



The influence of American Chestnut (*Castanea dentata*) on nitrogen availability, organic matter and chemistry of silty and sandy loam soils

Charles C. Rhoades*

US Forest Service, Rocky Mountain Research Station, 240 W. Prospect, Fort Collins, CO 80526, USA

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Summary

American chestnut trees once dominated vast areas of deciduous forest in eastern North America, but the exotic chestnut blight almost eliminated the species from the region. Introduction of blight-resistant American chestnut hybrids will probably start in the next decade after many years of tree breeding. What were the historic effects of chestnut on forest soils, and what changes may follow reintroduction of hybrid chestnuts? A site in southern Wisconsin provided an opportunity to examine the effect of chestnut trees on soil properties. At this site, 600 km northwest of chestnut's historic distribution, naturalized chestnuts have spread throughout an intact mixed-species forest from nine planted trees. The site contains soil developed on a silty loess-mantled ridge that abuts sandier hillslopes, allowing the effects of individual chestnuts to be examined on two soil types. I sampled and analyzed forest floor and mineral soils beneath canopies of individual American chestnuts and the surrounding mixed-species deciduous forest on fine-silt and sandy-loam soil types. On sandy loam soils, total soil carbon (C) and nitrogen (N), inorganic N and net mineralization and nitrification rates were 10–17% higher beneath chestnut canopies compared to soils beneath mixed-species deciduous forest. The pool of total soil N beneath chestnut canopies was positively related to the silt content of the sandy loam soils. In contrast, there were no differences between properties of chestnut canopy and mixed-species deciduous forest soils on the fine silt texture class. On sandy loam soil conditions common throughout the pre-blight distribution of American chestnut, soil biogeochemical processes differ beneath individual chestnut trees relative to a diverse mixture of deciduous species. These findings suggest that widespread chestnut reintroduction has the potential to alter both stand- and watershed-scale processes.

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*Tel.: +1 970 498 1250; fax: 1 970 498 1212.

E-mail address: crhoades@fs.fed.us.

Introduction

American chestnut (*Castanea dentata* [Marsh.] Borkh.), was a dominant component of the eastern deciduous forest until 1904 when chestnut blight caused by *Cryphonectria parasitica* (Murr.) Bar., was introduced to North America (Russell, 1987). Before the pathogen eliminated chestnut from the forest overstory, chestnut occupied a wide range of landscape positions and soil types and occurred within many forest associations (Braun, 1950; Keever, 1953; Russell, 1987). Throughout much of its native range, chestnut was an abundant overstory species on xeric ridges and more mesic hillslopes and coves (DeFries, 1884; Hawley and Hawes, 1912; Russell, 1987). Chestnut occurred on both north- and south-facing slopes and on soils formed from shale, sandstone, and occasionally limestone parent material (Braun, 1935), though the tree was most common on well-drained, acidic soils (Russell, 1987; Stephenson et al., 1991).

Blight-resistant hybrid chestnuts will be available for introduction to North American forests within the next decade (Hebard, 2001; McKinstry, 2005). Hybrid chestnuts are generated through a backcross breeding process that combines blight-resistance from Asian chestnuts (*C. mollissima* or *C. crenata*) with desired growth, form and nut characteristics of the American chestnut (Burnham, 1981). Potential for widespread dissemination of hybrid chestnut provokes questions regarding forest ecosystem dynamics and species replacement. Persistence of chestnut logs for a half-century (Hedman et al., 1996; Muller, 2003) combined with the previous abundance of the species suggests that biogeochemical characteristics of the American chestnut may have historically influenced soil properties.

Individual trees alter the biogeochemistry of soils within discrete zones of influence around trees isolated in savanna ecosystems (Belsky et al., 1989; Kellman, 1979) as well as those embedded within closed-canopy forest (Finzi et al., 1998; Zinke, 1962). Species-level variation in tree effects relate to differences in the amount and chemical composition of organic matter inputs, in nutrient uptake and in the capacity to fix atmospheric nitrogen, as well as secondary factors that follow from the effects of these differences on soil biota (Binkley, 1995; Rhoades, 1997). The resulting diversity of soil conditions has been described as a “mosaic of profiles reflecting the chemical characteristics of ground cover vegetation and individuals of the various tree species present” (Boettcher and Kalisz, 1990).

Characterization of tree effects on soil properties must consider species influences along with site conditions. For example, C and cation concentra-

tions differed between subcanopy soils beneath a variety of African savanna species and adjacent open areas to a greater extent in sandy soils as compared to fine-textured soils (Campbell et al., 1994; Charreau and Vidal, 1965; Kamara and Haque, 1992). Cation exchange capacity was lower in the sandy soils such that subcanopy organic matter inputs had greater effect on the size of the exchange complex (Campbell et al., 1994). Similarly, the N₂-fixing alder, *Alnus crispa* (Ait.) Pursh., significantly enriched soil N capital and availability on sandy, nutrient-poor floodplains but had little influence in upland sites with silty texture and higher N soils in northwestern Alaska (Rhoades et al., 2001). These studies indicate that antecedent soil properties that regulate exchange reactions and organic matter dynamics may determine the imprint of trees on soil biogeochemical processes.

Chestnut blight disease spared few locations where it is possible to estimate the potential of American chestnut to influence biogeochemical processes and edaphic patterns of forest ecosystems. An isolated stand of American chestnut located 600 km beyond the tree's native range in southwestern Wisconsin, affords a rare opportunity to investigate the effect of chestnut trees on soil chemistry and nutrient dynamics (Cummings-Carlson et al., 2002; McEwan et al., 2006; Paillet and Rutter, 1989). Chestnuts radiated from nine planted trees throughout 36 ha of mixed hardwood forest and now comprise about 30% of the overstory basal area (McEwan et al., 2006). Individual chestnuts are adequately dispersed so that soils beneath chestnut crowns can be compared to soils influenced by the mixture of species in the surrounding forest. The forest encompasses an abrupt transition between silt loess and sandstone parent materials thus allowing an assessment of the influence of individual American chestnut trees on the soil properties of silt and sandy loam soils. In the absence of common-garden plantation trials it is impossible to fully negate the possibility that effects attributed to individual chestnut may have resulted from a priori microsite soil differences. However, this disjunct stand provides a worthwhile first estimate of the potential for chestnut to influence soil properties differently than co-occurring hardwood species.

Materials and methods

Site description

The study was conducted in the Driftless Area of southwest Wisconsin, near West Salem (43° 57'N;

91° 03'W). Mean annual precipitation and temperature are 820 mm and 8.5 °C (at La Crosse, 10 km from site); half the annual precipitation occurs from May to August (NOAA, 2005). This region of bluffs and ravines remained unglaciated during the Pleistocene (Albert, 1995). The study area consists of a silt loess-mantled ridge and adjacent sandy loam hillslopes formed on sandstone residuum (Hole, 1976; Hole and Germain, 1994). The ridge-top Greenridge soil series are fine silty (28% sand, 65% silt and 7% clay) mesic Typic Hapludalfs (NRCS, 2005; Simonson 2006). The sideslope Council soil series are sandy loam (61% sand, 33% silt and 6% clay) mesic Typic Hapludalfs (Table 1). The ridgetop Greenridge loess soils also have higher pH, extractable cations (K^+ , Ca^{2+} , Mg^{2+}) and total N and C. Montmorillonite is the dominant clay mineral in Driftless Area loess soils, with lesser amounts of illite (NRCS, 2005). The textural and mineralogical differences between the loess and sandstone-derived substrates regulate a variety of soil processes that influence chemical exchange reactions, organic matter stabilization and aggregate structure, macro- and microbiological activity and plant-water relations (Coleman et al., 2004).

The Driftless Area is part of the maple-basswood forest region (Braun, 1950), where relatively xeric oak-hickory forest types intermix with more mesic northern species (Albert, 1995; Curtis, 1959). The West Salem site is situated within the Eau Claire Subsection of the Driftless Area, among forests dominated by *Quercus alba* L., *Q. rubra* L., *Carya cordiformis* Michx. and *Prunus serotina* Ehrh. Presettlement vegetation consisted of mixed oak forest, savanna and brushlands (Albert, 1995). West Salem forests intermingle northern broadleaf deciduous species such as *Populus grandidentata* Michx., *Q. ellipsoidalis* E.J. Hill and *Betula papyrifera* Marsh. and species common to chestnut's

native range such as *Tilia americana* L. and *Ulmus americana* L.

Sampling and analysis

Sampling was designed to compare the effects of individual chestnut trees on chemical properties of the litter layer and surface mineral horizon of two soil series with fine silt and sandy loam texture classes (Table 1). In May 2002, twenty chestnut trees were selected within the two areas mapped as (1) Greenridge fine silts on the broad central ridge and (2) Council sandy loams on the surrounding slopes. Crowns of sample trees were contiguous with adjacent deciduous species, but were at least two canopy heights (> 30 m) away from the nearest neighboring chestnut canopy. Sampled chestnuts averaged 44 cm diameter at 1.3 m height, had 4.5 m average canopy radius ($n = 40$). Sample trees ranged from 20 to 65 years old (McEwan et al., 2006).

Leaf litter and mineral soils were collected from 20 "chestnut canopy" and 20 "mixed deciduous canopy" locations on each soil series. Chestnut samples were located midway between the tree bole and the canopy dripline (approximately 2.5 m from the bole). Mixed deciduous samples were collected 15–25 m beyond the edge of the nearest chestnut crown, without regard for distance from the nearest tree bole. Chestnut samples were composited from two subsamples removed from opposing sides of each tree, parallel to the slope contour. Mixed deciduous samples were composited from two subsamples taken 10 m apart on the contour. The O horizon was sampled by removing a 20 × 20 cm quadrat using a serrated knife, and 0–10 cm mineral soil was collected from the same point with a 5-cm diameter corer.

Table 1. Physical and chemical properties of loess-derived Greenridge fine silt and sandstone-derived. Council sandy loam near West Salem, Wisconsin (mean and SE for 0–10 cm depth; $n = 20$ per soil series). Soil series differences (P value) were evaluated by one way analysis of variance.

Soil series	Particle size			pH	Extractable				Total	
	Sand	Silt	Clay		P	K^+	Mg^{2+}	Ca^{2+}	C	N
	%				$g\ m^{-2}$				$kg\ m^{-2}$	
Greenridge fine silt	28.6 (1.6)	64.6 (1.5)	6.9 (0.1)	5.9 (0.1)	7.0 (0.4)	20.0 (0.7)	29.9 (0.9)	188.8 (9.1)	3.8 (0.1)	0.28 (0.01)
Council sandy loam	61.3 (2.2)	33.1 (2.2)	6.1 (0.2)	5.6 (0.1)	9.5 (0.6)	17.3 (0.7)	24.2 (1.1)	159.5 (12.3)	3.4 (0.1)	0.24 (0.01)
P value	0.000	0.000	0.000	0.007	0.001	0.008	0.000	0.056	0.038	0.007

O horizon samples were rinsed with deionized water to remove adhering soil, then oven-dried for 48 h at 60 °C. Whole and identifiable chestnut leaf fragments were then hand-separated from mixed hardwood and unidentifiable leaf litter, and weighed to estimate the dry mass. Subsamples of chestnut and mixed deciduous leaf litter were then ground and digested in 18 M H₂SO₄ using the semi-micro Kjeldahl procedure (modified from Nelson and Sommers, 1980). Total N and P concentrations were analyzed by colorimetric spectrophotometer (Braun-Luebbe, Inc. Buffalo Grove, IL); cations were analyzed by atomic absorption (Perkin-Elmer Inc., Boston, MA).

Mineral soil samples were placed in plastic coolers immediately after sampling and stored at 4 °C. Ten-gram subsamples were extracted with 50 mL of 1 M KCl within 72 h of sampling, and extracts analyzed for NO₃⁻ and NH₄⁺ by colorimetric spectrophotometry (Bundy and Meisinger, 1994). Separate subsamples were oven-dried at 105 °C for 24 h to determine soil moisture content. A third set of 10 g subsamples was incubated for 28 days at 26 °C at field capacity (Binkley and Hart, 1989). Field capacity was approximated as the gravimetric water content of a subsample wetted to saturation then allowed to drain for 12 h (gravimetric moisture content of about 50%). After 28 days, the incubated subsamples were extracted and analyzed as described above. Net mineralization was calculated as the change in NO₃⁻ plus NH₄⁺, and net nitrification as the change in NO₃⁻ between initial and incubated extracts.

Mineral soil total C and N were analyzed by Dumas dry combustion (LECO CHN, 2000; St. Joseph, MI). Soil pH was analyzed in a 1:1 soil to deionized water slurry after one hour of agitation (Thomas, 1996). Exchangeable phosphorus and

cations were extracted with Mehlich-III reagents (0.2 N CH₃COOH, 0.25 N NH₄NO₃, 0.015 N NH₄F, 0.13 N HNO₃, and 0.001 M EDTA; Mehlich, 1984) and analyzed by colorimetry for P and atomic absorption for cations. Soil texture was measured with the Bouyoucos hydrometer method (Gee and Bauder, 1986).

The effect of chestnut on organic and mineral soil properties were compared among and within the two soil types. Two-way analysis of variance was used to evaluate the canopy type (chestnut versus mixed deciduous) and soil series main effects (SPSS Ver. 10.1.3, SPSS Inc., Chicago, IL). The interaction term between canopy type and soil series tests the consistency of chestnut effects across soil types. Where soil series by canopy type interactions were common, one-way analysis of variance was used to assess chestnut and mixed species forest soil differences within the individual soil series. Levene's statistic was used as a test of homogeneity of variance and data were log-transformed when necessary. Log transformation succeeded in reconciling violations of the assumption of homogeneity of variance. Significance is reported at the $\alpha = 0.05$ critical value unless noted otherwise. Relations between chestnut canopy soil properties and tree diameter and soil physical properties were evaluated using least-squares linear regression (SPSS Inc., Chicago, IL).

Results and discussion

Chestnut leaves from the O horizon had greater concentrations of most nutrients than the mixed deciduous species leaves (Table 2), reflecting either higher initial concentrations in fresh litterfall, or

Table 2. Chestnut and hardwood leaf litter nutrient concentrations on fine silt and sandy loam soils near West Salem, Wisconsin ($n = 20$ per soil series $\times$ canopy type). Within columns, similar letters indicate that means within soil series / canopy type combinations are equal ($\alpha = 0.05$).

Soil series	Canopy type	Leaf litter nutrients					Leaf litter mass	
		N	P	Ca	K	Mg	Total	Chestnut
		g kg ^{−1}					g m ^{−2}	
Greenridge fine silt	Chestnut	12.31a	1.18a	15.88b	2.83a	2.79a	615.99a	121.24b
	Mixed deciduous	10.82b	0.99b	18.16a	2.12b	2.28b	782.14a	39.95c
Council sandy loam	Chestnut	11.54ab	1.14a	15.15b	2.49ab	2.80a	800.29a	232.51a
	Mixed deciduous	11.42ab	1.01b	14.78b	2.16b	2.26b	628.83a	62.36bc
<i>P values for:</i>	Canopy type	0.035	0.000	0.088	0.000	0.000	0.973	0.000
	Soil Series/Texture	0.820	0.712	0.000	0.273	0.940	0.842	0.022
	Canopy × Texture	0.069	0.439	0.019	0.168	0.804	0.033	0.124

slower rates of nutrient loss in initial stages of decomposition. On silty soils, chestnut litter had higher N, P, K, and Mg and lower Ca concentrations compared to mixed deciduous litter. Concentrations of Mg and P were significantly higher in chestnut litter on sandy loam soils; K was marginally higher ($P = 0.055$). Mixed-species deciduous forest floor mass was similar on sandy and silty sites. However, chestnut leaf litter and total forest floor mass were twice as high under chestnuts growing on sandy rather than silty soils and chestnut litter represented a greater proportion of total litter (Table 2).

Variation in decomposition rates probably explains the different O horizon properties beneath individual chestnuts on the two soil texture classes. The elemental composition of chestnut leaf litter did not differ between the two soil types and litter mass is similar (Table 2). The mass of chestnut litter in the O horizon, as well as its proportion of total litter, increased with tree diameter (chestnut litter = $1.2\text{DBH} - 23$; $r^2 = 0.49$; $P = 0.001$). However, stem diameter was independent of soil texture at West Salem and the lower standing stock of chestnut litter on the fine silts probably relates to more rapid decomposition for the less acid, higher extractable cation and soil organic matter soils, rather than a difference in litter production. It is also notable that for each soil type, sand, silt and clay content did not differ beneath chestnut and mixed hardwood canopy types ($P > 0.2$).

Differences between chestnut and mixed deciduous forest mineral soil attributes were not consistent across soil types. Chestnut trees influenced organic matter content and N nutrition of sandy loam soils, but had no effect on the finer-textured Greenridge series (Table 3). Total soil C and N and extractable N ($\text{NH}_4^+ + \text{NO}_3^-$) were significantly higher (17%, 11%, and 12%, respectively) under chestnut trees compared to adjacent mixed-species deciduous forest and gravimetric soil moisture was marginally greater (14%; $P = 0.058$). The significant increase in total inorganic soil nitrogen beneath chestnut growing on sandy loam soils is aggregated from increases in nitrate (8%) and ammonium (15%). Nitrate represents 43% and 35% of the inorganic soil nitrogen pool in sandy loam and silty soils, respectively. Net mineralization and nitrification rates were 17% and 10% higher beneath chestnut canopies on the sandy loam. The similarity between net mineralization and nitrification rates (Table 3) indicates that most of the nitrogen mineralized was nitrified, irrespective of canopy location or soil type.

Individual chestnuts had little effect on soil acidity or exchangeable cations on either soil type

Table 3. Chestnut effects on mineral soil nutrient status on sandy loam and silt loam soils in western Wisconsin (0–10 cm depth). Canopy type differences (P value) were tested by one way analysis of variance ($n = 20$ per soil series x canopy type).

Soil series	Canopy type	pH	Extractable				Total		Inorganic N NH ₄ ⁺ + NO ₃ ⁻	Net	
			P	K ⁺	Mg ²⁺	Ca ²⁺	C	N		Mineralization	Nitrification
			g m ⁻²			kg m ⁻²		g m ⁻²		g m ⁻² 28d ⁻¹	
Greenridge fine silt	Chestnut	6.03	7.05	18.70	30.22	199.12	3.87	0.28	0.90	3.45	3.62
	Mixed deciduous	5.83	6.93	21.24	29.65	178.56	3.82	0.28	0.92	3.78	3.84
	<i>P value</i>	0.54	0.71	0.52	0.77	0.66	0.59	0.77	0.72	0.86	0.67
Council sandy loam	Chestnut	5.62	9.87	17.25	24.04	166.45	3.71	0.25	1.14	3.92	3.85
	Mixed deciduous	5.63	9.18	17.43	24.45	152.47	3.16	0.22	1.02	3.45	3.51
	<i>P value</i>	0.71	0.67	0.72	0.50	0.10	0.01	0.04	0.08	0.00	0.03

(Table 3). For comparison, on sandy loam soils in northern Michigan, extractable Ca^{2+} and Mg^{2+} were twice as high in the upper 40 cm of mineral soil beneath basswood (*Tilia americana* L.) compared to sugar maple (*Acer saccharum* Marsh.; Fujinuma et al., 2005). Even on steep slopes, sandy soil beneath individual yellow poplar (*Liriodendron tulipifera* L.) trees had significantly higher pH (0.6 units) and extractable cations (Ca^{2+} , Mg^{2+} and K^+ , increase 1.6-, 2.3- and 1.5-fold, respectively) compared to hemlock soil (*Tsuga canadensis* L.). However, yellow poplar did not differ from mixed deciduous species (Boettcher and Kalisz, 1990).

The chestnut effect on soil nitrogen availability was also low compared to the range of species effects reported among North American trees species. Net mineralization often differs by 50% or more between species growing in adjacent plantings (Binkley and Giardina, 1998) compared to the 17% difference measured between chestnut and a mixture of northern hardwoods on sandy loams at West Salem. On fine silty, loess-derived Alfisols at the Coulee Experimental Forest (~10 km south of West Salem, WI), for example, annual net mineralization and nitrification differed 2-fold between 28-year old stands of native broadleaf deciduous and conifer species (Gower and Son, 1992).

Controls on chestnut effects

The influence of American chestnut differed between the fine- and coarse-textured soils. Well-drained, sandy soils are commonly considered optimal for chestnut growth (Russell, 1987), so tree performance may explain the pattern; however, average diameter of sampled chestnuts was similar between soil types (43 cm vs. 45 cm on silt and sandy soils, respectively). Further, at a site 20 km east of West Salem, WI, mean height (6.4 m) and diameter (6.4 cm) of 7- and 8- year old chestnut seedlings differed little between planting blocks on coarse-loamy and fine-silty soils (Jacobs and Severeid, 2004).

An alternative explanation is that the influence of chestnut is more apparent in the coarser Council sandy loam soils, whereas the biogeochemical effect of the species is buffered by the higher cation exchange capacity, organic matter content and overall nutrient status of the Greenridge silt loam (Table 1). Soil texture contributes to regulation of soil chemistry, N cycling and organic matter content in a wide variety of forest ecosystems (Finzi et al., 1998; Fujinuma et al., 2005; Giardina et al., 2001; Pastor et al., 1984; Reich et al., 1997). For example, the combination of silt and clay

relates positively to net mineralization and nitrification rates in southern Wisconsin forest soils (Pastor et al., 1984), and variation in net N transformations are explained more by soil texture than by forest species composition (Reich et al., 1997). On the coarse-textured sandy loams at West Salem, silt content (but not clay) explained a significant amount of variation in both total and inorganic soil N pools and net nitrification rates (Fig. 1). Total soil N more than doubled across the 25% range in silt content found in the sandy loams; total soil C increased similarly ($\text{C Mg/ha} = 13 + 0.74 * \text{Silt } \%; r^2 = 0.58; P < 0.001$).

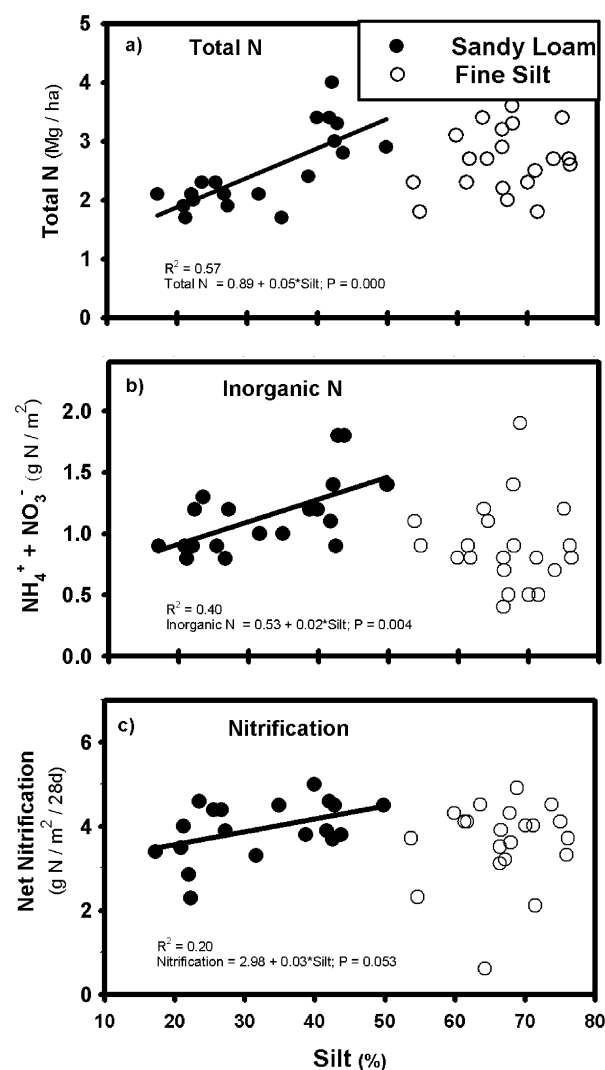


Figure 1. Least-squares linear relations between silt content and (a) total and (b) inorganic soil nitrogen and (c) net nitrification in surface mineral soils (0–10 cm depth) beneath the canopies of chestnut growing on sandy loam and fine silt soils. Regression line, equation and significance shown for sandy loam soil; similar relations were non-significant in fine silt soils.

However, these relations were absent in the fine-textured soils, where silt content exceeded 50%.

Soil changes with increased tree diameter may represent the cumulative influence of individual chestnuts. Based on diameter–age relations developed by McEwan et al. (2006), sample trees ranged from 20 to 65 years old. Stem diameter explained 25% of the variation in net mineralization (Fig. 2a), though it was unrelated to total soil C or N. Soil pH and extractable Ca^{2+} declined significantly with increasing tree girth (Fig. 2b and c) on sandy loam, though not on fine silt soils. Depletion of base cations from the soil exchange complex and storage in tree biomass may explain both the decline in

exchangeable soil calcium and the increased soil acidity measured beneath chestnut canopies on the sandy loam soils (Binkley and Valentine, 1991). Conversely, the greater amount of weatherable minerals may have buffered chemical changes associated with chestnut growth on the base cation rich loess soils.

Implications for chestnut restoration

Results from this single-tree study demonstrate the potential for chestnut to alter nutrient dynamics in the litter and mineral soil horizons relative to a diverse species mixture including oaks, hickory, aspen and birch. The effect of chestnut on soil chemistry, nitrogen transformations and other belowground attributes will continue to accrue as individual trees grow (Fig. 2) or as their relative abundance increases. While the West Salem stand allows a unique opportunity to study the effect of sizeable chestnut trees within a North American forest, the diameter of mature chestnut in pre-blight forests greatly exceeded the mean diameter of the trees included in this study. The largest tree sampled for this study had a 71 cm diameter and the largest of the nine original West Salem trees measured 135 cm in girth at 120 years. Mature chestnuts often exceed 1 m in diameter (Ashe, 1912; Smith, 2000), and in the absence of substantial chestnut blight disease (Cummings-Carlson et al., 2002), the West Salem chestnuts might have doubled or tripled their diameter in the coming two to three decades (McEwan et al., 2006).

Significant chestnut effects also may emerge once its abundance surpasses a certain threshold. With increased sugar maple (*Acer saccharum* L.) abundance for example, soil C:N and nitrification rates decline gradually (Finzi et al., 1998; Lovett et al., 2004), until the species exceeds 50% of the stand; at that point, nitrate leaching increases more than 10-fold (Mitchell et al., 2003). Unfortunately, the recent arrival of chestnut blight disease (Cummings-Carlson et al., 2002; Jarosz et al., 2002) will limit the long-term value of West Salem for assessing how further increases in density and size add to chestnut's influence on soil properties.

In future plantings, site and soil conditions may define the boundaries within which blight-resistant chestnut influence soils or other ecosystem attributes. At West Salem, texture determined the extent of chestnut's biogeochemical imprint on soils, but had no effect on tree growth. Across a broader range of edaphic conditions, texture may also determine chestnut performance. In pre-blight forests, chestnut dominance was often greatest

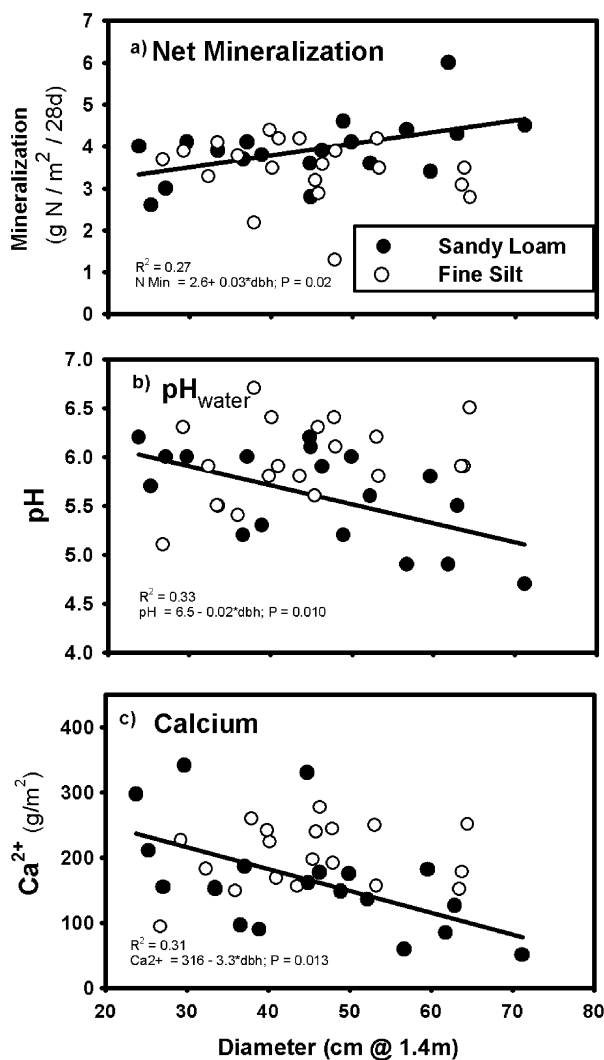


Figure 2. Linear relation between diameter and (a) net mineralization, (b) soil pH and (c) extractable calcium in mineral soils collected beneath canopies of American chestnuts on sandy loams and fine silts at West Salem. Regression line, equation and significance shown for sandy loams only; similar relations were non-significant in fine silt soils.

across a wide range of well-drained soils (Braun, 1935; McEwan et al., 2005; Rhoades and Park, 2001; Russell, 1987). On clayey, poorly drained or compacted soils chestnut growth and health were impaired by the prevalence of soil pathogens, such as phytophthora root rot (Anagnostakis, 2002; Rhoades et al., 2003).

This study examined soil patterns associated with several decades of chestnut development. I expect the single-tree patterns reflect chestnut's effect on soil properties more than the influence of previous soil characteristics on chestnut establishment; on both soil types, soil texture was similar beneath chestnut and mixed species canopies. Controlled experiments are needed to test this expectation, but until those experiments are developed and monitored for decades, this descriptive study provides the best available information on the likely effects of chestnut on soils. Replicated planting trials of blight-resistant chestnut and other appropriate species on a variety of soil types will also help separate chestnut and other species soil effects from site differences and will increase understanding of feedbacks between chestnut's influence on soil properties and the tree's fitness or abundance (Binkley and Giardina, 1998; Van Breeman and Finzi, 1998).

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References

- Albert, D.A., 1995. Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin: a working map and classification. Gen. Tech. Rep. NC-178. St. Paul, MN: USDA, Forest Service, North Central Forest Experiment Station.
- Anagnostakis, S.L., 2002. The effect of multiple importations of pests and pathogens on a native tree. *Biological Invasions* 3, 245–254.
- Ashe, W.W., 1912. Chestnut in Tennessee. Tennessee Geological Survey Bulletin 10-B, Nashville, TN.
- Belsky, A.J., Amundson, R.G., Duxbury, J.M., Riha, S.J., Mwonga, S.M., 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. *J. Appl. Ecol.* 26, 1005–1024.
- Binkley, D., 1995. The influence of tree species on forest soils: Processes and patterns. In: Mead, D.J., Cornforth, I.S. (Eds.), *Proceedings of the Trees and Soil Workshop*. Lincoln University Press, Lincoln University, New Zealand.
- Binkley, D., Giardina, C.P., 1998. Why do tree species affect soils? The Warp and Woof of tree–soil interactions. *Biogeochemistry* 42, 89–106.
- Binkley, D., Hart, S.C., 1989. The components of nitrogen availability assessments in forest soil. *Adv. Soil Sci.* 10, 57–112.
- Binkley, D., Valentine, D., 1991. Fifty-year biogeochemical effects of green ash, white pine, and Norway spruce in a replicated experiment. *For. Ecol. Manage.* 40, 13–25.
- Boettcher, S.E., Kalisz, P.J., 1990. Single-tree influence on soil properties in the mountains of eastern Kentucky. *Ecology* 71, 1365–1372.
- Braun, E.L., 1935. The vegetation of Pine Mountain, Kentucky: An analysis of the influence of soils and slope exposure as determined by geological structure. *Am. Midland Nat.* 16, 517–565.
- Braun, E.L., 1950. *Deciduous Forests of Eastern North America*. Blakiston Co, Philadelphia.
- Bundy, L.G., Meisinger, J.J., 1994. Nitrogen availability indices. In: Weaver, R.W., Angle, J.S., Bottomly, P.S. (Eds.), *Methods of soil analysis. Part 2. Agron. Monogr.* 5. Am. Soc. Agron. and Soil Sci. Soc. Am., Madison, pp. 951–984.
- Burnham, C.R., 1981. Blight-resistant American chestnut: there's hope. *Plant Disease* 65, 459–460.
- Campbell, B.M., Frost, P., King, J.A., Mwanza, M., Mhlanga, L., 1994. The influence of trees on soil fertility on two contrasting semi-arid soil types at Matopos, Zimbabwe. *Agroforestry Sys.* 28, 159–172.
- Charreau, C., Vidal, P., 1965. Influence de *L'Acacia albida* Del. sur le sol, nutrition minerale et rendements des mils *Pennisetum* au Senegal. *L'Agronomie Tropicale* 6–7, 600–626.
- Coleman, D.C., Crossley Jr., D.A., Hendrix, P.F., 2004. *Fundamentals of Soil Ecology*, 2nd Ed. Elsevier Publishing, San Diego.
- Cummings-Carlson, J.E., Paillet, F.L., Dahir, S.E., 2002. Ecological history and early disease management of an isolated stand of American chestnut in Wisconsin. *Phytopathology* 92, S94.
- Curtis, J.T., 1959. *The Vegetation of Wisconsin*. The University of Wisconsin Press, Madison, WI.

- DeFries, L.H., 1884. Report on the timbers of the north Cumberland: Bell and Harlan counties. Kentucky Geological Survey, Frankfort, KY.
- Finzi, A.C., Canham, C.D., Van Breeman, N., 1998. Canopy tree-soil interactions within temperate forests: species effects on pH and cations. *Ecol. Appl.* 8, 447–454.
- Fujinuma, R., Bockheim, J., Balster, N., 2005. Base-cation cycling by individual tree species in old-growth forest of Upper Michigan, USA. *Biogeochemistry* 74, 357–376.
- Gee, G.W., Bauder, J.W., 1986. Particle-size analysis. In: Klute, A. (Ed.), *Methods of Soil Analysis: Physical and Mineralogical Methods*, Part 1. 2nd Ed. Am. Soc. of Agron., Madison, pp. 383–412.
- Giardina, C.P., Ryan, M.G., Hubbard, R.M., Binkley, D., 2001. Tree species and soil textural controls on carbon and nitrogen mineralization rates. *Soil Sci. Soc. Am. J.* 65, 1272–1279.
- Gower, S.T., Son, Y., 1992. Differences in soil and leaf litterfall nitrogen dynamics for five forest plantations. *Soil Sci. Soc. Am. J.* 56, 1959–1966.
- Hawley, R.C., Hawes, A.F., 1912. *Forestry in New England: A Handbook of Eastern Forest Management*, 1st ed. Wiley, New York.
- Hebard, F.V., 2001. Backcross breeding program produces blight-resistant American chestnuts. *Ecol. Restoration* 19, 252–254.
- Hedman, C.W., Van Lear, D.H., Swank, W.T., 1996. In-stream large woody debris loading and riparian forest seral stage associations in the southern Appalachian Mountains. *Can. J. For. Res.* 26, 1218–1227.
- Hole, F.D., 1976. *Soils of Wisconsin*. University of Wisconsin Press, Madison.
- Hole, F.D., Germain, C.E., 1994. Natural divisions of Wisconsin. Madison, WI: Wisconsin Department of Natural Resources. Map and accompanying text.
- Jacobs, D.F., Severeid, L.R., 2004. Dominance of inter-planted American chestnut (*Castanea dentata*) in southwestern Wisconsin, USA. *For. Ecol. Manage.* 191, 111–120.
- Jarosz, A.M., Dahir, S.E., Double, M.L., 2002. Spatial patterns of blight and hypovirus spread within the West Salem chestnut stand. *Phytopathology* 92, S94.
- Kamara, C.S., Haque, I., 1992. *Faidherbia albida* and its effects on Ethiopian highland Vertisols. *Agroforestry Sys.* 18, 17–29.
- Kellman, M., 1979. Soil enrichment by neotropical savanna trees. *J. Ecol.* 67, 565–577.
- Keever, C., 1953. Present composition of some stands of the former oak-chestnut forest in the southern Blue Ridge Mountains. *Ecology* 34, 44–54.
- Lovett, G.M., Weathers, K.C., Arthur, M.A., Schultz, J.C., 2004. Nitrogen cycling in a northern hardwood forest: Do species matter? *Biogeochemistry* 67, 289–308.
- McEwan, R.W., Rhoades, C.C., Beiting, S., 2005. *Castanea dentata* ([Marsh.] Borkh.) in the pre-settlement vegetation of Mammoth Cave National Park, central Kentucky. *Natural Areas J.* 25, 275–281.
- McEwan, R.W., Keiffer, C.H., McCarthy, B.M., 2006. Dendrochronology of American chestnut (*Castanea dentata*) in a disjunct stand of oak-chestnut forest. *Can. J. For. Res.* 36, 1–11.
- McKinstry Jr., R.B., 2005. Ecosystem restoration and federal land policy: Reexamination in light of the American Chestnut restoration effort. In: Steiner, K.C., Carlson, J.E. (Eds.), *Proceedings of the Conference on Restoration of American Chestnut on Forest Lands*. May 2004. Asheville, NC.
- Mehlich, A., 1984. Mehlich 3 soil test extractant: A modification of Mehlich 2 extractant. *Comm. Soil Sci. Plant Anal.* 15, 1409–1416.
- Mitchell, M.J., Driscoll, C.T., Inamdar, S., McGee, G.G., Mbila, M.O., Raynalm, D.J., 2003. Nitrogen biogeochemistry in the Adirondack Mountains of New York: Hardwood ecosystems and associated surface waters. *Env. Poll.* 123, 355–364.
- Muller, R.N., 2003. Landscape patterns of change in coarse woody debris accumulation in an old-growth deciduous forest on the Cumberland Plateau, south-eastern Kentucky. *Can. J. For. Res.* 33, 763–769.
- Nelson, D., Sommers, L., 1980. Total nitrogen of soil and plant tissue. *J. Assoc. Anal. Chem.* 63, 770–778.
- NOAA, 2005. *Midwestern Regional Climate Center*. 2005. Historical Climate Data; Station: 474370 La Crosse, WI 1971–2000 NCDC. http://sisyphus.sws.uiuc.edu/climate_midwest/historical/temp/wi/474370_tsum.html.
- NRCS, 2005. La Crosse County, Wisconsin, Tabular Data Version 3. USDA Natural Resources Conservation Service.
- Paillet, F.L., Rutter, P.A., 1989. Replacement of native oak and hickory species by the introduced American chestnut (*Castanea dentata*) in southwestern Wisconsin. *Can. J. Bot.* 67, 3457–3469.
- Pastor, J., Aber, J.D., McClaugherty, C.A., Melillo, J.M., 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology* 65, 256–268.
- Reich, P.B., Grigal, D.F., Aber, J.D., Gower, S.T., 1997. Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. *Ecology* 78, 335–347.
- Rhoades, C.C., 1997. Single-tree influences on soil properties in agroforestry: lessons from natural forest and savanna ecosystems. *Agroforestry Sys.* 35, 71–94.
- Rhoades, C.C., Park, A.C., 2001. Pre-blight abundance of American chestnut in Kentucky. *J. Am. Chestnut Found.* 15, 36–44.
- Rhoades, C.C., Oskarsson, H., Binkley, D., Stottlemeyer, R., 2001. Alder (*Alnus crispa*) effects on soils in ecosystems of the Agashashok River valley, northwest Alaska. *Ecoscience* 8, 89–95.
- Rhoades, C.C., Brosi, S.L., Dattilo, A.J., Vincelli, P., 2003. Soil compaction and moisture controls on incidence of Phytophthora root rot on American Chestnut seedlings. *For. Ecol. Manage.* 184, 47–54.

- Russell, E.W.B., 1987. Pre-blight distribution of *Castanea dentata* (Marsh.). Borkh. Bull. Torrey Bot. Club 114, 183–190.
- Simonson, D.T., 2006. Soil survey of La Crosse County, Wisconsin, Subset of Major Land Resource Area 105. USDA Natural Resources Conservation Service, in cooperation with the University of Wisconsin.
- Smith, D.M., 2000. American chestnut: Ill-fated monarch of the eastern hardwood forest. J. For. 98, 12–15.
- Stephenson, S.L., Adams, H.S., Lipford, M.L., 1991. The present distribution of chestnut in the upland forest communities of Virginia. Bull. Torrey Bot. Club 118, 24–32.
- Thomas, G.W., 1996. Soil pH and soil acidity. In: Sparks, D.L. (Ed.), Methods of Soil Analysis: Part 3. Chemical Analysis. Soil Sci. Soc. Am., Madison, pp. 475–490.
- Van Breeman, N., Finzi, A.C., 1998. Plant–soil interactions: ecological aspects and evolutionary implications. Biogeochemistry 42, 1–19.
- Zinke, P.J., 1962. The pattern of influence of individual forest trees on soil properties. Ecology 43, 130–133.