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Characterization and ecological significance of a seed bank from the Upper Pennsylvanian Wise Formation, southwest Virginia

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ABSTRACT. Soil seed banks are important to the maintenance and restoration of floras. Extant seed banks exhibit unique characteristics with regard to the distribution of seed size and seed density. Seeds were recovered from the Upper Pennsylvanian Wise Formation in southwest Virginia. Structurally preserved seeds were also examined from coal balls of the Pennsylvanian Pottsville and Allegheny Groups, Ohio. The size distribution of the seeds from the Wise Formation is similar to that of structurally preserved seeds of the Upper Pennsylvanian Pottsville and Allegheny Group coal balls. In contrast, the seed size distributions in extant wetland, grassland, woodland and forest habitats are significantly narrower than that of seeds from the Pennsylvanian seed banks. Larger seeds are less dependent on light for germination, and aid in seedling establishment more than smaller seeds, especially in dense stable forests where disturbance events are rare. Large seed size may contribute to increased seed longevity, which reduces the effect of environmental variability on seed germination and development. The significantly larger size of the Palaeozoic seeds may have imparted an advantage for seedling establishment in the dense Palaeozoic forests. The preponderance of large seeds may be a result of the absence of large seed predators (e.g. herbivorous tetrapods), and may have been an evolutionary strategy to minimize damage to the embryo from a predator population dominated by small invertebrates with chewing or sucking mouthparts.

The estimated seed density of 192 seeds/m^2 in the Palaeozoic seed bank falls within the range of modern seed banks, but at the lower end of modern seed bank densities in a variety of habitats.

KEYWORDS: Seed bank, Pennsylvanian, ecological significance, seed size, seed density

INTRODUCTION

A soil seed bank represents a reservoir of viable seeds derived from the surrounding flora, with the potential to restore the flora in a disturbance event or to replace aging members of the population (Darwin 1859, Thompson 1987, Baskin & Baskin 1998, Hopfensperger 2007, Saatkamp et al. 2014). Many processes serve to bury seeds in plant communities; for example, soil drying, cracking, soil freezing/thawing and animal activities contribute to seed burial and the establishment of a soil seed bank (Benvenuti 2007a, b). Seeds act as diaspores and can remain viable for long periods of time in the soil (Baskin & Baskin 1998).

The origin of the seed was a major evolutionary event in plants. Seeds are first recognized in the fossil record in the late Devonian (Rothwell & Scheckler 1988). Seed-bearing plants of the Palaeozoic include the Medullosaleans, Lyginopteridaleans, Callistophytaleans, conifers, cycads and gymnosperms, and subsequently the ginkgos, cycadeoids and angiosperms in

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the Mesozoic. These taxa have seeds that vary in size, shape, seed coat thickness and accessory structures such as wings, parachutes and internal air channels that aid in seed dispersal. Angiosperm seeds are often shed within a fruit, which can exhibit a wide range of accessory structures for abiotic or biotic dispersal that fall well outside of the morphological diversity of seeds in the Palaeozoic. Even though Palaeozoic seeds have been studied (Arnold 1938, Harper et al. 1970), basic aspects of the seed banks (species composition, seed size distribution, seed density) associated with Carboniferous habitats are not well known due to low sample size.

A significant number of seeds from a single lithological unit in the Upper Pennsylvanian Wise Formation in southwest Virginia were collected over a 1–2 day period during a mountaintop mining operation. The purpose of this study was to determine the characteristics of an Upper Pennsylvanian (Palaeozoic) seed bank and to compare them with extant seed banks, in order to better understand the carboniferous plant communities.

MATERIALS AND METHODS

GEOLOGY

Economically important coal deposits occur in three areas in Virginia: the Triassic Richmond and Farmville basins, the Mississippian Valley coal field, and the Pennsylvanian southwest Virginia coal field (Eby et al. 1923). The southwest Virginia coal field is the source of all current coal production in Virginia, and ranges in type from high- to low-volatile bituminous coal. The coal-bearing strata are generally horizontal to gently dipping. The Pennsylvanian Formations in the southwest coal field are, in ascending geological order, the Pocahontas Formation/Lee Formation, Norton Formation, Wise Formation and Harlan Formation. These formations are comprised of sequences of non-marine coal, sandstone, siltstone and shale, and are occasionally intercalated with thin clastic calcareous sediments of marine origin. The fossil seeds used in this study are from the Upper Pennsylvanian Wise Formation. The seeds were collected over a 1–2 day period during a mountaintop mining operation at the A & G Coal Corporation, Black Mountain, Virginia, by Mr. B. Tussing of Wise, Virginia. A total of 77 seeds were extracted from the matrix, cleaned and labeled, and a number of seeds were examined *in situ*.

The Pennsylvanian sediments in Ohio belong to the Pennsylvanian Pottsville and Allegheny Groups. These sediments are comprised of sandstone, limestone, shale and coals, and are of both terrestrial and marine origin. Coal balls collected from these sediments in southeastern Ohio were cut, polished, etched in HCl and peeled in order to examine the structurally preserved seeds microscopically. Processing and identification of the structurally preserved seeds were done in the lab of Thomas N. Taylor, University of Kansas, Lawrence, Kansas, and the coal balls are deposited in the palaeobotanical collections at the University of Kansas. A total of ten seeds were investigated from the coal ball peels (Tab. 2).

The seed-bearing sediments from the Wise Formation represent an *in situ* seed bank, based on these observations: the sediments are unsorted, the seeds are randomly oriented, and the range of seed size is highly variable and comparable to the range of sizes observed in the autochthonous assemblage of seeds from the Pennsylvanian coal balls of southeastern Ohio.

MODERN SEED WEIGHT MEASUREMENTS

Tiffney (1984) calculated the volume of angiosperm seeds using the ellipsoidal-ovoid volume estimation formula ($V = 4/3\pi abc$, where a is seed length, b is seed width, c is seed breadth) (see also Erickson et al. 2000, Sims 2012). Tiffney (1984) tested the assumption that volume and weight are related in seeds using 52 angiosperm taxa, and found a log-linear relationship between seed volume and seed weight. In this study we examined seeds of 62 gymnosperm species from eight families from a wide range of habitats (Tab. 1). The seeds were obtained from the West Virginia University Herbarium (WVU) in Morgantown, WV; Montgomery Botanical Center, Coral Gables, FL; Huntington Botanical Gardens, San Marino, CA; the USDA; and the US National Herbarium at the Smithsonian Institution, Washington, DC. Seed weight was measured using a Toledo scale to 0.00001 g accuracy. A minimum of 10 and a maximum of 100 seeds per species were weighed, and the dry weight of the seeds was recorded (Tab. 1). For seeds of each species we recorded the length (mm), width (mm), breadth (mm), sphericity index, volume (mm^3) and weight measurements (Tab. 1). The sphericity index of the seeds was determined according to Mohsenin (1986), who expressed the degree of sphericity as follows:

$$\Phi = (ABC)^{0.333}) / A \times 100$$

where Φ represents the sphericity index, A is seed length, B is seed width, and C is seed breadth.

All seeds from the species examined having a sphericity index above 50% were regarded as spherical, and the ellipsoidal-ovoid volume method could then be applied.

FOSSIL SEED MEASUREMENTS

The fossil seed length (A), width (B) and breadth (C) were measured using a digital caliper to 0.1 mm accuracy. Sphericity was calculated according to Mohsenin (1986). Volume (V) was estimated using the ellipsoid-ovoid volume estimation formula (Tiffney 1984, Eriksson et al. 2000, Sims 2012). Tiffney (1984) documented a log-linear relationship between the volume (mm^3) and dry weight (grams) of modern angiosperm seeds ($n = 52$ species, $R^2 = 0.928$). We assessed this relationship in modern gymnosperms in this study. The linear

Table 1. Gymnosperm species examined in this study to determine if seed volume is correlated with seed weight

Gymnosperm Species	Average Length (mm)	Average Width (mm)	Average Breadth (mm)	Sphericity Index	Volume (mm^3)	Volume (mm^3) Log	Average Weight (g)	Weight (g) Log
Abies balsamea	5.048	2.691	1.712	56.486	97.366	1.988	0.008	–2.097
Abies bornmuelleriana	11.583	5.109	3.114	49.044	771.514	2.887	0.073	–1.137
Abies eraseri	5.045	2.553	1.427	52.259	76.949	1.886	0.007	–2.155
Abies fraseri	5.116	2.818	1.856	58.400	112.026	2.049	0.007	–2.155
Abies grandis	9.004	3.829	2.234	47.185	322.457	2.508	0.027	–1.569
Abies homolepis	6.436	3.047	1.910	51.924	156.816	2.195	0.021	–1.678
Abies nordmanniana	11.552	5.124	3.040	48.787	753.370	2.877	0.083	–1.081
Araucaria araucana	3.026	2.628	1.850	80.903	61.593	1.790	0.003	–2.523
Cedrus deodara	14.896	6.061	3.163	44.125	1195.588	3.078	0.097	–1.013
Chamaecyparis sp.	4.939	2.337	1.947	57.078	94.088	1.974	0.003	–2.523
Chamaecyparis thyoides	2.367	1.936	0.945	68.828	18.130	1.258	0.001	–3.000
Cupressus arizonica	4.697	3.520	1.621	63.643	112.206	2.050	0.009	–2.046
Dioon spinulosum	49.555	30.003	27.549	69.315	171485.098	5.234	13.630	1.134
Encephalartos ferox	28.253	15.794	13.628	64.417	25459.930	4.406	4.262	0.630
Epedra viridis	6.621	2.980	1.571	47.390	129.773	2.113	0.005	–2.301
Ephedra antisyphilitica	6.308	3.566	1.780	54.167	167.634	2.224	0.008	–2.097
Ephedra nevadensis	6.814	3.170	2.496	55.368	225.722	2.354	0.008	–2.097
Ephedra trifurca	9.025	2.495	2.215	40.733	208.814	2.320	0.002	–2.699
Ginkgo biloba	20.461	17.027	13.434	81.522	19594.705	4.292	1.594	0.202
Juniperis virginiana	3.574	2.221	1.807	67.922	60.052	1.779	0.007	–2.155
Juniperus ashei	5.404	3.898	2.793	71.874	246.318	2.391	0.038	–1.420
Juniperus communis	4.353	2.389	1.944	62.519	84.639	1.928	0.008	–2.097
Juniperus occidentalis	5.919	4.013	2.941	69.482	292.470	2.466	0.035	–1.456
Juniperus pinchotii	5.427	3.976	3.291	76.196	297.305	2.473	0.031	–1.509
Juniperus scopulorum	4.053	3.173	2.515	78.520	135.411	2.132	0.017	–1.770
Junperus osteosperma	6.153	4.711	4.141	80.043	502.543	2.701	0.070	–1.155
Kousa × balsam fir	5.116	2.797	1.487	54.109	89.085	1.950	0.009	–2.046
Larix kaempferi	4.584	2.530	1.650	58.292	80.116	1.904	0.005	–2.301
Picea abies	4.625	2.238	1.702	56.206	73.756	1.868	0.010	–2.000
Picea engelmannii	3.159	1.710	1.182	58.691	26.732	1.427	0.003	–2.523
Picea glauca	3.088	1.796	1.394	63.990	32.368	1.510	0.003	–2.523
Picea mariana	2.581	1.697	0.875	60.605	16.045	1.205	0.001	–3.000
Picea meyeri	4.104	2.134	1.434	56.590	52.580	1.721	0.006	–2.222
Picea pungens	3.902	1.917	1.375	55.690	43.061	1.634	0.004	–2.398
Picea ruben	3.474	1.867	1.495	61.336	40.596	1.608	0.004	–2.398
Pinus albicaulis	8.918	5.376	4.812	68.648	965.875	2.985	0.034	–1.469
Pinus banksiana	3.831	1.945	1.093	52.481	34.097	1.533	0.004	–2.398
Pinus cembroides	11.269	7.310	6.311	71.205	2176.553	3.338	0.164	–0.785
Pinus clausa	4.854	2.771	1.934	60.976	108.908	2.037	0.011	–1.959
Pinus echinata	4.491	2.704	1.897	63.291	96.446	1.984	0.008	–2.097
Pinus elliottii	6.060	3.729	2.839	65.968	268.596	2.429	0.029	–1.538
Pinus flexilis	7.891	5.374	3.405	66.374	604.526	2.781	0.085	–1.071
Pinus palustris	15.828	6.591	3.694	45.885	1613.402	3.208	0.084	–1.076
Pinus ponderosa	5.798	3.916	2.803	68.765	266.448	2.426	0.033	–1.481
Pinus resinosa	4.213	2.558	1.712	62.659	77.244	1.888	0.008	–2.097
Pinus rigida	4.671	2.438	1.504	55.133	71.707	1.856	0.007	–2.155
Pinus strobus	6.419	3.837	1.587	52.806	163.646	2.214	0.025	–1.602
Pinus sylvestris	4.704	2.782	1.504	57.340	82.403	1.916	0.009	–2.046
Pinus taeda	5.401	4.490	3.264	79.381	331.390	2.520	0.025	–1.602
Pinus taeda	5.401	4.490	3.264	79.381	331.390	2.520	0.025	–1.602
Pinus virginiana	4.557	2.704	1.789	61.467	92.292	1.965	0.009	–2.046
Pordocarpus falcastus	12.999	11.646	10.862	90.577	6884.381	3.838	0.725	–0.140
Pordocarpus macrophyllus	9.322	7.005	6.844	81.850	1871.094	3.272	0.259	–0.587
Pseudotsuga menziesii	5.887	3.198	1.713	54.007	135.020	2.130	0.011	–1.959
Pseudotsuga taxifolia	6.365	3.387	2.049	55.467	184.937	2.267	0.012	–1.921
Sequoia sempervirens	4.602	3.651	0.981	55.249	69.007	1.839	0.004	–2.398
Sequois sp.	4.585	3.214	1.011	53.619	62.374	1.795	0.005	–2.301
Taxodium ascendens	13.576	6.429	4.332	53.158	1582.968	3.199	0.088	–1.056
Taxodium distichum	14.627	7.710	4.268	53.468	2015.127	3.304	0.077	–1.114
Taxodium macrosatum	6.332	2.974	2.757	58.838	217.364	2.337	0.007	–2.155
Thuja occidentalis	4.463	1.778	0.449	34.208	14.917	1.174	0.001	–3.000
Tsuga canadensis	3.456	1.611	1.055	52.177	24.592	1.391	0.001	–3.000

Table 2. Estimated weight of fossil seeds, based on the log-linear relationship between seed volume and seed weight. Note: the fossil seeds identified in the table are from coal balls of the Ohio Pennsylvanian Pottsville and Allegheny Groups. Seeds examined from coal ball peels exhibited a size range similar to that of fossil seeds from the Wise Formation. Incomplete data from the coal balls were not included in estimating the weight of the fossil seeds from the Wise Formation

Fossil Seeds	Average Length (mm)	Average Width (mm)	Average Breadth (mm)	Sphericity Index	Volume (mm^3)	Volume (mm^3) Log	Estimated Seed Weight (g)	Estimated Seed Weight (g) Log
1	59.05	46.03	39.81	80.39	452985.88	5.66	41.4925	1.62
2	11.80	7.74	6.79	72.13	2595.24	3.41	0.2134	–0.67
3	19.33	10.49	7.46	59.24	6327.19	3.80	0.5320	–0.27
4	14.77	10.11	3.77	55.80	2356.10	3.37	0.1943	–0.71
5	6.43	4.87	3.08	71.19	402.41	2.60	0.0320	–1.49
6	10.95	6.43	3.84	58.94	1131.94	3.05	0.0918	–1.04
7	11.00	8.36	4.39	67.05	1687.48	3.23	0.1400	–0.85
8	6.64	5.52	1.56	57.95	238.99	2.38	0.0191	–1.72
9	10.70	7.77	3.64	62.63	1266.99	3.10	0.1033	–0.99
10	13.96	9.92	4.43	60.73	2567.14	3.41	0.2134	–0.67
11	12.04	7.63	6.74	70.64	2592.26	3.41	0.2134	–0.67
12	14.64	8.09	7.53	65.60	3730.23	3.57	0.3104	–0.51
13	11.94	7.88	6.68	71.59	2628.56	3.42	0.2185	–0.66
14	8.82	5.48	4.74	69.28	958.63	2.98	0.0780	–1.11
15	32.90	21.89	11.00	60.41	33146.62	4.52	2.8721	0.46
16	38.25	25.32	21.39	71.56	86710.72	4.94	7.6802	0.89
17	32.67	24.80	17.37	73.66	58908.97	4.77	5.1578	0.71
18	34.32	28.68	11.81	65.79	48631.96	4.69	4.2766	0.63
19	39.63	22.92	9.56	51.70	36328.13	4.56	3.1541	0.50
20	31.58	19.71	10.80	59.59	28132.73	4.45	2.4378	0.39
21	32.23	21.46	13.37	64.93	38695.46	4.59	3.3837	0.53
22	35.21	27.10	20.91	76.78	83532.93	4.92	7.3288	0.87
23	35.65	25.38	18.47	71.49	69942.31	4.84	6.0766	0.78
24	31.02	21.79	14.62	68.97	41351.97	4.62	3.6300	0.56
25	28.98	18.69	15.81	70.38	35851.55	4.55	3.0811	0.49
26	24.22	14.11	6.41	53.47	9158.94	3.96	1.2924	–0.11
27	28.34	18.23	14.59	68.98	31541.67	4.50	2.7406	0.44
28	29.01	19.03	11.22	63.13	25928.23	4.41	2.2198	0.35
29	37.84	20.54	12.06	55.54	39212.46	4.59	3.3837	0.53
30	36.47	28.03	15.58	68.77	66658.83	4.82	5.7986	0.76
31	29.05	25.65	17.74	81.12	55315.70	4.74	4.8079	0.68
32	32.04	21.49	13.35	65.17	38469.44	4.59	3.3837	0.53
33	33.86	20.50	15.45	64.92	44888.15	4.65	3.8942	0.59
34	30.75	22.96	11.68	65.50	34496.66	4.54	3.0098	0.48
35	37.81	23.41	10.18	54.87	37724.57	4.58	3.3054	0.52
36	31.39	26.34	12.73	69.60	44066.02	4.64	3.8040	0.58
37	34.02	21.57	13.96	63.65	42881.94	4.63	3.7160	0.57
38	36.48	22.33	15.23	63.26	51917.01	4.72	4.5879	0.66
39	35.75	27.81	12.44	64.49	51780.45	4.71	4.4817	0.65
40	31.70	27.29	11.14	66.92	40315.62	4.61	3.5459	0.55
41	27.09	24.07	19.87	86.42	54232.69	4.73	4.6966	0.67
42	31.89	31.22	18.94	83.18	78913.54	4.90	6.9934	0.84
43	37.86	29.69	15.51	68.27	72969.35	4.86	6.3680	0.80
44	34.09	24.65	15.10	68.19	53095.45	4.73	4.6966	0.67
45	32.80	29.49	13.21	71.05	53486.75	4.73	4.6966	0.67
46	26.59	25.49	10.00	70.95	28356.60	4.45	2.4378	0.39
47	39.07	23.88	18.99	66.51	74152.29	4.87	6.5189	0.81
48	33.29	26.72	12.91	67.56	48061.62	4.68	4.1776	0.62
49	29.97	20.79	15.07	70.18	39292.20	4.59	3.3837	0.53
50	34.39	23.89	13.09	63.99	45009.30	4.65	3.8942	0.59
51	29.72	21.68	14.55	70.73	39249.98	4.59	3.3837	0.53
52	39.92	23.19	12.20	56.02	47274.38	4.67	4.0809	0.61
53	38.42	30.18	13.05	64.17	63340.80	4.80	5.5332	0.74
54	32.86	23.09	11.36	62.21	36085.96	4.56	3.1541	0.50
55	32.36	22.30	14.50	67.37	43782.71	4.64	3.8040	0.58
56	34.09	26.04	18.67	74.55	69387.41	4.84	6.0766	0.78
57	32.83	25.44	15.10	70.67	52772.07	4.72	4.5879	0.66
58	32.74	18.79	18.18	68.09	46804.31	4.67	4.0809	0.61

Table. 2. Continued

Fossil Seeds	Average Length (mm)	Average Width (mm)	Average Breadth (mm)	Sphericity Index	Volume (mm^3)	Volume (mm^3) Log	Estimated Seed Weight (g)	Estimated Seed Weight (g) Log
59	29.61	27.09	16.52	79.66	55442.25	4.74	4.8079	0.68
60	32.29	24.40	20.59	78.14	67901.15	4.83	5.9360	0.77
61	33.30	22.43	10.25	59.00	32030.01	4.51	1.2074	0.08
62	35.22	28.71	13.58	67.78	57471.61	4.76	5.0384	0.70
63	30.81	23.53	14.69	71.18	44554.66	4.65	3.8942	0.59
64	24.45	17.83	12.71	72.16	23191.15	4.37	2.0213	0.31
65	30.61	19.85	13.31	65.37	33850.17	4.53	2.9401	0.47
66	22.54	16.32	14.29	76.92	21996.08	4.34	1.8841	0.28
67	30.13	21.13	12.13	65.41	32312.96	4.51	2.8056	0.45
68	32.67	21.44	19.27	72.65	56509.83	4.75	4.9218	0.69
69	29.64	20.61	9.23	59.88	23606.21	4.37	2.0213	0.31
70	27.37	15.50	13.77	65.61	24443.97	4.39	2.1182	0.33
71	29.97	18.89	13.26	65.13	31408.84	4.50	2.7406	0.44
72	25.29	19.07	12.89	72.49	26011.56	4.42	2.2724	0.36
73	28.33	20.45	12.03	67.22	29172.10	4.46	2.4955	0.40
74	26.03	19.35	10.76	67.30	22685.71	4.36	1.9745	0.30
75	27.45	19.56	11.18	66.02	25131.67	4.40	2.1684	0.34
76	28.74	18.90	16.02	71.35	36404.36	4.56	3.1541	0.50
77	25.61	19.18	11.99	70.30	24635.79	4.39	2.1182	0.33
Pachytesta vera	39.00	29.00	22.44	ND	159712.96	5.20	14.1195	1.15
Pachytesta stewartii	26.00	13.00	8.58	ND	12141.50	4.08	1.0249	0.01
Pachytesta saharasperma	7.00	6.00	3.96	ND	696.33	2.84	0.0562	–1.25
Pachytesta hoskinsii	9.00	6.00	3.96	ND	895.28	2.95	0.0727	–1.14
Pachytesta illinoensis	6.00	3.00	1.98	ND	149.21	2.17	0.0117	–1.93
Pachytesta gigantea	66.00	32.00	21.12	ND	186748.11	5.27	16.6348	1.22
Pachytesta muncii	34.00	27.00	17.82	ND	68488.68	4.84	6.0766	0.78
Conostoma oblongum	3.00	2.00	1.32	ND	33.16	1.52	0.0026	–2.59
Stephanosperma elongatum	2.00	1.00	0.66	ND	5.53	0.74	0.0004	–3.39
Hexapterospermum delevoryii	20.00	15.00	9.90	ND	12434.40	4.09	1.0492	0.02

regression equation $y = 1.0171x + 4.13191$ is solved by substituting the volume (Log) of the fossil seeds for x, giving an estimation of fossil seed weight (Log). The weight in grams was determined by the equation W = 10^X, where X = the weight (Log) and W = weight in grams. Direct weight measurements of fossil seeds are not useful on account of seed permineralization (Tab. 2).

MODERN SEED BANK AND DATA COLLECTION

The published reports of modern seed banks used for comparison in this study are those with known species composition and seed density. Seed weights of species occurring in modern seed banks were compiled from the Royal Botanic Gardens Kew Seed Information Database (SID) (Royal Botanic Gardens Kew 2008). The weight for each species is the reported weight for 1000 seeds. The weight of an individual seed was determined as 1/1000th of the reported weight from the Royal Botanic Gardens SID. Species whose seed weight could not be found were eliminated from this study.

DETERMINATION OF FOSSIL SEED DENSITY

Seed density is reported as the number of seeds per square meter of sediment (Tab. 3). The methods used for determining seed density include the germination method and elutriation method. The elutriation method is a direct method which separates all of the seeds from a soil sample. The germination method gives an estimate of seed density of viable seeds in a known volume of soil, and not of all the seeds present in that volume of soil. We could not determine the Palaeozoic soil area and could not determine the depth of the paleosol from which the sample was taken (seed density decreases with depth). We calculated the number of seeds per meter squared (Gross 1990). The frequency of seeds per square meter of sediment was determined by measuring the displacement of a known volume of water by blocks of sediment that contain seeds. None of the blocks of sediment containing seeds was less than 10 cm in any dimension. The volume of all usable samples with seeds was determined by their displacement of a volume of water (final water level minus initial water level).

Seed density per square meter was determined using the formula:

$$\underset{\text{(seed density)}}{\text{SD}} = \frac{\text{\# of seeds sample 1} + \text{\# of seeds sample 2}}{\text{\# ml displaced by sample 1} + \text{\# ml displaced by sample 2}}$$

Using this formula, the frequency distribution of seeds per square meter of sediment can be extrapolated to determine the seed density in one square meter of soil for the Pennsylvanian seed bank by multiplying the total number of seeds in all fragments by 10,000 centimeters (the number of centimeters in one square meter) divided by the total volume of sediment (1 ml = 1 cubic centimeter). All samples were taken from one sediment type during mountaintop mining operations.

STATISTICAL ANALYSIS

All statistical analyses were run using PAST v. 3.14 (Hammer 1999–2016). The Shapiro-Wilks test was used to determine if the data was normally distributed. To test the assumption of a log-linear relationship between gymnosperm seed volumes (mm^3) and the gymnosperm seed weights (g), the data were transformed to log data, and we used a log-linear regression model ($y = 1.0171x - 4.13191$, $R^2 = 0.9306$).

To determine similarity in seed size distribution and seed density, ANOVA was applied to the Pennsylvanian seed bank and modern seed banks.

RESULTS

A log-linear regression of volume versus weight of seeds of 62 modern gymnosperm species yields $R^2 = 0.9306$ (Tab. 1, Fig. 1), supporting the hypothesis of a log-linear relationship between the volume and weight of gymnosperm seeds (Tiffney 1984). Tiffney (1984) studied the log-linear relationship between the volume and weight of 52 propagules of extant angiosperm species, obtaining $R^2 = 0.928$, similar to the result from our data. The log-linear relationship between volume and weight in gymnosperm seeds provides the basis for estimating the weight of the perminerized fossil seeds, using the regression equation $y = 1.0171x - 4.13191$ (Tab. 2, Fig. 1).

Fossil seeds from the Pennsylvanian Wise Formation of the Black Mountain mine in Virginia have seed sizes ranging from 0.0026 g to 41.49 g (Tab. 2). Of the 87 fossil seeds for which we estimated seed weight, only 18 seeds were estimated to weigh less than 1 g. The fossil seed bank was dominated by seeds estimated to weigh more than 1 g (Tab. 2, Fig. 2). There was a significant difference in seed weight between the extant habitats (wetland, grassland, woodland, forest) and the fossil seed bank assemblage of the Pennsylvanian Wise Formation (ANOVA, F = 94.68, p = 4.529E-65) (Tab. 3, Fig. 2).

The average seed density of modern seed banks ranges from 262 seeds/m^2 to 50,060 seeds/m^2 associated with the woodland habitat (Tab. 3, Fig. 4). Seed density does not significantly differ between seed banks from different habitats (Kruskal Wallis, $p = 0.086$). Palaeozoic seed density had only a single data point represented as an average (Fig. 3). Estimated seed density per square meter was 192 seeds/m^2 in the sediments of the Pennsylvanian Wise Formation from the Black Mountain Mine; this falls within the range of modern seed banks (Tab. 3, Fig. 3).

DISCUSSION

In this study we assessed two characteristics of the Palaeozoic seed bank: seed size (weight) and seed density. Palaeozoic seed size (weight) differed significantly from that of seeds in extant seed banks (Tab. 2, Fig. 2). The wetland, grassland, woodland and forest seed banks are dominated by small seeds (<1 g) (Tab. 3, Fig. 3) and the fossil habitat was dominated by seeds approximately 1000 times heavier (>1 g) (Fig. 2). Fossil seed density was at the low end of seed densities observed in extant seed banks but did not differ significantly (Fig. 3).

Thompson et al. (1993) suggested that size and shape are of some predictive value for the persistence of seeds in the seed bank. Other factors such as germination requirements and resistance to pathogens and predation are also important to seed persistence (Moles et al. 2005). Larger seeds often originate from shade-tolerant climax species (forest habitat) and are better adapted for low-light germination than smaller seeds. These seeds can germinate in the understory (Schupp et al. 1989). Insect predation was the major type of seed predation during the Pennsylvanian. There is evidence that insects with sucking and piercing mouthparts preyed upon a number of seed-bearing plants in the Palaeozoic (Labandeira & Phillips 1996, Labandeira 1998, 2007). There is also evidence of boring in pteridosperm stems and petioles, and external feeding of pteridosperm foliage (Labandeira & Phillips 1996). The

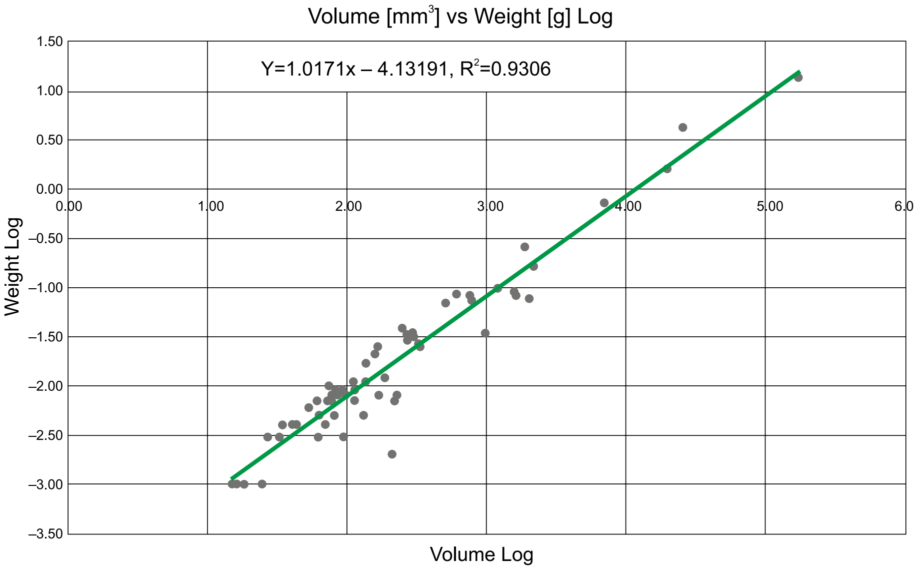

Fig. 1. Log – linear regression showing the relationship between volume and seed weight of the 62 gymnosperms species studied

earliest indication of seed predation consists in circular holes in *Trigonocarpus* from the Early and Mid-Pennsylvanian of Illinois and England (Scott & Taylor 1983). The occurrence of larger seeds in the Pennsylvanian may have been affected by the preponderance of invertebrate predators. Larger seeds can better tolerate small predators by satiating them before

Table 3. Average seed weight and seed density per square meter for seed banks from a variety of habitats

Seed Bank Location	Habitat	Average Seed Weight (g)	Seed Density/m^2	Reference
Belgium	Forest	0.00127	12426	Bossuyt et al. 2005
France	Forest	0.00229	8296	Decocq et al. 2004
Estonia	Forest	0.00294	900	Zobel et al. 2007
Canada	Forest	0.01233	900	Leckie et al. 2000
USA	Forest	0.00368	1031	Korb et al. 2005
New Zealand	Forest	0.00409	8841	Moles & Drake 1999
New Zealand	Forest	0.03993	1131	Enright & Cameron 1988
USA	Forest	0.00692	262	Matlack & Good 1990
Africa	Forest	0.02238	3492	Wassie & Teketay 2006
Belgium	Forest	0.00854	9192	Gosdefroid et al. 2006
USA	Grassland	0.00089	6470	Rabinowitz 1981
Argentina	Grassland	0.00174	28523	Boccanelli & Lewis 1994
USA	Grassland	0.00235	2019	Johnson & Anderson 1986
USA	Wetland	0.00017	4197	Middleton 2003
USA	Wetland	0.00031	25511	Tu et al. 1998
Canada	Wetland	0.00067	2726	Pederson 1981
USA	Wetland	0.00076	700	Hopkins & Parker 1984
USA	Wetland	0.00112	12860	Baldwin et al. 2001
USA	Wetland	0.00260	29753	Van der Valk & Davis 1978
USA	Wetland	0.00310	26956	Leck & Simpson 1987
USA	Wetland	0.00733	2430	Parker & Leck 1985
USA	Wetland	0.00414	7369	Galatowitsch et al. 1996
USA	Wetland	0.00546	467	Titus & Titus 2008
USA	Wetland	0.03296	4159	Schneider & Sharitz 1986
England	Woodland	0.00070	21950	Warr et al. 1994
England	Woodland	0.00085	20993	Warr et al. 1994
England	Woodland	0.00086	50060	Warr et al. 1994
England	Woodland	0.00117	45896	Warr et al. 1994
England	Woodland	0.00586	5105	Warr et al. 1994
Palaeozoic, Virginia, USA	Palaeozoic	3.74000	192	Present study

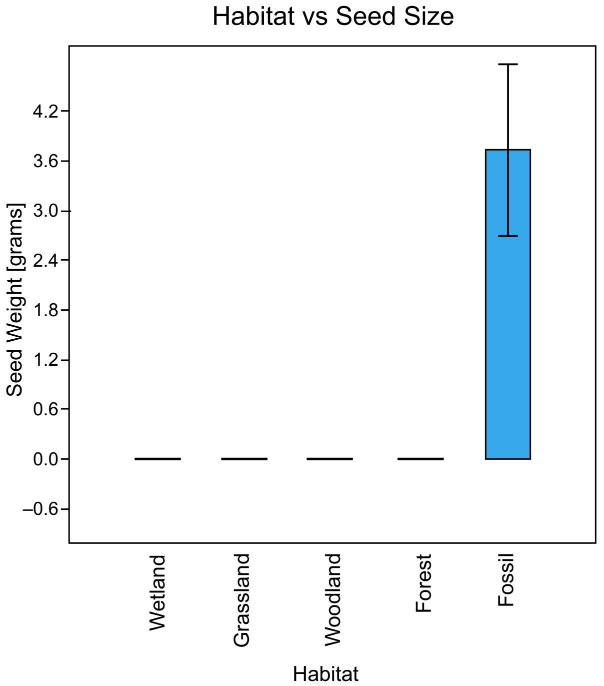

Fig. 2. Histogram showing seed size from various habitats (Wetland Mean Weight = 0.008; Grassland Mean Weight = 0.002 g; Woodland Mean Weight = 0.003 g; Forest Mean Weight = 0.011 g; Fossil Mean = 3.74 g); bars indicate standard error. Seed size differs significantly between the extant habitats and the fossil seed assemblage

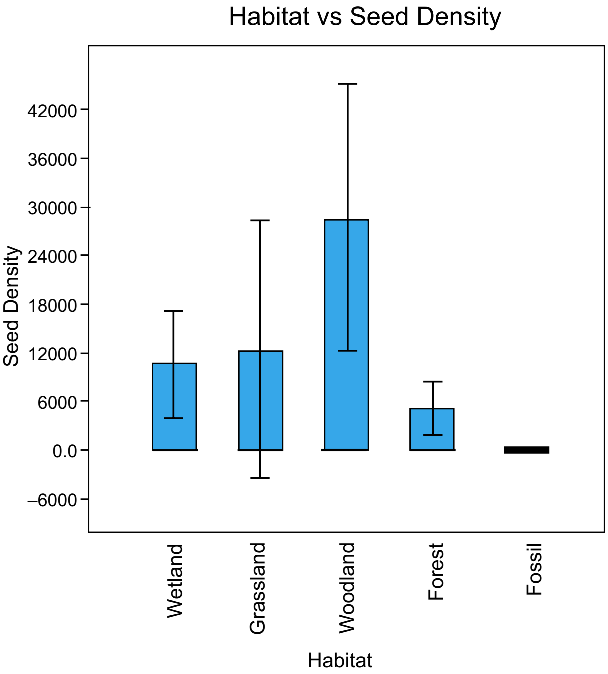

Fig. 3. Histogram showing differences in seed density among various habitats. Seed density does not differ significantly between the extant habitats and the fossil seed assemblage

they damage the embryo. Moreover, maternal investment of resources in the endosperm or cotyledonary tissue above the minimum requirement is insurance against destructive seed predators (Mack 1998). Studies of predation in modern seed banks have shown that birds and mammals have a preference for larger seeds (Westoby et al. 1996); however, large herbivorous tetrapods evolved in the late Carboniferous and may not have been an important factor in the evolution of seed size in the Pennsylvanian (Sues & Reisz 1998).

Small and spherical seeds are capable of incorporation into the soil profile more easily than large seeds (Thompson et al. 1993, Bekker et al. 1998, Benvenuti 2007a). Palaeozoic seeds exhibit sphericity, but their size would suggest that fewer Palaeozoic seeds were incorporated deep in the soil column. The Palaeozoic seed size spectrum is significantly different, shifted to the higher end of the seed size gradient than is observed in extant seed banks (ca 1000-fold difference, Fig. 3). It must be considered that the finding of large seed size does not necessarily represent all of the seed sizes produced by Palaeozoic seed-bearing taxa. The full Palaeozoic seed size spectrum may not be preserved in the death assemblage, and seed size may vary between Palaeozoic habitats as it does in modern seed banks. Some studies have shown taphonomic bias of preservation in the fossil record; only a fraction of the organisms that lived at that time may be preserved (Lawrence 1971). Sims (2012) indicated lower preservation probability for smaller seed lineages than larger seeded lineages in the Pennsylvanian Sub period. The structurally identified seed fossils from the Ohio coal balls, however, have a seed size range and small:large seed ratio similar to those observed in seeds recovered from Virginia (Tab. 2).

The preponderance of larger seeds suggests that the formation of the Palaeozoic seed bank occurred in a closed-canopy tropical forest (Baker 1972). Although the species composition, size and density of seed banks vary in extant tropical forests, many investigated sites show a tendency toward large seeds and lower seed density (Hopkins & Graham 1983, Garwood 1989, Dalling et al. 1997, Dalling & Denslow 1998). The Pteridosperms broadened their role as canopy-dominant taxa during the Pennsylvanian (DiMichele et al. 2006). The prevalence of large seeds may have been a strategy to produce shade-tolerant juveniles below the forest canopy, awaiting the formation of a gap or to capture space in forest gaps by more rapid seedling establishment (Schupp et al. 1989, van Ulft 2004). The stored reserves in large seeds promote quick germination and rapid seedling establishment in a population of transient seeds (Foster & Janson 1985, Rees 1996, Turnbull et al. 1999, Nathan & Muller-Landau 2000, Yu et al. 2007).

Seed density has been shown to vary between habitats and within habitat. There was no significant difference in seed density between habitats ($p = 0.074$) (Fig. 3), although the seed density reported for the Palaeozoic seed bank is at the low end of the seed density range (Fig. 3). Palaeozoic seed density is most similar to the density described for the forest habitats examined in this study (Tab. 3, Fig. 3) (Hall & Swaine 1980, Kramer & Johnson 1987). The Palaeozoic community that led to the formation of this seed bank has been reconstructed as climax forest–wetland (Leck et al. 1989). Many Palaeozoic coal swamps were coastal and may have been exposed to disturbances such as storms, storm surges or fires, which may also affect seed density (Middleton 1999).

Although seed size (weight) was significantly larger than that of extant seed bank assemblages, seed density fell within the range of modern seed banks, suggesting that seed banks and seed bank dynamics were being established early after the evolution of seeds and in response to their ecological context. The seed density of extant forests is similar to that of the Palaeozoic habitat, and the latter may be characterized as tropical or subtropical forest. It would be interesting to know what evolutionary changes in seed physiology accompanied the establishment of the first seed banks. The variation in the characteristics observed in modern seed banks may be influenced by the unique ecological context of the individual habitats. In the case of the Palaeozoic habitat, large seed size, coupled with low seed density, may be influenced by the absence of large predators, the preponderance of small invertebrate predators, disturbance factors (e.g. fire, storm surges), and may have aided germination and early seedling establishment in the forest understory or in forest gaps in these dense, stable tropical–subtropical wetland Palaeozoic forests.

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