (Rajora *et al.* 2002, Noland *et al.* 2006), our forest floor

Fig. 1. Seasonal patterns of seed production per unit area for (a) three stands harvested using the structural retention (SR) system and (b) three unharvested (UC) old-growth white pine stands. Vertical bars present mean values (and standard deviation) for each of seven seed trap collection dates ($n = 15$).

Table 2. Variation in mean total seed production, total seed production per unit pine basal area, and cone predation in old-growth white pine stands (a) harvested by the structural retention system (SR) and (b) unharvested (UC). Least squares (LS) means ($n = 3$), standard error (SE) of least square means, and the $p > F$ values for treatment comparisons are presented.

Treatment	Stand	Seed production (# ha ⁻¹)	Seed production (# m ⁻²)	Cone predation (# ha ⁻¹)
(a) SR	1	495 179	34 872	8 276
	2	588 025	31 278	3 608
	3	835 614	65 796	2 759
LS Mean	–	639 606	43 982	4 881
SE	–	145 041	8 473	4 639
(b) UC	1	2 661 585	68 421	28 436
	2	2 149 742	68 901	19 099
	3	2 704 437	83 214	6 578
LS Mean	–	2 505 255	73 512	18 038
SE	–	145 041	8 473	4 639
$p > F$	–	0.0008	0.069	0.12

Fig. 2. Relationship of seed production per unit basal area with white pine basal area for structural retention harvested (SR) and unharvested (UC) old-growth white pine stands. Regression equations and coefficients of determination (r^2) are presented ($n = 45$).

survey suggested that pre-dispersal seed predation by squirrels may have been as high as 245 000 (SR) to 900 000 seeds per hectare (UC), slightly more than 25% of estimated total seed production of these two treatments.

Silvicultural treatments can modify seed production of forest tree species (Sarvas 1962, Lee 1979, Owens and Blake 1985). Thinning and release from competition can temporar-

ily stimulate cone and seed production by conifer species, presumably due to positive effects of increased resource availability on tree vigour and reproductive growth in more open-grown trees (Lee 1979, Krannitz and Duralia 2004, Karlsson 2006). This response is generally transient and more strongly expressed during years of above-average seed crops (Phares and Rogers 1962, Stephenson 1963, Reukema 1982). In our study, conducted in a year of a relatively large seed crop, SR stands showed a strong trend towards the opposite response, suggesting that 16 years after harvesting seed production per unit pine basal area was reduced.

Causal factors for treatment differences in seed production per unit pine basal area were not examined in our study, but could be due to harvest effects on the fecundity of parent trees, microsite factors that influence tree size and seed yield, and/or the level of pre-dispersal seed predation (Nathan and Mueller-Landau 2000). Mean annual seed production of individual trees is proportional to leaf mass (and basal area) (Greene *et al.* 1999) but tree size and live crown length were unaffected by harvest and are an unlikely cause of treatment effects. Alternatively, the purposeful retention of trees for structural attributes rather than seed-bearing potential during the SR harvest may have inadvertently created stands with a comparatively lower genetic and/or physiological capacity for reproduction. Differential expression of the many environmental factors (e.g., seasonal temperature and precipitation or frost events) that influence the multi-phased 26-month reproductive cycle may also be partly responsible for the observed treatment effects (Puritch 1977, Lee 1979, Owens and Blake 1985).

Higher pre-dispersal seed predation in harvested stands is a less plausible explanation for observed treatment differences. Although pre-dispersal seed losses to red squirrels can be significant, estimated cone predation did not differ with treatment. Many insect species feed on the reproductive structures of conifers and can reduce annual cone crops from 10% to 100% (Mattson 1978, Turgeon *et al.* 1994). In *Pinus* species, recently thinned and lower-density stands exhibited a higher incidence of cone damage by insects (Kraft 1968, Barnes 1969, Stiell 1971). Our findings that more open-grown trees exhibited higher seed production in both treatments, and, regardless of density, trees in UC stands produced more seed, suggest pre-dispersal seed loss to insects was not a major factor reducing seed production in SR stands.

White pine trees growing in localized areas of lower pine basal area produced more seed, regardless of harvest treatment. Our findings that seed production per unit pine basal area was more strongly influenced by pine than total stand basal area suggests this response is primarily associated with pine density effects on microenvironment and crown size of seed-bearing trees, rather than interspecific competition of pine with subordinate canopy trees. Within temperate and boreal conifer species,

Table 3. Variation in seed characteristics, peak value (PV), germination value (GV), and final percent germination after 28 days (G28) for old-growth white pine stands (a) harvested by the structural retention system (SR) and (b) unharvested (UC). Least squares (LS) means ($n = 3$), standard error (SE) of least squares means, and the $p > F$ values for treatment comparisons are presented.

Treatment	Stand No.	Full (%)	Partial (%)	Empty (%)	Mass (mg)	PV	GV	G28 (%)
(a) SR	1	78.8	2.8	18.4	13.9	4.59	15.20	95.6
	2	80.2	5.1	14.7	16.1	5.22	18.44	95.7
	3	72.7	4.7	22.6	15.5	5.11	17.63	96.6
LS Mean	–	77.2	4.2	18.6	15.1	4.97	17.09	96.0
SE	–	2.1	0.5	2.1	0.5	0.29	1.26	0.9
(b) UC	1	87.9	3.3	8.8	15.9	5.16	17.38	97.5
	2	82.3	3.5	14.3	15.2	6.41	22.39	98.8
	3	82.4	2.4	15.2	16.1	5.69	18.77	94.7
LS Mean	–	84.2	3.1	12.8	15.7	5.75	19.51	97.0
SE	–	2.1	0.5	2.1	0.5	0.29	1.26	0.9
$p > F$	–	0.08	0.22	0.13	0.46	0.13	0.25	0.47

dominant, vigorous trees with large diameters and exposed crowns typically produce more seed (Lee 1979, Wendel and Smith 1990, Greene *et al.* 1999, Krannitz and Duralia 2004). More open-grown or widely spaced trees may also produce larger numbers of cones and seeds (Stiell 1971, Sutton *et al.* 2002, Krannitz and Duralia 2004), provided spacing is not so wide as to increase self-fertilization (Smith *et al.* 1988, Mitton 1992, Rajora *et al.* 2002). In 80-year-old white pine stands, higher total seed production in areas of intermediate ($28 \text{ m}^2 \text{ ha}^{-1}$) compared with high ($43 \text{ m}^2 \text{ ha}^{-1}$) basal area was attributed to smaller crowns and fewer cones per tree where density was higher (Graber 1970).

Seed characteristics and germination performance

The *Pinaceae* are monoecious, wind-pollinated, and capable of both outcrossing and selfing, with outcrossing being favoured as the size and density of the breeding population increases (Mitton 1992, Rajora *et al.* 2002). The sound, partially filled, and empty seed percentages of the old-growth study stands were within the range reported in above-average seed years for unmanaged and shelterwood second-growth white pine stands in Ontario (Rajora *et al.* 2002, Noland *et al.* 2006). The slightly higher proportion of sound seed formed in UC stands may be due to greater outcrossing in stands of higher pine density (Mitton 1992), but the percentage of empty seeds formed by selfing did not differ with harvest treatment. The comparatively low percentages of empty seed in these old-growth white pine stands support the finding that self-fertilization and inbreeding seldom occur in white pine unless stands are small, isolated, and/or of very low density (Rajora *et al.* 2002, Marquardt *et al.* 2007). Similar proportions of partially filled seeds in SR and UC stands suggest no major treatment differences in resource availability and microclimatic conditions that influenced embryo development and morphological seed maturation (Edwards 1980, Owens and Blake 1985).

Stand density and thinning of conifer stands have comparatively less effect on seed germinability and mass than on seed production (Barnes 1969, Graber 1970, Karlsson 2006). In our study, harvesting of old-growth white pine stands had no effect on seed germination performance and seed mass, with

values for both similar to those reported for second-growth stands (Graber 1970; Parker *et al.* 2004, 2006; Noland *et al.* 2006). Where seedbed and understory environmental conditions are favourable for germination, emergence, and early establishment, our results suggest it is unlikely that the viability and mass of seed produced by old-growth white pine stands will compromise natural regeneration potential (Baskin and Baskin 1998, Greene *et al.* 1999).

Conclusions

Ontario's provincial policy for conservation and management of old-growth white and red pine forests seeks to maintain or increase the area of old growth on public land while allowing for the sustainable management for timber and other values (OMNR 2003, Latremouille *et al.* 2008). Presently, about 4% (50 000 ha) of total white and red pine dominated forests in Ontario are classified as old growth (OMNR 2006). In the absence of periodic disturbance by fire or management intervention to provide the environmental conditions needed to secure and promote the growth of pine regeneration, it is unlikely that old-growth stands will retain white and red pine as a keystone species (Barnes 1989, Day and Carter 1990, Zenner and Peck 2009). With an average of 80% sound seed and a 96% germination rate, the SR and UC stands dispersed about 491 000 and 1 924 000 viable seeds per hectare, respectively. Even if 95% of the viable seed suffered post-dispersal predation by small mammals (Cornett *et al.* 1998, Duchesne *et al.* 2000), the surviving 25 000 and 96 200 seed per hectare would likely be sufficient to establish a fully stocked cohort of white pine natural regeneration given suitable seedbed and environmental conditions. Although limited to six stands in a single location, our results indicate that in the absence of severe fragmentation, isolation, or reduction in size of breeding populations, seed production will likely not limit natural regeneration in unmanaged and partially harvested old-growth white pine stands in years of mast seeding.

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