Journal of the Torrey Botanical Society 147(3): 222–231, 2020.

Influence of stand age, soil attributes, and cover type on *Rubus* (Rosaceae) seed bank abundance

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Abstract. We assessed *Rubus* seed bank abundance and variability in 39 stands located throughout northern Pennsylvania as part of a replicated chronosequence of age classes. Seed abundance declined precipitously after stand age 60 in the Allegheny hardwoods or after stand age 50 in the northern hardwood and oak forests. Variability among sites increased with stand age, resulting in less predictability of *Rubus* seed abundance. *Rubus* seed banks were more than twice as abundant in Allegheny and northern hardwoods as in mixed oaks. *Rubus* seed bank abundance decreased as percent clay in the soil increased. Given that *Rubus* seed bank abundance declines with age and seed abundance becomes more variable, we suggest that there will be less *Rubus* immediately following the stand-replacing disturbances in older stands, potentially changing plant competition dynamics and wildlife food sources.

Key words: *Rubus*, seed bank, seed longevity, temperate forests

Blackberries and raspberries (hereafter referred to as *Rubus*) have long been recognized as one of the most common genera that dominate forest understories after significant canopy disturbance regardless of their abundance in the undisturbed forest community (Olmsted and Curtis 1947). In early successional communities, the rapid establishment of dense *Rubus* cover imparts multiple benefits to the forest ecosystem (Donoso and Nyland 2006). For example, given the high mobility of nitrate in soils, *Rubus* serves an important ecological role of retaining nitrogen on-site (Bormann and Likens 1979; Whitney 1982; Truax *et al*. 1994; Lautenschlager 1999). This role may be increasingly important given that nitrate and nitrite inputs to northeastern forests have declined in the two decades since the Clean Air Act amendments (Li *et al*. 2016; Lloret and Valiela 2016). In addition, *Rubus* thickets provide an important source of browse and soft mast for wildlife utilizing early successional communities. Indeed, Greenberg *et al*. (2007, 2012) estimated that *Rubus allegheniensis* thickets can produce 4–10 kg/ha of dry pulp per year with birds consuming over 70% of the fruit in some landscapes (McCarty *et al*. 2002). *Rubus* cover also tempers the microclimatic conditions (*e.g*., light, temperature) found in disturbed forests, thereby promoting tree regeneration (Boring *et al*. 1981; Adams *et al*. 1991; Balisky and Burton 1993). Hay-scented fern (*Dennstaedtia punctilobula* (Michx.) T. Moore) covers an estimated 33-60 percent of Pennsylvania's forest understories as a result of deer preferentially browsing the shrubs that naturally compete with it (McWilliams *et al*. 1995; Royo and Carson 2006). *Rubus* can reduce the abundance of hay-scented fern, which interferes with tree regeneration by growing above it and eventually displacing it by shading (Marquis and Grisez 1978; Horsley and Marquis 1983; de la Cretaz and Kelty 2002). Hay-scented fern interference problems are typically controlled using broadcast herbicides because other means of control are not effective (Horsley 1988, 1991; Ristau *et al*. 2011). More *Rubus* in the forest understory could substantially reduce the total land area where herbicide is required to control interfering ferns.

Following a canopy disturbance (*e.g*., harvesting or windthrow), *Rubus* seedlings emerge from a persistent seed bank, expand coverage through layering and other vegetative means, and form new independent plants (Whitney 1982). Viable seeds stored in forest soils will germinate when cues such as increased temperature, increased light quantity and quality (*e.g*., ratio of red to far-red), and nutrient flux (increased nitrate nitrogen) occur following a disturbance (Leck *et al*. 1989). The dependability of the seed bank as a source of new *Rubus* germinants, however, is variable because the abundance and distribution of buried seeds varies with stand age. For example, Graber and Thompson (1978) found that in forests of New Hampshire, *Rubus* seed bank density progressively declined from 1,047, 452, 89, and 12 seeds·m^{-2} in

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doi 10.3159/TORREY-D-17-00015.1

Received for publication March 28, 2017, and in revised form March 6, 2020; first published November 18, 2020.

stands aged 5, 38, 95, and > 200, respectively. Data from northern hardwood old growth forests in Michigan and Pennsylvania suggest that viable *Rubus* seed storage in soils is minimal (Mladenoff 1990; Peterson and Pickett 1995). Collectively, this evidence suggests that at some point during stand development, the abundance of viable *Rubus* seed declines and reduces the likelihood of its dominating the postdisturbance community. In fact, Peterson and Carson (1996) hypothesized that, over time, diminishing availability of viable seeds would shift regeneration patterns following stand-replacing disturbance from initial dominance by seed-banking species, including *Rubus* and pin cherry (*Prunus pensylvanica* L.), to dominance by wind-dispersed species, such as the birches (*Betula lenta* L. and *B. allegheniensis* Britt.).

In addition to stand age, the composition and abundance of forest seed banks is influenced by several additional factors, including soil properties, forest type, and disturbance history (Pickett and McDonnell 1989; Eyre 1980; Baskin and Baskin 2001). Soil properties such as pH and soil moisture can influence seed bank composition, with more neutral pH typically supporting higher aboveground diversity and therefore higher seed bank species richness and density (Brown and Oosterhuis 1981), and higher soil moisture may result in shorter seed bank persistence due to fungal pathogen development (Wagner and Mitschunas 2008), although increased moisture results in increased plant productivity once seedlings become established (Whitney 1982). *Rubus* is best adapted to fine- to medium-textured soils (USDA NRCS 2019). High white-tailed deer browse pressure can suppress *Rubus* abundance and reproductive output, leading to less replenishment of the seed bank (Marquis and Grisez 1978; Horsley and Marquis 1983; Horsley *et al*. 2003).

Given the potential importance of edaphic factors and prior stand history in altering *Rubus* seed bank availability, even among stands of the same age, any study that compares seed bank densities within and among stand ages should be replicated, and these potential sources of variability in seed bank abundance should be quantified. In fact, *Rubus* seed bank can vary by several orders of magnitude (0 to nearly 5,000 seeds·m^{-2}; Oosting and Humphreys 1940; Olmsted and Curtis 1947; Livingston and Allessio 1968; Leckie *et al*. 2000; Yorks *et al*. 2000; Sullivan and Ellison 2006). However, those studies evaluated stands that vary greatly in forest type, age, and disturbance history, making generalizations about the expected *Rubus* seed abundance across stands varying in age, type, and edaphic conditions impossible. Well-replicated chronosequence data are required to make such generalizations, and these are rare in the literature. We conducted the first rigorous and well-replicated assessment of the seed bank in forest stands focused on *Rubus* abundance.

We used predictions from the literature with regard to time since disturbance and evidence that forest cover type and soil properties can influence the seed bank to formulate objectives. Our main objective was to assess the abundance and variability of *Rubus* seed among stands in a replicated chronosequence of forests in three forest types while also accounting for soil conditions at 39 stands in north-central Pennsylvania. We tested the hypothesis of Peterson and Carson (1996) that the *Rubus* seed bank would decrease in abundance as stand age increased, implicitly reducing the role of *Rubus* in stand recovery after disturbance in older stands. We expected to find higher abundance of *Rubus* in finer-textured, more mesic soils associated with Allegheny hardwoods than in oak forests based on anecdotal field observations. Results of this study have the potential to help improve prediction of stand establishment outcomes following timber harvesting or natural disturbances in these forests.

Methods. Study Sites and Sampling. We used 39 second-growth Allegheny hardwood (*Prunus serotina–Acer saccharum*), mixed oak (*Quercus rubra*, *Q. alba*, *Q. velutina*, *Q. montana*), or northern hardwood (*Fagus–Betula–Acer–Tsuga*) stands in northern and northwestern Pennsylvania, USA, ranging in age from 43 to 120 yr when data were collected in 2008. All stands originated following complete overstory removal after or independent of prior partial harvests. None of the sites were fenced to exclude deer, so they established under varying ambient deer densities. None had a significant stand altering disturbance since establishment. We established a single 0.4-ha rectangular sample plot in each forest stand and embedded a 10 × 10-m grid within it (Fig. 1). We measured all trees ≥ 2.5 cm diameter at breast height using a 0.24-ha interior sample plot to quantify overstory composition and relative density as a measure of canopy crowding (Roach and Gingrich 1968; Stout and Nyland 1986). Overstory

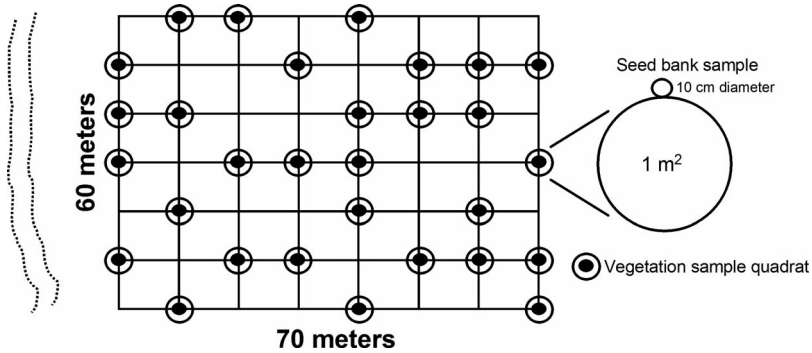

FIG. 1. Sampling grid layout within a 0.4-ha plot. Thirty intersection points were selected randomly from 56 possible points and used as centers of circular 1-m^2 quadrats for estimating percent cover by species. Seed bank samples were obtained using a 10-cm-diameter sample adjacent to the vegetation quadrat.

composition was a mix of *Acer rubrum* L., *Acer saccharum* Marsh., *Betula allegheniensis* Britt., *B. lenta* L., *Fagus grandifolia* Ehrh., *Magnolia acuminata* (L.) L., *Prunus serotina* Ehrh., *Quercus alba* L., *Q. coccinea* Muench., *Q. montana* L., *Q. rubra* L., and *Q. velutina* Lam. with some various minor species.

We established 30 1-m^2 circular quadrats at intersection points of gridlines randomly selected from a total of 56 possible center points to assess aboveground *Rubus* coverage by species (later combined as *Rubus* spp.) (Fig. 1). Seed bank samples were taken using a 5-cm-deep, 10-cm-diameter PVC corer at the outside edge of each of the 30 quadrats. To obtain a standwide estimate of *Rubus* seed bank density, the 30 cores from within a site were bulked and thoroughly mixed, and six 405-cm^3 subsamples per site were used to estimate seed bank composition by the seedling emergence method (Roberts 1981). Each subsample provided a standwide estimate due to the mixing of soil from 30 locations within the stand. Within-site variability was not of interest in this work and was assumed to be high (Plue and Hermy 2012). Each subsample was placed in a 25 × 25-cm square tray with approximately 2.54 cm of sterile sand covering the bottom. Soil trays were watered after installation and then watered daily in the morning. We identified all germinants to species as they emerged, counted them, and removed them from trays until no new emergents appeared. This germination period was followed by a 90-day cold stratification period at 4 °C. Afterward, the emergence methods were repeated. For ease of interpretation and applicability, we expressed *Rubus* seed bank densities as seeds·m^{-2}. We did not count ungerminated seeds, only those that germinated and emerged.

At each site, we excavated a soil pit in the center of the 0.4-ha sample plot to a depth of up to 60 cm or an impermeable layer if present. We recorded horizon depths, depths to mottling or impermeable layer if present, and percent coarse fragments in each horizon. Soil from the combined Oa and A (Oa/A) and upper B horizons were collected, dried, and sieved to 2 mm. We determined soil texture using the hydrometer method (Bouyoucos 1951) and percent organic matter using loss on ignition in a muffle furnace (Allison 1965). We estimated percent soil moisture available to plants using the soil water characteristics model based on texture, percent organic matter, and coarse fragments (Saxton and Rawls 2006). For site characteristics, see Table 1. All soil variables, seed bank abundance estimates, and aboveground vegetation measures were collected at the site level with comparisons among age classes coming from replicates within a class.

STATISTICAL ANALYSES. For all analyses, we categorized stands into 10-yr age classes (*i.e.*, 40–49, 50–59, 60–69, 70–79, 80–89, 90–99, and 100+), thereby providing replication within a 10-yr age class chronosequence and allowing for estimates of variability. We used multiple regression and the stepwise parameter selection technique in PROC GLMSELECT with the Schwarz Bayesian select criterion and CHOOSE=AICc criterion (SAS Institute Inc. 2014) to identify which variables best predicted *Rubus* density in the seed bank. We included stand age class, forest type, pH, texture (percent clay), percent organic matter, percent coarse fragments, stand relative density

Table 1. Stand vegetation, soils, and *Rubus* seed bank data for 39 stands ordered by forest type and age.

Age class	County stand ID	Latitude (N)	Longitude (W)	Forest type[a]	Relative density	Available moisture (%)	Soil pH	Sand (%)	Silt (%)	Clay (%)	Organic matter (%)	*Rubus* cover (%)	*Rubus* seeds ($\cdot m^{-2}$)
40–49	Tioga 2	41.61083	−77.2175	AH	114	7.92	4.27	77	5	18	3.79	0.25	1336
40–49	Tioga 3	41.60944	−77.2169	AH	96	6.62	4.58	79	3	18	3.07	0.00	349
50–59	Tioga 4	41.60833	−77.2139	AH	93	6.62	4.50	77	5	18	2.48	0.00	1042
50–59	Tioga 5	41.74139	−79.0903	AH	91	7.84	4.46	71	5	24	2.62	0.08	870
50–59	Tioga 6	41.69611	−77.1025	AH	92	6.81	4.43	77	3	20	1.83	0.00	3022
50–59	Tioga 7	41.59611	−78.7436	AH	99	8.51	4.57	67	5	27	3.29	0.00	767
50–59	Tioga 8	41.51083	−79.1525	AH	93	7.92	4.48	69	7	23	3.09	0.19	2227
60–69	Venango 3	41.70528	−77.1106	AH	111	10.14	4.40	53	13	33	3.79	1.18	55
70–79	Elk 5	41.29389	−79.8764	AH	58	8.04	4.58	71	3	26	2.55	0.70	260
70–79	Tioga 9	41.34000	−78.4386	AH	91	6.62	4.48	77	5	18	4.40	3.11	411
70–79	Tioga 10	41.94750	−77.9644	AH	84	5.32	4.31	83	5	11	3.65	4.16	1521
70–79	Tioga 11	41.70583	−77.1050	AH	83	6.41	3.94	67	5	27	2.45	3.96	226
80–89	Warren 2	41.29361	−79.8622	AH	99	8.21	4.55	67	11	22	3.92	0.00	0
80–89	Tioga 12	41.68417	−79.2675	AH	68	8.52	4.30	67	5	27	3.02	0.00	103
90–99	Forest 1	41.70472	−77.1053	AH	115	7.92	4.62	69	7	23	4.07	1.34	158
90–99	Elk 6	41.29222	−79.8672	AH	96	8.90	4.55	65	7	28	2.38	1.00	55
40–49	Tioga 1	41.34667	−78.4433	NH	101	8.52	4.56	69	7	23	2.97	1.03	1350
50–59	Venango 2	41.34000	−78.4450	NH	112	12.12	4.45	47	13	39	3.98	2.57	212
60–69	Elk 2	41.34028	−78.4481	NH	105	10.42	4.29	55	13	31	3.62	0.04	41
90–99	Potter 1	41.32056	−78.9792	NH	77	6.48	4.65	77	5	17	4.27	0.00	452
90–99	Tioga 13	41.31528	−78.9775	NH	108	8.06	4.62	69	7	24	2.13	2.55	137
90–99	Venango 7	41.31722	−78.9778	NH	84	10.84	4.66	65	7	27	2.38	2.54	185
100+	Tioga 14	41.73833	−79.2697	NH	95	7.93	4.24	69	7	23	2.09	0.08	185
100+	Warren 3	41.26639	−79.8608	NH	97	6.22	4.51	79	5	16	2.25	0.14	55
40–49	Venango 1	41.28139	−79.8506	Oak	85	9.32	4.51	57	13	30	2.67	24.18	432
60–69	Elk 1	41.26861	−79.8672	Oak	96	11.07	4.34	49	23	27	2.79	0.03	0
60–69	Elk 3	41.31806	−78.9803	Oak	104	10.00	4.38	57	13	29	5.06	0.00	212
60–69	Elk 4	41.32667	−78.9881	Oak	70	8.19	4.42	67	9	23	4.34	0.00	48
70–79	Jefferson 1	41.28528	−79.8592	Oak	88	11.40	4.32	77	9	14	1.38	0.04	55
70–79	Jefferson 2	41.32583	−78.9872	Oak	79	13.13	3.96	43	27	30	3.49	0.00	34
70–79	Jefferson 3	41.61083	−77.2175	Oak	76	6.33	4.17	47	27	26	2.61	0.04	151
70–79	Warren 1	41.60944	−77.2169	Oak	106	8.33	4.61	67	9	24	3.17	0.00	55
80–89	Venango 4	41.60833	−77.2139	Oak	87	9.16	4.54	63	9	28	2.66	0.00	110
80–89	Venango 5	41.74139	−79.0903	Oak	129	10.99	4.39	53	11	35	3.24	0.00	82
80–89	Venango 6	41.69611	−77.1025	Oak	71	9.71	4.52	59	11	29	3.39	0.17	27
80–89	Jefferson 4	41.59611	−78.7436	Oak	87	12.10	4.18	37	27	36	3.57	0.00	21
90–99	Venango 8	41.51083	−79.1525	Oak	111	8.75	4.44	61	13	26	1.84	0.00	75
90–99	Jefferson 5	41.70528	−77.1106	Oak	121	8.62	4.36	65	11	24	2.39	0.00	16
100+	Jefferson 6	41.29389	−79.8764	Oak	102	5.84	4.60	81	5	14	1.73	0.00	7

[a] AH = Allegheny hardwood; NH = northern hardwood; Oak = mixed oak.

(*sensu* Stout and Nyland 1986), and moisture availability as potential site predictors. Following initial variable selection, we tested for differences in *Rubus* density per m^2 using mixed-model analysis of covariance (PROC GLIMMIX) (SAS Institute Inc. 2014). Age class and forest type were modeled as fixed factors and percent clay as a continuous covariate. *Rubus* seed bank density was modeled using a gamma distribution because data were overdispersed and right skewed. All analyses were conducted using SAS 9.4 (SAS Institute Inc. 2014). P-values of < 0.05 were considered significant, while values from 0.05 to 0.1 were considered marginally significant for main effects and values up to 0.2 considered interesting for interactions (Stehman and Meredith 1995).

Results. Across forest types and stand ages included in this study, we identified six *Rubus* species in our seed bank emergence study: *R. allegheniensis* Porter, *R. flagellaris* Willd., *R. hispidus* L., *R. idaeus* L., *R. occidentalis* L., and *R. odoratus* L. Of *Rubus* species, 97.6% of the emergents were *R. allegheniensis*. For this reason, we conducted all analyses on total *Rubus* abundance combined. Within our sample stands, aboveground *Rubus* coverage (also mostly *R.*

Table 2. Stepwise regression predictors to model *Rubus* spp. seed bank density. Step refers to the order of inclusion in the model selection, and values in bold represent the predictor variables that maximize goodness of fit using the fewest predictors as assessed by the Akaike information criterion (AICc). Means and ranges for predictors are presented.

			Rubus spp. seed abundance		
Predictors	Mean	Range	Step	R^2 adj.	AICc
Stand age	74	43–106	**1**	**0.27**	**247.99**
Percent clay (%)	8.61	5.32–13.13	**2**	**0.39**	**242.29**
Forest type	—	Northern hardwood, Allegheny hardwood, mixed oak	**3**	**0.46**	**239.49**

allegheniensis) ranged from 0% to 24%, with most stands having less than 5% cover (Table 1).

Age, forest type, and percent clay were identified by multiple regression as significant predictors of *Rubus* abundance, and these three predictors explained 46% of the variability in *Rubus* seed density (Table 2). An analysis of covariance revealed that *Rubus* seed bank density was related to both stand age class and marginally to forest type (Table 3). Seed abundance declined with increasing stand age and ranged from 0 to 3,022 seeds·m^{-2}. Seed abundance was greatest in Allegheny hardwood forest types and lowest in the oak types (Fig. 2A–C). Seed abundance declined precipitously rather than gradually after stand age 60 in the Allegheny hardwoods or after stand age 50 in the northern hardwood and oak forests (Fig. 2). There was a spike in average abundance at age 70 in the Allegheny hardwoods stands driven by one stand with abundant viable *Rubus* seed.

Within any given age class, there was considerable among-stand variability in the amount of seed present, with estimates often differing by ≥ 1 order of magnitude (Table 1). Despite the sharp decrease in *Rubus* seed numbers for stands older than age 60, one 90-yr-old northern hardwood stand had 452 seeds·m^{-2} (Table 1; Fig. 2).

Discussion. Persistent seed-banking species such as *Rubus* are typically most abundant within the first decade after heavy overstory disturbance (Whitney 1978; Bicknell 1979), but some plants are present throughout later stages of stand development in gaps and in small patches having favorable light levels and soil conditions (Bicknell 1979). Like those two studies, most of the seeds in our forests were likely deposited up to 60–70 yr earlier and began losing viability over time (Marks 1974; Truax *et al*. 1994; Lautenschlager 1999).

Table 3. Mixed-model analysis of covariance results of the effect of predictor variables on *Rubus* spp. seed density in soils as calculated by seedling emergence trials. Values in bold are significant at $p \leq 0.1$.

	Rubus spp. seed density	
Predictors	*F* value	*P* value
Forest type	$F_{2,21} = 3.04$	**0.069**
Stand age class	$F_{6,\ 21} = 3.54$	**0.014**
Percent clay	$F_{1,\ 21} = 0.10$	0.755
Forest type × age	$F_{8,\ 21} = 1.00$	0.467

Our data showed a dramatic *Rubus* seed bank decline after age 50–60 in our replicated age class chronosequence. We observed a *Rubus* seed bank abundance peak at age 40–49 in all but Allegheny hardwoods, a timing similar to that shown elsewhere (15–35 yr) (Bicknell 1979; Tierney and Fahey 1998). Other studies found declines in stored *Rubus* seeds after approximately 50 yr (Marks 1974; Bormann and Likens 1979; Whitney 1982; Truax *et al*. 1994; Lautenschlager 1999; Donoso and Nyland 2006). Large-scale disturbances are rare in forests prior to stand maturity, with management activities limited to precommercial thinning and crop tree release in the years up to age 50 and commercial thinning from age 50 to maturity (Nyland 2002). The lack of light in the forest understory during this period prevents input of additional seed produced within the stand. We observed a spike in average seed bank abundance at age 70 for Allegheny hardwoods driven by one stand, which may have been due some undocumented non–stand-replacing disturbance, such as defoliation or mortality events triggering a *Rubus* response earlier that resulted in some seed bank replenishment. Gaps from individual tree mortality would be similar to the steady-state or old-growth stage, where soils within canopy gaps (higher light levels and soil disturbance) often have more abundant viable seed than adjacent areas (Oosting and Humphreys 1940; Marquis 1975b; Mladenoff 1990). We found less *Rubus* seed in oak stands than beneath Allegheny or northern hardwoods.

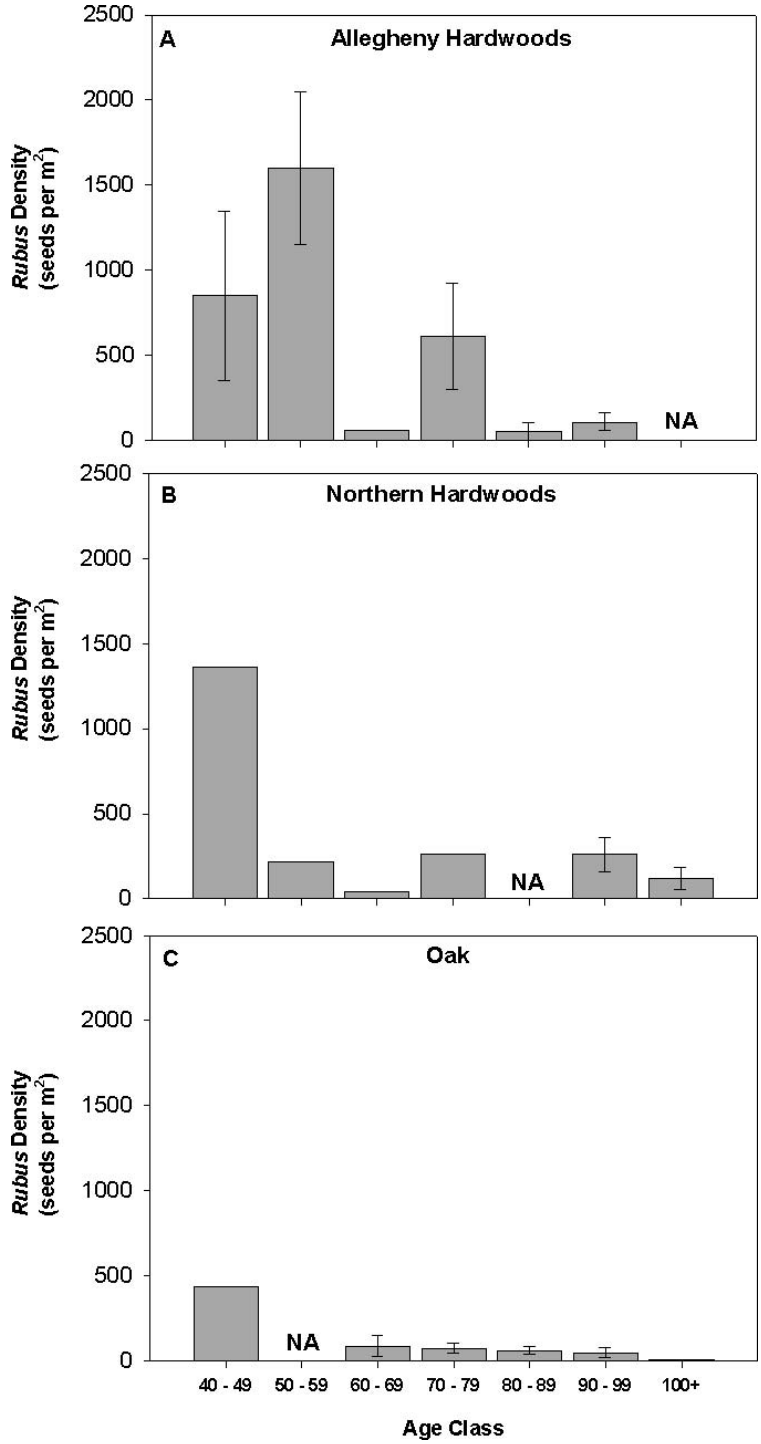

FIG. 2. Mean *Rubus* spp. (± 1 SE) seed bank densities as estimated by greenhouse emergence trials for stands within different age classes in (A) Allegheny hardwood, (B) northern hardwood, and (C) oak forests. Counts are expressed as seeds·m^{-2}. Estimates with an *N* of 1 do not have an error bar, and categories without any representative stands are labeled NA.

Moreover, we found that stands with a clay texture (higher plant available moisture) had less *Rubus* across all forest types (Table 2), suggesting that there may be both dry and wet thresholds that limit *Rubus* development and its persistence in the seed bank. Our oak stands had higher plant-available moisture levels than the Allegheny and northern hardwoods stands based on the texture-driven soil water characteristics model we used. This was somewhat surprising given that oak stands typically occur on more xeric sites than characterize northern hardwood forests (Braun 1964; Eyre 1980). Presence of more sandy and thus more well-drained soils in our Allegheny and northern hardwood stands may be the reason for this difference. In the lake states, geographic location as well as soil drainage negatively affected tree regeneration on poorly drained, very dry, or shallow soil, but *Rubus* persisted on all sites with its greatest abundance on poorly drained soils (Metzger and Tubbs 1971; Godman and Tubbs 1973).

Rubus seedlings can grow through and eventually will displace dense shade-producing species, such as hay-scented fern, by intercepting light above the fern canopy and casting their own shade (Marquis and Grisez 1978; Horsley and Marquis 1983; de la Cretaz and Kelty 2002). Some land managers have wondered if a longer waiting period following a partial cut might result in less fern without a need for herbicide use since seedlings typically grow through *Rubus* unless it is extraordinarily dense (Horsley 1991). It is unknown how many seeds and what distribution of seeds within a stand is required for there to be enough *Rubus* to grow through and displace ferns, but the phenomenon has been observed in the field (Horsley and Marquis 1983). Our data show that the high variability in *Rubus* seed bank abundance makes generalizations about expected outcomes difficult, though older stands and oak forests are less likely to have abundant *Rubus*. This might reflect factors related to erratic seed bank replenishment during early stand development due to the variation in the distribution and abundance of seed-bearing *Rubus* individuals as well as herbivory on those individuals (Harper 1980; Hulme 1996, 1998). Additional research, perhaps using experimental additions of varying numbers of *Rubus* canes in a fern field, is needed to determine how much *Rubus* is needed to displace ferns and how long the process takes.

In addition to its potential as a natural control of dense species such as the ferns, *Rubus* functionally acts to hold nitrogen on-site by its rapid vegetative reproduction (Bormann and Likens 1979; Whitney 1982; Truax *et al*. 1994; Lautenschlager 1999). Reduced *Rubus* seed in older stands may result in increased loss of nitrogen on a given site following harvests or other disturbances. A reduced *Rubus* seed bank response has important wildlife consequences in early successional stands where the wildlife species consume large quantities of fruit (McCarty *et al*. 2002; Greenberg *et al*. 2007, 2012).

Historic browsing by white-tailed deer in Pennsylvania (Marquis 1975a; Redding 1987) along with the fact that most forests are of a similar and older age makes the Peterson and Carson (1996) hypothesis even more dramatic because seed banks have already been limited by past browsing. Our data support their hypothesized decline of early successional species such as *Rubus* across the forest types we studied, making it more likely that the next disturbance will result in a smaller seed bank response than the large *Rubus* establishments typically observed following large-scale disturbances, often in excess of 1,000 seeds·m^{-2} (Olmsted and Curtis 1947; Graber and Thompson 1978). Also, in support of the second part of Peterson and Carson (1996), we have observed an increased regeneration response of more intermediate species such as the birches and red maple with the lowered number of pioneer propagules following disturbances, including harvests (Albright *et al*. 2017).

Conclusions. The abundance of *Rubus* seeds in north-central Pennsylvania forests was related to stand age, soil texture or moisture, and forest cover type. *Rubus* seedling establishment is more likely when a disturbance reduces overstory relative density to $\leq$ 60% (Barrett 1962; Nyland 2002), and our data show that seed bank abundance diminishes greatly and becomes more variable in its distribution as stands age. Hence, land managers cannot rely on *Rubus* establishment and development as an alternative for controlling ferns in second-growth stands, especially under high deer impact. Browsing in the stand establishment phase reduces abundance of reproductive *Rubus* and prevents a rebuilding of the seed bank (Horsley *et al*. 2003). Implications for reduced seed bank abundance in older stands include

potential nitrogen loss, reduced wildlife food, and reduced competition with recalcitrant fern understories. Most forest management practices occur in older stands when the *Rubus* seed bank is reduced, so if *Rubus* were used as a means to displace fern, preplanning that includes intermediate treatments, such as thinning at age 50 to levels that would replenish the seed bank, would be required, as would controlling deer impact. Reduced seed bank abundance of early successional species favors intermediate shade-tolerant species such as birches and red maple and supports the hypothesis of Peterson and Carson (1996) that the next forest will be dominated by birch and red maple.

Acknowledgments. This work was supported by a grant from the Pennsylvania DCNR Bureau of Forestry Grant and the USDA Forest Service Northern Research Station. We thank Mary Ann Fajvan, James Finley, Robert Long, Ralph Nyland, Scott Stoleson, Susan Stout, and three anonymous reviewers for assistance that greatly improved this manuscript.

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