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Cleavitt and Fahey

Masting in the northern hardwood forest

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Seed production of sugar maple and American beech in northern hardwood forests,
New Hampshire, USA.

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20 **Abstract.** Mast seeding is the synchronous production of large seed crops in plant
21 populations and for many tree species is known to be determined by the interaction between
22 weather cues and internal plant resources. We use a 24-year record of seed fall for sugar maple
23 and American beech across a northern hardwood forest landscape to quantify their masting
24 patterns and explore the relationship between mast years, resources and weather cues,
25 particularly the difference between summer temperatures in the two years prior to the seed fall
26 year (ΔT). We found clear evidence of masting in these species and mast years were often
27 coincident in the two species; masting was best predicted by ΔT or ΔT plus previous-year seed
28 fall. We saw no evidence for correspondence of masting in these trees to precipitation cues. A
29 soil calcium addition modified elevation effects on seed production. Clarification of the
30 controls on mast seeding for these important tree species will aid in predicting such resources as
31 mast for wildlife and maple sugar production in northern hardwood forests.

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33 **Keywords:** masting, ΔT model, *Acer saccharum*, *Fagus grandifolia*, temperature cue

1. Introduction

Masting is the synchronous and highly variable seed production among years by populations of plant species and is common among wind-pollinated trees. Selection pressure for masting is thought to involve such functional roles as predator satiation (Janzen 1971) and enhanced dispersal (Jansen et al. 2004). Weather cues clearly play a key role as proximate environmental cues for masting (Kelly et al. 2013), but internal plant resource dynamics also have been shown to influence the timing and magnitude of mast events (Pearse et al. 2016). In addition to effects on tree reproduction, masting has important implications for animal populations and trophic dynamics in forests (Ostfeld and Keesing 2000).

Northern hardwood forests dominated by sugar maple (*Acer saccharum* Marsh.; ACSA) and American beech (*Fagus grandifolia* Ehrh.; FAGR) are widely distributed across northeastern North America, and both species are regarded as putative masting tree species (*sensu* Kelly 1994). Although studies from the region provide a record of high seed years for these species, affording a nearly 50 year signal (Table S1), the relationships between masting by these two species have not been explored quantitatively, and the cues and internal controls of masting are not entirely clear. Masting by American beech is particularly important for wildlife population dynamics in this region (Bergeron et al. 2011; Jakubas et al. 2005) in the absence of other “hard” mast species (e.g., oaks), and variation in seed production in northern hardwood forests has wide and interacting effects on trophic relations (Bergeron et al. 2011; Jensen et al. 2012) and tree recruitment dynamics (Cleavitt et al. 2008; Cleavitt et al. 2011).

In general, weather cues exert primary control over masting in perennial plants, and Kelly et al. (2013) presented a strong case for a ΔT model in which the difference in temperature between the two previous years regulates subsequent-year masting in a wide suite of plants.

Additional internal cues related to plant resource balance (e.g., carbon, nitrogen (N), phosphorus (P)) have been shown to exert a complementary influence on masting (Crone and Rapp 2014, Pearse et al. 2016); for example, negative correlations between seed production in the current year to that in the previous year have been reported (Kelly 1994). Variation in seed production for sugar maple and American beech has received limited analysis in relation to weather cues, and the ΔT model has not been tested for these tree species. Seed production for FAGR has been related to midsummer water stress in the year preceding the seed year, as well as to July temperature two years preceding the seed year (Piovesan and Adams 2001). The role of drought in signaling mast years for ACSA also has been suggested based on correlations between the Palmer Drought Severity Index (PDSI) and high seed years in Pennsylvania (Long et al. 1997, 2011). The relative predictive power of standard meteorological variables (e.g., preceding year conditions) versus differential variables (e.g., ΔT model) for masting has implications for the sensitivity of seed production to climate change (Kelly et al. 2013; Koenig et al. 2016).

The possible role of resource balance influencing masting in these species also has been indicated. In particular, negative correlations have been observed between current- and previous-year seed production of FAGR in Michigan (Piovesan and Adams 2001), and maple sugar production in Vermont was lower in the year following mast years of ACSA (Rapp and Crone 2015). The magnitude and frequency of masting also may be reduced in the stressful environment near a species' range limits (Kelly and Sork 2002) suggestive of resource limitation. The role of nutrient (N, P) limitation in masting has been indicated by nutrient depletion the year after masting occurs (Pearse et al. 2016), and liming of severely calcium (Ca)-deficient sites resulted in increased seed production of ACSA in Pennsylvania (Long et al. 2011) and New

Hampshire (Halman et al. 2013). Calcium addition apparently influenced seed production through increased flower production on in both of these studies.

We use a 24-year record of seed fall for ACSA and FAGR collected at Hubbard Brook Experimental Forest (HBEF) to address several questions. At the forest level: 1) Does masting occur in these two tree species and are their mast years coincident? 2) Can we predict seed production in these two species from exogenous (e.g., temperature, precipitation) and endogenous (e.g., negative correlation) cues? At the site level: 3) How do parameters of masting (e.g., synchronicity, frequency, magnitude) change near the elevation limits of these species? and 4) Did a watershed-scale Ca addition affect seed production, particularly for ACSA, a calcium sensitive species?

2. Materials and Methods

The Hubbard Brook Experimental Forest (HBEF) is located in north-central New Hampshire, USA (43° 56' N, 71° 45' W). The overstory vegetation is dominated by northern hardwoods: sugar maple, American beech, and yellow birch (*Betula alleghaniensis* Britt.), which together comprise over 90% of the forest basal area (van Doorn et al. 2011). Detailed descriptions of soils, hydrology, topography, and vegetation of the HBEF are presented in Likens and Bormann (1995). The climate is humid continental with short, cool summers and long, cold winters. Annual precipitation averages 140 cm; mean annual temperature is 5.5 °C; and daily temperatures average from –8.5 °C in January to 18.8 °C in July (Bailey et al. 2003).

We measured seed fall using seed trap arrays distributed in nine plots in a stratified (by elevation zone), random design (Fahey et al. 2005). Seed fall was estimated for a 24-year period (1993–2016) from a maximum of 102 seed traps (0.1 m² catch site) positioned in three elevations

zones: 500m (500-525 m); 600m, (600-625 m); and 700m, (700-725 m) within three study sites, two reference sites and one Ca treated site (Table 1). The calcium silicate mineral, wollastonite, was applied to Watershed 1 (hereafter referred to as “CAL”) by helicopter in October 1999 with a uniform delivery rate of 1028 kg Ca ha⁻¹ (Peters et al. 2004). This treatment was explicitly designed to replace the Ca that was lost from the Hubbard Brook forest as a result of human activity during the 20th century and thereby to evaluate the likely effects of anthropogenic soil Ca depletion on forest ecosystem dynamics (Battles et al. 2014). The pool of exchangeable Ca increased significantly after treatment, peaking in the O horizons by 2002 and in the upper mineral soil by 2006 (Johnson et al. 2014).

In each year, all seeds and leaves were collected from the baskets, sorted, and counted three times a year: early May, late August and after leaf-off in early November. All collections were pooled by year for analysis. To standardize for differences in species abundance among plots we also express seed fall per unit of leaf fall for each species (i.e., relative seed production) for between plot tests.

We followed existing conventions to define masting species (Kelly 1994) and mast years (LaMontagne and Boutin 2009). For the forest-level analyses we pooled all reference site data from 1994, 1995, 1997-2016 to calculate the long-term mean and annual standard deviation (ASD) of seedfall (seeds per m⁻²). Pooling the data reduced the occurrence of zero counts and matched the scale of available meteorological data (see below). In addition, this forest-level approach should make for a more robust comparison to mast years reported in other studies (Table S1). We examined the coefficient of variation (CV; long-term standard deviation divided by the mean) for the two species and the annual deviate from the long-term mean; species with CV >1 are defined as masting species (Kelly 1994). Mast years were defined as years when seed

production is greater than the absolute value of the minimum standardized deviate (LaMontagne and Boutin 2009). To test for concordance in seed production for ACSA and FAGR, we looked for shared mast years and Spearman rank correlations (LaMontagne and Boutin 2007).

We used a 19-year (1998-2016) seed fall record for reference sites together with temperature and precipitation records from the HBEF (http://www.hubbardbrook.org/data/dataset_search.php) to explore relationships between weather cues and seed production. Temperature data were mean monthly temperatures (°C) averaged for two stations (stations 1 and 6, which span the elevation range of the seed collectors; Bailey et al. 2003). The precipitation data (mm) were growing season (15 April – 15 November) totals for each year from the mean of three stations (stations 9-11; nearly coincident with our collection sites; Bailey et al. 2003). Therefore, the seedfall and metrological data sets covered similar landscape variability.

We focus on a limited set of weather cues that are well documented in the literature; we acknowledge that this approach may miss other potential biological cues. Here we tested the ΔT model (Kelly et al. 2013), which uses the temperature difference between the two previous summers (sum of mean monthly temperatures for June-August) to predict seed production in the third year. We also evaluated possible effects of precipitation variation (Piovesan and Adams 2001), and summer temperature two years previous (2T model in Kelley et al. (2013)). Finally, we evaluated the possible effects of previous-year seed production as evidence of resource balance controls on seed production (Kelly 1994). Generalized Linear Models (GLMs) analyzing the logarithm of seeds m^{-2} were run in JMP Pro 11 for Windows (SAS Institute Inc., Cary, NC) and compared using the reduction in model deviance and bias corrected Akaike's Information Criterion (AIC_c).

At the site-level ($N=9$; **Table 1**), we examined the synchrony of seed production across sites for both species using Spearman rank correlations (LaMontagne and Boutin 2007) and the ASD (described above) to delineate mast years for comparison of masting frequency. To test for differences in variability, we calculated site-level CV (CV_s) using the full data set for each site (**Table 1**; 19-24yrs). To compare the magnitude of seed production between sites (including Ca treatment) and elevations, we used the balanced data set for 19 years of seed fall (1998-2016). For these analyses, relative seed production (seeds leaf⁻¹) was more appropriate as these values account for differences in species abundance among the sites. In a mixed model analyzing the logarithm of relative seed production, year was a random factor and site and elevation with their interaction were fixed factors to test for site and elevation differences. Significance tests were followed by Tukey-Kramer HSD multiple comparisons.

3. Results

During the 19-year record, both ACSA and FAGR had a $CV > 1$ and five mast years with four of these years coincident for both species (**Fig. 1**). The synchronicity of seed production between the species was highly significant for both reference sites, but higher at REF1 (Spearman corr. = 0.673; $p < 0.0001$) than at REF 2 (0.3349; $p = 0.0060$).

The best overall model for predicting seed fall in ACSA was the ΔT model and for FAGR the best model included both ΔT and previous year's seed fall (**Table 2**; **Fig. 2**). The ΔT model was a better overall predictor than the standard weather variables (**Table 2**). Summer temperature in year⁻² was a significant predictor for both species, and neither species was significantly related to the other precipitation or temperature variables tested, including differential precipitation (**Table 2**). The best models predicted higher seed fall for ACSA in 2008 and 2013 and for FAGR in 2012 than was actually observed (**Fig. 2**).

Moderate to high synchrony was observed between sites for seed fall of both ACSA and FAGR (**Table 3**). Within sites, the 700m elevation site had the lowest correlation to seed production in other sites, particularly at REF2 for both species and CAL for FAGR (**Table 3**). Frequency of mast years was not significantly different among elevation zones (Contingency X^2 : ACSA = 1.66; $p = 0.437$; FAGR = 2.42; $p = 0.300$) though they occurred more often in low elevation sites for all areas except at CAL for ACSA.

ACSA had a higher CV_s than FAGR at all but one site, and FAGR had $CV_s < 1$ at one high elevation site (**Table 3**). The CV_s values tended to be higher at high elevation sites for ACSA as years with moderate seed production were lacking (**Table 3**; **Fig. S1**). In contrast, the CV_s for FAGR was lower at high elevation sites with more years of moderate seed production (**Table 3**; **Fig. S1**). There was no evidence for increased seed fall of ACSA in the CAL site; however, FAGR had highest relative seed fall (seeds leaf⁻¹) at 700m in CAL (**Tables 3 and 4**). Relative seed fall of ACSA was greater at REF1 than the other sites (**Table 3**). Elevation effects were stronger for ACSA than for FAGR; however, both species had a significant elevation interaction term (**Tables 3 and 4**). At both REF sites, ACSA relative seed fall decreased significantly at 700m; however, on CAL the decrease was not significant (**Tables 3 and 4**). The largest elevation effect for FAGR was higher relative seed fall on CAL at 700m (**Table 3**).

Discussion

Both species displayed masting (Kelly 1994) (**Fig. 1**; **Table 3**). The coincidence of mast years (4 years: 2000, 2002, 2006, and 2011) and significant correlation between species suggested that the two species were responding, at least in part, to a common cue. In particular, application of the ΔT model indicated that masting in both species was probably responding

193 primarily to the difference in temperature between the previous two years as a proximate cue
194 (Kelly et al. 2013). In contrast to some previous reports (Long et al. 2011; Piovesan and Adams
195 2001), we found no evidence of precipitation or drought effects on masting of either species.
196 However, soil characteristics and bedrock depth are particularly important for delineating
197 drought conditions in New Hampshire and indexes such as the PDSI based mainly on
198 precipitation perform poorly (Davis and Stampone 2014). The predictive power of the ΔT model
199 for FAGR could allow wildlife managers to better predict seed crops for wildlife (Jensen et al.
200 2012). Moreover, maple sugar producers could use the ΔT model for ACSA to predict sap
201 quality, given the reported relationship to mast years (Rapp and Crone 2015).

202 The role of internal controls and resource balance in regulating masting of these species
203 was suggested by the significance of previous-year seed fall as a predictor; particularly for
204 FAGR (Table 2). Previous studies have also indicated a strong effect of previous year seed fall in
205 regulating masting of *Fagus* spp. (Jakubas et al. 2005; Wagner et al. 2010), but the actual
206 resource that contributes to this apparent constraint on seed production is not known. This effect
207 of previous seed production has not been quantified previously for ACSA, but indications of
208 resource constraints were suggested by reduced maple sugar production in the year following
209 masting (Rapp and Crone 2015). For ACSA, resource allocation to seeds in the previous year is
210 complicated by an unknown and variable proportion of the seeds being unfilled perhaps
211 contributing to the weakness of the relationship found here.

212 Because the magnitude and frequency of masting may be reduced in the stressful
213 environment near a species' range limits (Kelly and Sork 2002), we expected seed fall and
214 masting to vary with elevation. In fact, we observed contrasting patterns of seed fall in relation to
215 elevation for the two species. Relative seed production was lower at the highest elevation at both

reference sites for ACSA, but at none of the reference sites for FAGR. Thus, there was support for decreased seed production near the elevation limits for ACSA, but not for FAGR. Moreover, there were several other intriguing trends with elevation, which should be further considered for biological significance. Frequency of mast years and synchronicity between sites both decreased at high elevation (**Table 3**). At high elevations sites, the occurrence of moderate seed years was lessened for ACSA and enhanced for FAGR, as reflected by differences in their CV_s values (**Table 3; Fig. S1**).

Previous plot-level studies in Pennsylvania (Long et al. 1997, 2011) and HBEF (Halman et al. 2013) indicated that seed production by ACSA was stimulated by Ca additions, but we observed limited effects of Ca treatment on seed production parameters in this highly Ca-sensitive species (Schaberg et al. 2006). The difference between our study and the Pennsylvania studies may reflect treatment intensity as about five times more Ca was added than in the present study. However, Ca addition rate in the plot-level study at HBEF (Halman et al. 2013) was comparable to our watershed-level application. Thus, local site-level factors also appear to influence the response of ACSA seed production to mitigation of soil Ca depletion.

The Ca addition ameliorated elevation effects on seed production for both species (i.e. causing significant interaction term; **Table 4**), but to a much greater extent for FAGR (**Table 3**). Some weak evidence for amelioration of seed production limits at high elevation due to Ca addition was observed for ACSA, while relative seed production for FAGR was highest at 700m and lowest at 500m on CAL; the reverse of the expected pattern (Kelly and Sork 2002; Piovesan and Adams 2001). The stronger Ca effect on FAGR seed fall at high elevation was surprising given the many studies showing ACSA to be more sensitive to Ca amendments than FAGR, but

in agreement with greater overall forest response from the Ca addition at higher elevation on CAL reported previously (Battles et al. 2014; Minocha et al. 2010).

The synchronicity of mean seed production at three sites distributed over several km in the HBEF was moderate to high (**Table 2**; Koenig et al. 2003). Several of our mast years also coincided with those reported as high seed years from other sites in the Northeast (**Table S1**). The comparison of predicted versus actual seed production (**Fig. 2**) highlighted one apparently failed mast year. For ACSA, the year 2013 was predicted to be a mast year; this year also exhibited high between-site variability in seed production in Vermont (Rapp and Crone 2015). Overall, the model predictions were fairly close to actual seed production patterns and show promise for forecasting seed production and related variables for these two important tree species.

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Table 1. Descriptions of seed trap collection sites in Hubbard Brook Experimental Forest, NH. The species data is meant to summarize abundance of species in the collection sites: Leaf (percent of leaves that are target species out of all leaves over time in the collections); Rel. abund (the relative abundance by tree density in the collection site). Seed data are means (1SE) and are given as seeds m⁻².

Sites	Elev class	<i>Acer saccharum</i> (ACSA)			<i>Fagus grandifolia</i> (FAGR)		
		Leaf (%)	Rel. abund (%)	Seeds m ⁻²	Leaf (%)	Rel. abund (%)	Seeds m ⁻²
REF1 (1993-present; 12 traps per elevation)	500m	19.8	39.5	38 (4.5)	29.6	30.2	19 (4.0)
	600m	72.7	82.6	194 (22)	27.3	13.0	16 (4.1)
	700m	29.8	41.3	22 (3.1)	27.6	21.7	5.7 (1.0)
REF2 (1994, 1995, 1997-present; 10 traps per elevation)	500m	41.5	20.0	49 (6.2)	27.9	72.0	20 (3.5)
	600m	39.1	35.3	50 (7.5)	32.6	47.1	14 (3.5)
	700m	1.9	3.1	0.8 (0.3)	68.3	71.9	33 (4.1)
CAL (1998-present; 12 traps per elevation)	500m	50.8	62.3	65 (7.4)	18.2	15.6	3.8 (0.7)
	600m	35.0	43.9	29 (3.7)	50.1	49.5	19 (2.5)
	700m	39.2	16.1	21 (3.4)	23.9	19.5	23 (3.6)

Table 2. Comparisons of generalized linear models predicting seed production (seeds m⁻²) in sugar maple (ACSA) and American beech (FAGR) over 19-yrs (1998-2016). Significance of the deviance reduction was evaluated by likelihood ratio chi square (X²) test: * p <0.05; **p<0.01; ***p<0.001. Akaike’s information corrected criterion (AIC_c) used to compare fit between models, where the model with the lowest was set to “zero” and all other models compared by the difference in model AIC_c (Δ AIC_c). The best model for each species is in bold. Model abbreviations: ΔT (difference in summer temperatures for year⁻¹ and year⁻²); Ppt (growing season precipitation); Δ Ppt (difference in growing season precipitation for year⁻¹ and year⁻²); T (temperature); summer (sum of the mean temperatures for June-August).

Model	ACSA		FAGR	
	Likelihood		Likelihood	
	ratio	X ² Δ AIC _c	ratio	X ² Δ AIC _c
ΔT	22.9***	0	18.2***	1.1
ΔT + previous seed	22.9***	3.2	22.9***	0
Previous seed	9.4**	13.6	16.9***	2.4
Summer T yr ⁻²	7.5**	15.4	7.5**	11.8
July T yr ⁻²	8.1**	17.0	5.8*	17.0
Summer T yr ⁻¹	5.7*	17.2	4.1*	18.7
July T yr ⁻¹	1.9	21.1	0.5	18.8
Ppt yr ⁻¹	0.2	22.7	0.1	19.2
Δ Ppt	0.2	22.8	0.1	19.2

Table 3. Site-level comparisons of seed production by sugar maple (ACSA) and American beech (FAGR) in Hubbard Brook

Experimental Forest, NH. The average Spearman correlation to all other sites and the coincidence of mast years were used to assess synchronicity and frequency of masting. Mast years for sites are delineated in **Figure S1**. The coefficient of variation (CV) and relative seed production (Rel. seeds: seeds per 100 leaves in the same collectors) compare the magnitude of masting. Tukey-Kramer post-hoc subsets for relative seed production are given by letter superscripts within the column ($\alpha = 0.05$).

Site	Elev class	ACSA				FAGR			
		Ave. Corr.	Mast years	CV	Rel. seeds (per 100 lvs)	Ave. Corr.	Mast years	CV	Rel. seeds (per 100 lvs)
REF1	500m	0.844	1994, 1996, 1998, 2000, 2002, 2006, 2011	1.33	15.3 (2.1) ^a	0.767	1996, 2002, 2006, 2011, 2013, 2015	1.30	2.5 (0.4) ^{bc}
	600m	0.862	1994, 1996, 2002, 2006, 2011	1.46	14.0 (1.6) ^a	0.782	2000, 2002, 2006, 2011	1.42	2.1 (0.5) ^{bc}
	700m	0.806	1994, 1996, 2002, 2006, 2011	1.57	4.6 (0.7) ^{bc}	0.751	1995, 1996, 2006, 2011, 2013	1.04	0.9 (0.1) ^c
REF2	500m	0.882	1994, 1998, 2000, 2002, 2006, 2011	1.42	8.9 (1.3) ^{ab}	0.758	2000, 2002, 2006, 2011, 2013	1.24	3.0 (0.5) ^{ab}
	600m	0.857	1994, 2000, 2002, 2006	1.74	7.4 (1.1) ^b	0.739	2000, 2002, 2006, 2013	1.80	1.9 (0.4) ^c
	700m	0.621	1994, 2000, 2011	2.33	1.6 (1.0) ^c	0.685	2002, 2011, 2015	0.87	2.9 (0.3) ^b
CAL	500m	0.846	2002, 2006, 2011	1.59	7.6 (1.2) ^b	0.750	1998, 2000, 2002, 2006, 2011, 2013, 2015	1.15	0.9 (0.2) ^c
	600m	0.855	2002, 2006, 2011	1.63	4.9 (0.6) ^{bc}	0.722	2000, 2002, 2008, 2011, 2013	1.20	1.9 (0.2) ^{bc}
	700m	0.838	2006, 2011, 2013	1.73	4.8 (1.3) ^{bc}	0.670	2006, 2011, 2013, 2015	1.07	4.5 (0.7) ^a

Table 4. Summary of mixed models for between site comparisons of seed production and relative seed production (seed leaf⁻¹) in sugar maple (ACSA) and American beech (FAGR) from three sites in HBEF, NH for 19-ys (1998-2016). Significance of the F ratio: * p <0.05; **p<0.01; ***p<0.001. Post-hoc separation is presented in **Table 3**.

Fixed effect:		Site	Elevation	Site x Elevation
Test variable	df den	df 2	df 2	df 4
ACSA seeds leaf ⁻¹	751	16.5***	6.49**	5.15**
FAGR seeds leaf ⁻¹	621	1.97	6.45**	11.2***

Figure Legends

Figure 1. Seed production for sugar maple (ACSA) and American beech (FAGR) at Hubbard Brook Experimental Forest, NH from 1994-2016: **A.** Bars show the annual means ($\pm$ 1SE) for all reference site collectors (N=66) and asterisks denote mast years. The long-term mean is shown by a solid line. **B.** the standardized deviation of annual seed production from the long-term means (ASD) and coefficient of variation (CV). Years with ASD values above the minimum standardized deviate (dotted line) were considered mast years.

Figure 2. Actual (heavy solid line) and predicted logarithm of seed production for sugar maple (ACSA) and American beech (FAGR) at Hubbard Brook Experimental Forest, NH from 1998-2016. For both species the predicted values from model: ΔT + previous seed production are the light dashed lines. For ACSA, the light gray line is ΔT alone and for FAGR light gray line represents the previous seed production alone. See **Table 3** for model comparison and statistics of fit.

Figure 1. Seed production for sugar maple (ACSA) and American beech (FAGR) at Hubbard Brook Experimental Forest, NH from 1994-2016: A. Bars show the annual means ($\pm$ 1SE) for all reference site collectors (N=66) and asterisks denote mast years. The long-term mean is shown by a solid line. B. the standardized deviation of annual seed production from the long-term means (ASD) and coefficient of variation (CV). Years with ASD values above the minimum standardized deviate (dotted line) were considered mast years.

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Table S1. Summary of studies reporting seed production data for sugar maple (ACSA) and American beech (FAGR) from 1959 through the present in the Northeast portion of their range.

Study	Years of record	High seed year(s)	Location	Method	“High” seed production (seeds m ⁻²)
ACSA seed production:					
Forcier 1973	1967-1969	1969	HBEF, NH	Seed traps	154
Nothnagle 1980	1975-1977	1976	HBEF, NH	Seed traps	407
Hughes and Fahey 1988	1984-1985	1984	HBEF, NH	Seed traps	264
Graber and Leak 1992	1971-1981	1971, 1974, 1976, 1979, 1981	Bowl, NH	Seed traps	613-1186
Garrett and Graber 1995	1971-1981	1971, 1974, 1976, 1979, 1980, 1981	Bartlett, NH	Seed traps	220-301
Marks and Gardescu 1998	NA	1984, 1989, 1992, 1994	Upstate, NY	Seedling cohort size	NA
Houle 1999	1988-1994	1988, 1990, 1992, 1994	Québec	Seed traps	93-194
McCarthy and Keiffer 2004	1996-2000	1998	Ohio	Seed traps	271

Gardescu 2003	NA	1984, 1988	Upstate, NY	Seedling cohort size	NA
Long et al. 2011	1987-2008	1989, 1992, 2000, 2003, 2006	Pennsylvania	Index 0-7	NA
Graignic et al. 2014	NA	1996, 2002, 2003, 2006	Québec	Age structure of seedlings	NA
Rapp and Crone 2015	1998-2013	1998, 2000, 2006, 2011	Vermont	Proportion of trees with seeds	NA
This study	1993-2016	1994, 1996, 2000, 2002, 2006, 2011	HBEF, NH	Seed traps	140-253
FAGR seed production:					
Gysel 1971	1959-1968	1960, 1964	Michigan	Seed traps beneath FAGR canopy	275-474
Forcier 1973	1968-1969	none	HBEF, NH	Seed traps	---
Nothnagle 1980	1975-1977	1976	HBEF, NH	Seed traps	68
Hughes and Fahey 1988	1984-1985	1984	HBEF, NH	Seed traps	59
Graber and Leak 1992	1971-1981	1971, 1978	Bowl, NH	Seed traps	30, 43

Leak and Graber 1993	1976-1981	1976, 1978, 1980, 1981	Bartlett, NH	Seed traps	50-108
McCarthy and Keiffer 2004	1996-2000	1998, 2000	Ohio	Seed traps	112-127
Jakubas et al. 2005	1988-2003	1988, 1994, 1996, 1998, 2000, 2002	Adirondacks, NY	Seed traps	32-64
Bergeron et al. 2011	2005-2009	2006, 2008	Québec	Seed traps beneath FAGR canopy	135-246
This study	1993-2016	2000, 2002, 2006, 2011, 2013	HBEF, NH	Seed traps	39-56

Additional references for Table S1.

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Legend

Figure S1. The standardized deviation of annual seed production from the long-term means (ASD) for nine sites at Hubbard Brook Experimental Forest, NH. Years with ASD values above the minimum standardized deviate (dotted line) were considered mast years (as listed in **Table 3**).

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Figure S1. The standardized deviation of annual seed production from the long-term means (ASD) for nine sites at Hubbard Brook Experimental Forest, NH. Years with ASD values above the minimum standardized deviate (dotted line) were considered mast years (as listed in Table 3).

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