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ARTICLE

Frequency of sprout-origin trees in pre-European settlement forests of the southern Appalachian Mountains

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Abstract: We hypothesized that tree form, recorded in historical public land surveys, would provide a valuable proxy record of regeneration patterns during early-European settlement of North America's eastern deciduous forest. To test this hypothesis, we tallied stem form from witness trees used in land survey records in the southern Appalachian Mountains from 13 counties spanning four physiographic provinces: Piedmont, Blue Ridge, Ridge and Valley, and Cumberland Plateau. A total of 3% of witness trees used in the land surveys were of sprout origin. American basswood (*Tilia americana* L.) exhibited the highest proportion of sprout-origin trees at 12%. Other overstory species with a high proportion of sprout-origin trees were hickory (*Carya* sp.), red maple (*Acer rubrum* L.), and sycamore (*Platanus occidentalis* L.), all with 6% of stems being from sprout origin. Blue Ridge had significantly more sprout-origin trees compared with the other three physiographic provinces. Forests in the southern Appalachian Mountains during the pre-European settlement period had a suite of disturbances that controlled their growth and regeneration; however, most of these disturbances did not result in large-scale tree mortality, and therefore, sprouts were not an important source of regeneration.

Key words: forest disturbance, oak regeneration, eastern deciduous forest, forest structure.

Résumé : Nous avons posé l'hypothèse que la forme des arbres notée dans les relevés historiques des terres publiques constitue une source indirecte précieuse de données sur les patrons de régénération présents au début de la colonisation européenne des forêts décidues de l'est de l'Amérique du Nord. Pour tester cette hypothèse, nous avons recensé la forme de la tige d'arbres témoins dans les relevés d'inventaire des terres dans la partie sud des Appalaches, qui couvrent 13 comtés répartis dans quatre provinces physiographiques : Piedmont, Blue Ridge, Ridge and Valley, et Cumberland Plateau. Au total, 3 % des arbres témoins utilisés dans l'inventaire des terres provenaient d'un rejet de souche. Le tilleul d'Amérique (*Tilia americana* L.) était l'espèce ayant la plus forte proportion d'arbres provenant de rejets, soit 12 %. Les autres espèces du couvert dominant ayant une forte proportion d'arbres provenant de rejets étaient le caryer (*Carya* sp.), l'érable rouge (*Acer rubrum* L.) et le platane (*Platanus occidentalis* L.), dont 6 % des tiges provenaient de rejets. Il y avait significativement plus d'arbres provenant de rejets dans la région du Blue Ridge comparativement aux autres provinces physiographiques. Les forêts dans la partie sud des Appalaches ont subi une séquence de perturbations qui ont influencé leur croissance et leur régénération pendant la période d'établissement des premiers colons européens. Cependant, la plupart de ces perturbations n'ont pas engendré de mortalité des arbres à grande échelle de telle sorte que les rejets de souche n'ont pas été une source importante de régénération. [Traduit par la Rédaction]

Mots-clés : perturbation forestière, régénération du chêne, forêt décidue de l'est, structure forestière.

Introduction

European settlement of North America provided a unique opportunity to quantify how substantial shifts in human land use impacted terrestrial ecosystems. The environmental conditions prior to European settlement serve as baseline conditions with which to compare present-day ecosystems. Differences in species composition, species distribution, forest structure, and disturbance regimes between these two time periods have been attributed to the introduction of intensive agriculture, large-scale timber harvesting, exotic species, loss of native species, and fire exclusion (McEwan et al. 2011). As scientists have reconstructed pre-European settlement environmental conditions to better understand human impacts on the environment, land managers have appropriated these baseline reconstructions and are using them as goals for habitat restoration (Brose et al. 2001). The use of an arbitrary reference period as a restoration baseline has been criticized in some situations (Jachowski et al. 2015). However, in eastern deciduous forests, the baseline of European settlement is often applied because the perceived attributes of this period, specifically oak dominance, match forest management goals (Brose 2014).

Reconstructions of historical vegetation and disturbance regimes are founded on proxy records. In eastern deciduous forests, the most valuable proxy sources include the following: paleoecological records preserved in soils and lake sediments; spatially explicit demographic data from trees; fire scars and dendroecological analysis of tree-ring growth patterns; historical forest measurements; and original land survey records (Russell 1997). Often two proxy sources are compared to validate reconstructions. For example, land survey records (Abrams and McCay 1996) and historical forest measurements (Burke 2011) reveal the same influence of topographic position on species distribution. Occasionally, different proxy sources yield conflicting representations of pre-European settlement baseline conditions, which requires researchers to

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reconstruct environmental conditions from an amalgamation of multiple proxy sources.

The importance of disturbance in eastern deciduous forests has become a source of discussion because different proxy sources provide conflicting reconstructions of types of disturbance and patterns of forest regeneration common in pre-European settlement times. Annual fire scars and land survey records provide evidence of a fire-based disturbance regime with a modal fire return interval of 7 years and a predominance of sprout-origin, fire-adapted tree species (Shumway et al. 2001; Thomas-Van Gundy and Nowacki 2013; Aldrich et al. 2014). Paleoecological records (Clark and Royal 1996) and dendroecological patterns (Copenheaver et al. 2014) reveal an oak-dominated forest where fire was infrequent at some locations and the forest canopy remained undisturbed for long periods. The differences among proxy reconstructions of disturbance may be attributed to higher levels of regional variation in pre-European settlement forests (Matlack 2013). In present-day forests, widespread agricultural disturbance, associated with European settlement, has homogenized the forested landscape (Thompson et al. 2013). Thus, perhaps the varied reconstructions of disturbance identified in the various proxy sources accurately reflect a historically heterogeneous forest.

In this study, we examine a commonly used proxy, land surveys, but extract new information on tree form or architecture with the hope of contributing to the ongoing discussion about the nature of disturbance and regeneration in the eastern deciduous forest during the period of European settlement. Public and private land surveys allowed the purchase of property by new landowners and were archived as public records. Most land surveys contain parcel descriptions that reference trees blazed by the surveyor to "witness" survey points. Forest historians in the early 1900s realized the ecological value of witness trees, because they provided a reference point of forest species composition during a period when European land uses had not substantially altered the North American landscape (Sears 1925). Witness tree records, although not originally intended to sample historic forest conditions, remain one of the most valuable quantitative records of the forest condition from the period of European settlement (Liu et al. 2011). In this study, we propose to use the frequency of sprout-origin trees used for witness trees as a representation of importance of disturbance on the pre-European settlement landscape. Trees sprout in response to damage to the main stem (Lamont et al. 2011); therefore, frequency of sprout-origin trees indicates a history of tree damage that can serve as a proxy for frequency of disturbance (Del Tredici 2001).

In the North American eastern deciduous forest, many tree species have the ability to stump sprout after the main stem is damaged by fire, wind, or harvesting. In management of forests for timber production, stump sprouts provide a valuable source of regeneration, especially on infertile sites (Lamson 1976). Their economic importance means we have fairly accurate measurements of stump sprouting rates following timber harvesting. Following clear-cutting, 72% of yellow poplar (*Liriodendron tulipifera* L.), 90% of red maple (*Acer rubrum* L.), and 84% of chestnut oak (*Quercus montana* Willd.) stumps produced at least one sprout (Mann 1984). After thinning, stump sprout rates were 91% for yellow poplar, 95% for red maple, and 86% for chestnut oak (Keyser and Zarnoch 2014). Surveys of postharvest sites report that 10%–53% of the reproduction is in the form of double- or multiple-sprouts originating from the single stem form (Wendel and Trimble 1968). In western conifer forests, the multiple-stem form occasionally results from germination of several seeds from a wildlife food cache; however, in eastern forests, sprout-origin trees are an indication of sprouting following damage to the original parent tree (Linhart and Tomback 1985).

Sprouting behavior following natural disturbance is less well documented than sprouting following harvesting. Much of what we know about non-harvest-related sprouting comes from experiments where researchers mimicked natural disturbance events to study regeneration patterns. In two studies of artificially created canopy gaps, sprouts accounted for 26%–87% of initial regeneration; however, survivorship of sprouts was not sustained, and by the time stems reached >5 cm diameter at breast height (dbh, 1.3 m), sprouts only accounted for 11% of surviving trees (Dietze and Clark 2008; Barker Plotkin et al. 2013). With controlled burning, vigorous sprouting occurred in fire-damaged trees, but repeated controlled burns reduced the vigor and frequency of sprouting, perhaps because of a lack of belowground carbon reserves (Arthur et al. 2015). One of the only studies that examined historical fire and long-term survivorship of sprouts found that black oak (*Quercus velutina* Lam.) developed multiple sprouts 1–2 years after the fire and that multiple sprout origin stems from a common parent survived to maturity (Dinh et al. 2015).

In post-European settlement, sprout-based regeneration of hardwood trees dominates large areas of the southern Appalachian Mountains because forests regularly experience a suite of interacting disturbances (Dietze and Clark 2008). Dendroecological reconstructions of disturbance have identified disease, drought, fire, hurricanes, ice storms, individual tree gap dynamics, and insect outbreaks as factors that regularly impact tree growth and mortality (Lafon 2004; van de Gevel et al. 2012; Butler et al. 2014; Copenheaver et al. 2014). In lands that are not actively managed for timber production, forests have increased in the frequency of hardwood species capable of vigorous sprouting following periods of forest clearance, agriculture, and land abandonment (Flatley and Copenheaver 2015). In managed forests, sprouts from cut stumps are often relied on as important source of regeneration (Keyser and Loftis 2015). In present-day eastern deciduous forest of the southern Appalachian Mountains, sprouts are the primary form of regeneration; however, we do not know whether this represents a shift in regeneration patterns associated with European settlement.

Therefore, the objectives of this project were to (*i*) evaluate the potential of using tree form in witness tree records to quantify disturbance in the southern Appalachian Mountain region during early European settlement; (*ii*) identify species differences in sprout-origin trees from land survey records; and (*iii*) compare the frequency of sprout-origin trees across four physiographic provinces (Piedmont, Blue Ridge, Ridge and Valley, and Cumberland Plateau) to identify potential landscape differences in historical disturbance regimes.

Methods

Study area and historical dataset

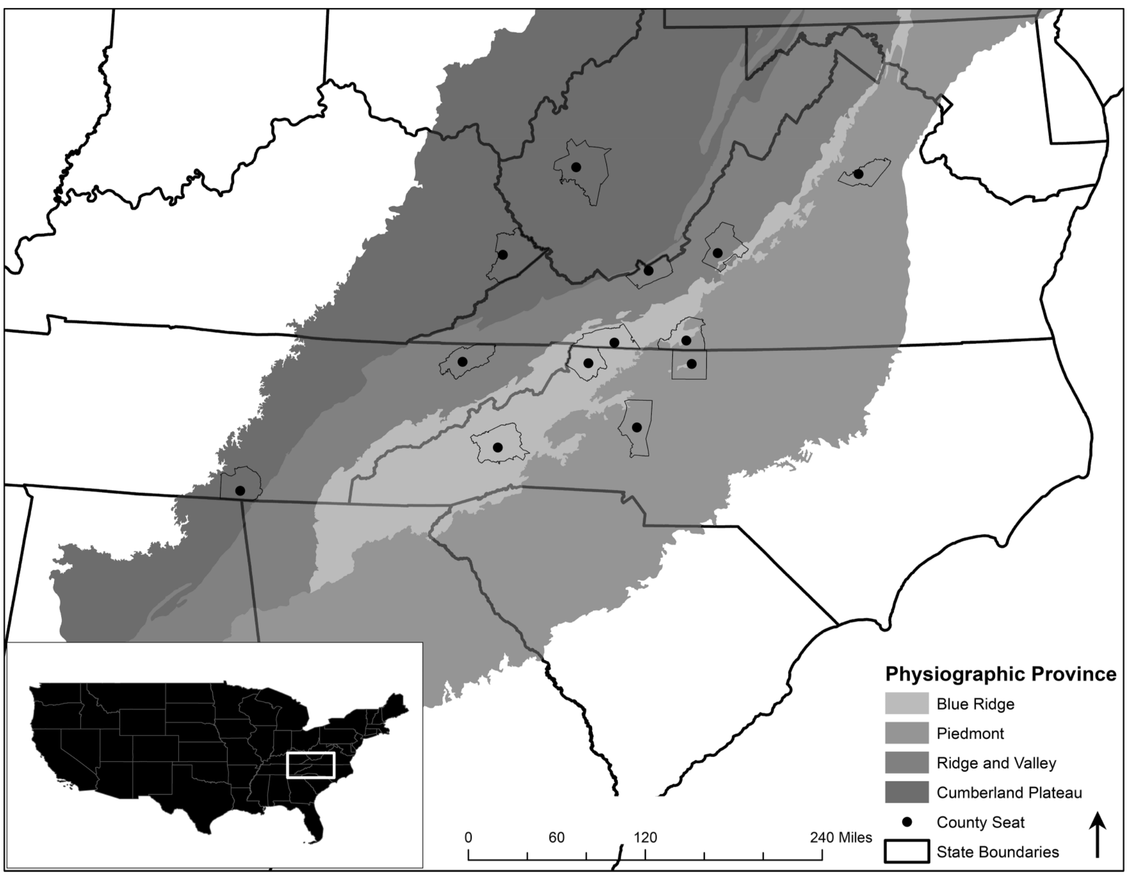
We selected 13 counties spanning four physiographic provinces that are centered on the southern Appalachian Mountains: Piedmont, Blue Ridge, Ridge and Valley, and Cumberland Plateau (Table 1; Fig. 1). The physiographic provinces are a part of the eastern deciduous forest, but there are slight variations in species dominance caused by topography and associated edaphoclimatic gradients. Forests of the rolling Piedmont physiographic province are uniformly dominated by white oak (*Quercus alba* L.), with other important species being black oak, chestnut oak, mockernut hickory (*Carya tomentosa* (Lam.) Nutt.), pignut hickory (*Carya glabra* (Mill.) Sweet), red maple, scarlet oak (*Quercus coccinea* Muenchh), shagbark hickory (*Carya ovata* (Mill. K. Koch), sycamore (*Platanus occidentalis* L.), white ash (*Fraxinus mericana* L.), and yellow poplar (Gemborys 1974; Farrell and Ware 1991). The forests of the more mountainous Blue Ridge physiographic province are dominated by red oak (*Quercus rubra* L.), sugar maple (*Acer saccharum* Marshall.), sweet birch (*Betula lenta* L.), and white ash (Abrams et al. 1997; van de Gevel et al. 2012). Forest composition in the Ridge and Valley is dominated by chestnut oak, red maple, red oak, scarlet oak, and white oak (Adams and Stephenson 1983). The Cumberland Plateau's forests are dominated

Table 1. Counties from which witness trees were collected from land survey records.

State	County	County seat	Location of county seat	Time period of land records	Total no. of witness trees
Piedmont					
Virginia	Orange	Orange	38.2458°N, 78.1097°W	1734–1737	1258
Virginia	Patrick	Stuart	36.6403°N, 80.2739°W	1790–1800	3454
North Carolina	Stokes	Danbury	36.4094°N, 80.2089°W	1788–1793	1430
North Carolina	Iredell	Statesville	35.7867°N, 80.8786°W	1788–1793	1710
Blue Ridge					
Virginia	Grayson	Independence	36.6228°N, 81.1517°W	1793–1802	2995
North Carolina	Ashe	Jefferson	36.4200°N, 81.4689°W	1799–1802	2059
North Carolina	Buncombe	Asheville	35.5800°N, 82.5558°W	1805–1808	1985
Ridge and Valley					
Virginia	Botetourt	Fincastle	37.4994°N, 79.8767°W	1770–1773	3290
Virginia	Giles	Pearisburg	37.3292°N, 80.7325°W	1806–1818	5612
Tennessee	Hawkins	Rogersville	36.4167°N, 83.0000°W	1788–1801	2029
Cumberland Plateau					
West Virginia	Kanawha	Charleston	38.3472°N, 81.6333°W	1790–1801	2166
Kentucky	Pike	Pikeville	37.4772°N, 82.5300°W	1822–1833	3358
Tennessee	Marion	Jasper	35.0750°N, 85.6281°W	1819–1830	1457

Note: Physiographic provinces (Piedmont, Blue Ridge, Ridge and Valley, and Cumberland Plateau) are listed from east to west, and within physiographic provinces, counties are listed from north to south.

Fig. 1. The historical land survey data were gathered from 13 counties that spanned four physiographic provinces in the southern Appalachian Mountains.



by beech (*Fagus grandifolia* Ehrh.), black oak, chestnut oak, mockernut hickory, red maple, red oak, scarlet oak, shagbark hickory, shortleaf pine (*Pinus echinata* Mill.), sourwood (*Oxydendrum arboreum* (L.) DC), sugar maple, and white oak (Hart and Grissino-Mayer 2008; Hart et al. 2012).

Each county government archives land survey books that date from the establishment of the county. We transcribed all of the witness trees from land survey descriptions included in the oldest deed book from each county (the one exception was Buncombe County, North Carolina, where we transcribed the first two books because the first book contained relatively few land surveys). The land descriptions contained distances, directions, and references to witness trees used to identify the location of survey points. For example, a 31 ha land parcel sold in Giles County, Virginia, on 29 September

1806, was described as follows (n.b., bearings are abbreviated as N47W for north 47 degrees west):

> "beginning at a black oak corner to Thomas Shannon's land and runneth thence N47W 34 poles to a lynn and two chestnuts N82W 88 poles to a chestnut and 2 dogwoods S50W 20 poles thence N70W 30 poles to two chestnuts growing from one root S9W 26 poles to two chestnuts S27E 122 poles crossing Sugar Run to a chestnut and cucumber in a hollow S77E 56 poles to a chestnut and cucumber in a hollow S77E 56 poles to a chestnut oak on a north hill side N10E 48 poles to a lynn and white walnut on a line of his own lands and running N71W 80 poles to two poplars and running thence N67E 123 poles to the beginning". (Giles County Deed Book A, page 50)

For each county, all witness trees were tallied, by species, into four categories: single-stem tree, sprout-origin tree, sapling, and dead. When only the species was identified, the tree was classified as a single-stem tree. Sprout-origin trees were identified in different ways depending on the surveyor. We classified a tree as being of sprout origin if it was described as bunch, bush, cluster, double, forked, grub, three forked, three pronged, triple, twin, shrub, two from one root, three from one root, four from one root, or a bunch growing from one root. It was not unusual for a survey point to include more than one witness tree, e.g., the two yellow poplars mentioned in the above example. However, these were not classified as sprout-origin trees because the surveyors differentiated between two trees witnessing the same survey point and two stems that shared a common root. This is evidenced in a land description from Grayson County, Virginia's Deed Book 1, page 500, which identifies a survey point as witnessed by "two white oaks, one of them double". A tree was classified as a sapling if it was identified as small or a sapling. Dead trees were described by surveyors as broke, dead, dry, fallen, fallen down, lying down, stumps, or thunderstruck.

The handwritten deeds recorded in county courthouses provided substantially more detailed information about individual witness trees than the more commonly employed connected drafts or township contiguous warrantee maps (Black and Abrams 2001; Thomas-Van Gundy and Strager 2012). The connected drafts only report the tree species, but deed records were intended for land surveyors to be able to relocate specific witness trees. Therefore, they commonly included detailed descriptions of individual trees, e.g., "a black oak with a flint stone growing in its base" (Iredell County, North Carolina's Deed Book A, page 492) and "a white oak marked T with a tomahawk" (Kanawha County, West Virginia's Deed Book A, page 217). However, the metes-and-bounds witness trees lack information included with "bearing trees" recorded in the rectangular land survey system and some private land surveys that would have allowed quantification of surveyor biases in selection of trees. Bearing trees from the rectangular survey system have distance and bearing from the survey point and often included a diameter measurement of the tree (White 1991). This additional information is used to identify surveyor biases (Kronenfeld and Wang 2007). Favored species or tree sizes will have a longer average distance because surveyors traveled further to select those individuals. Because metes-and-bounds witness trees lack this additional information, it is not possible to identify tree-specific biases from the survey data. Thus, it was impossible to ascertain whether surveyors would have favored single-stem trees, sprout-origin trees, saplings, or dead trees. Another resource commonly employed to identify potential biases in tree selection by land surveyors are government manuals that outline the standards and methods for surveying public and private lands. The survey manual that would have been current with the collection of this data was the Land Ordinance of 1785, which provided surveyors with explicit instructions about how to establish the rectangular survey system in new territory (Cazier 1978). However, our study site in the southern Appalachian Mountains was already settled. Therefore, surveyors continued to use the less formalized, colonial-era, metes-and-bounds survey method. For the land surveys used in this study, it is not possible to identify whether surveyors were biased for or against the use of multiple-stemmed trees as witness trees from survey instructions. The inability to quantify a potential bias in selection of witness trees based on tree form does not negate the value of examining patterns of tree form from witness tree records, but it does suggest that we should view the results with the understanding that biases may have existed.

Data analysis

We used χ^2 contingency table analysis to evaluate whether tree species varied in the distribution of tree type (single stem, sprout origin, or sapling) used in the historical land surveys. One of the assumptions of the χ^2 contingency table test is that fewer than 20% of the expected values should be less than five individuals and none should be less than one individual (Devore and Farnum 2005). Therefore, we discarded all dead trees and were unable to include minor tree species in this analysis, because they did not have a sufficiently large sample size to meet this assumption. Thus, this analysis was completed with 23 of the most frequently occurring tree species used by the land surveyors.

We used χ^2 contingency table analysis to evaluate whether the distribution of witness tree type (single stem, sprout origin, sapling, or dead) used in historical land surveys varied across the four physiographic provinces: Piedmont, Blue Ridge, Ridge and Valley, and Cumberland Plateau. The witness tree data served as the observed values for this test, and the test was evaluated at an α level of 0.05. The sample size was sufficiently large that we met all of the requirements for this test.

Results

Species-level analysis

A total of 58 species were identified by land surveyors and used as witness trees in the 13 counties examined in this study. Witness trees varied significantly ($\chi^2 = 1062$, $P < 0.00001$), by species, in their distribution across stem form classes. Basswood (*Tilia americana* L.) had the highest proportion (12%) of witness trees of sprout origin (Table 2). There were three trees that had a modest proportion of sprout origin stems: hickory (6%), red maple (6%), and sycamore (6%). White oak and hickory had the highest proportion of saplings (both 11%) used as witness trees. Black oak and locust (*Robinia pseudoacacia* L.) had a moderate (9%) proportion of saplings. Note that rare species, dead trees, and species that never had sprout-origin trees in the witness tree record were not included in this analysis. One minor species that had a high proportion of sprout-origin tree was red bud (*Cercis canadensis* L.) with 15%. Dead trees were seldom used as witness trees; however, they were present in some land survey records. Butternut (*Juglans cinerea* L.) had the highest proportion of witness trees that were dead snags or stumps (2%). There were 15 species used as witness trees with no stems described as being of sprout origin. However, it should be noted that most of these species were rarely selected as witness trees. Therefore, the lack of sprout-origin trees is more likely an indication of inadequate representation of a species rather than inability to sprout following damage. Note the small sample sizes for those species that lacked individuals of sprout origin: boxelder ($n = 19$, *Acer negundo* L.), crab apple ($n = 8$, *Pyrus coronaria* L), eastern red cedar ($n = 16$, *Juniperus virginiana* L.), hackberry ($n = 30$, *Celtis occidentalis* L.), hawthorne ($n = 3$, *Crataegus* spp.), holly ($n = 24$, *Ilex opaca* Aiton.), ironwood ($n = 44$, *Carpinus caroliniana* Walter.), mountain ash ($n = 9$, *Sorbus americana* Marshall.), mountain laurel ($n = 3$, *Kalmia latifolia* L.), pawpaw ($n = 18$, *Asimina triloba* (L.) Dunal.), pin oak ($n = 7$, *Quercus palustris* Muenchh.), swamp white oak ($n = 6$, *Quercus bicolor* Willd.), sweet gum ($n = 52$, *Liquidambar styraciflua* L.), water oak ($n = 58$, *Quercus nigra* L.), and wahoo ($n = 3$, *Euonymus atropurpureus* Jacq.).

Landscape-level analysis

The ratio of stem form used for witness trees was not the same across all four physiographic provinces ($\chi^2 = 814$, $P < 0.00001$). The

Table 2. Common witness trees reported in land surveys from 1734 to 1830 in 13 counties in the southern Appalachian Mountains.

Common name	Scientific name	Single-stem trees	Sprout-origin trees	Saplings
Ash	*Fraxinus* L.	511 (90%)	14 (3%)	39 (7%)
Basswood	*Tilia americana* L.	349 (87%)	48 (12%)	4 (1%)
Beech	*Fagus grandifolia* Ehrh.	1976 (96%)	23 (1%)	57 (3%)
Black gum	*Nyssa sylvatica* Marshall.	557 (91%)	4 (1%)	45 (7%)
Black oak	*Quercus velutina* Lam.	2074 (89%)	36 (2%)	204 (9%)
Black walnut	*Juglans nigra* L.	400 (93%)	11 (3%)	17 (4%)
Buckeye	*Aesculus flava* Aiton.	319 (94%)	8 (2%)	9 (3%)
Chestnut	*Castanea dentata* (Marshall) Borkh	1996 (95%)	80 (4%)	24 (1%)
Chestnut oak	*Quercus montana* Willd.	609 (94%)	16 (3%)	21 (3%)
Dogwood	*Cornus florida* L.	723 (90%)	36 (5%)	49 (6%)
Elm	*Ulmus* L.	249 (90%)	8 (2%)	21 (8%)
Hickory	*Carya* Nutt.	1844 (87%)	45 (6%)	238 (11%)
Locust	*Robinia pseudoacacia* L.	257 (89%)	2 (1%)	27 (9%)
Pine	*Pinus* L.	1447 (95%)	14 (1%)	50 (3%)
Post oak	*Quercus stellata* Wangenh.	856 (92%)	12 (1%)	57 (6%)
Red maple	*Acer rubrum* L.	617 (89%)	41 (6%)	33 (5%)
Red oak	*Quercus rubra* L.	1474 (95%)	20 (1%)	64 (4%)
Scarlet oak	*Quercus coccinea* Muenchh	1195 (94%)	22 (2%)	43 (3%)
Sourwood	*Oxydendrum arboretum* (L) DC	216 (93%)	5 (2%)	12 (5%)
Sugar maple	*Acer saccharum* Marshall.	943 (95%)	17 (2%)	27 (3%)
Sycamore	*Platanus occidentalis* L.	360 (94%)	24 (6%)	1 (0.3%)
Yellow poplar	*Liriodendron tulipifera* L.	1207 (94%)	43 (3%)	21 (2%)
White oak	*Quercus alba* L.	8472 (87%)	182 (2%)	1047 (11%)

Note: Values are presented at total number (proportion). Species did not have the same ratio of individuals in each stem form (single stem trees, sprout-origin trees, or saplings), indicating some species were more likely to have reproduced from sprouts than others. Witness trees classified as dead are not shown in this table.

Blue Ridge had the highest proportion of witness trees that were of sprout origin (3.6%) and the Piedmont had the lowest proportion at 1.4% (Table 3). The higher proportion of sprout-origin trees does not appear to be attributed to a transition in species, because common species that grew in all four physiographic provinces showed a general pattern of a higher proportion of sprout-origin stem form in the witness trees from the Blue Ridge (Table 4). The Ridge and Valley had the highest proportion of witness trees that were saplings (9.8%), and this was closely followed by the Blue Ridge with 9.7% (Table 3). The lowest percentage was found in the Cumberland Plateau, where only 2.3% of the witness trees were saplings. All four physiographic provinces had a small proportion of dead trees that were used to witness a survey point, and these percentages ranged from 0.2% in the Cumberland Plateau to 0.4% in the Blue Ridge.

Table 3. Witness trees used in land surveys in 13 counties between 1734 and 1830.

Physiographic province	Single-stem trees	Sprout-origin trees	Saplings	Dead
Piedmont	7493 (95.4%)	113 (1.4%)	222 (2.8%)	23 (0.3%)
Blue Ridge	6081 (86.3%)	257 (3.6%)	684 (9.7%)	28 (0.4%)
Ridge and Valley	9604 (87.6%)	258 (2.4%)	1073 (9.8%)	30 (0.3%)
Cumberland Plateau	6738 (95.9%)	113 (1.6%)	162 (2.3%)	14 (0.2%)

Note: Values are presented at total number (proportion).

Discussion

Witness tree records from metes-and-bounds surveys have always been more challenging to use as a proxy record of pre-European settlement forest conditions compared with bearing tree records from rectangular public land surveys. Cogbill et al. (2002) described witness tree data from the northeastern United States as being "unregulated and unstandardized…obscure and found in widely scattered repositories". These challenges explain why most northeastern researchers use secondary sources, known as connected drafts or township contiguous warrantee maps, rather than the original handwritten deeds (Black and Abrams 2001; Thomas-Van Gundy and Strager 2012). However, in the southeastern United States, so many courthouse records were destroyed during the Civil War that it is impossible to reconstruct a connected draft of original land surveys because of the extensive spatial gaps in the data. In Virginia, 45 counties experienced catastrophic or considerable loss of courthouse records, e.g., in Caroline County, "deed books prior to 1836…were stolen, mutilated, and (or) destroyed by Union troops who ransacked the courthouse in May 1864" (Anonymous 2010). Despite the limitations and challenges of using metes-and-bounds witness tree records in the southeastern United States, the information uncovered in this study reveals unexpected shifts in patterns of forest regeneration that we would not have been able to discover without the use of historical metes-and-bounds survey records.

Sprout-origin trees represent only 3% of the witness trees used in land survey records from the period of early European settlement in the southern Appalachian Mountains. This indicates that most trees did not depend on sprouting for regeneration. We recognize that the proportion of sprout-origin trees was likely higher than 3%, because not all sprouts survive to maturity. However, survival of double or triple stems to maturity is the norm for eastern deciduous forests. Trees initially produce multiple sprouts from a cut or damaged stump, and although there is a high rate of mortality among this initial cohort of sprouts, more than one sprout typically survives to maturity. Red oak has the highest survivorship of sprouts, with mature, sprout-origin red oak averaging four stems per stump (Johnson 1975). Sprout-origin black oak, chestnut oak, and white oak are more likely to be double stemmed rather than multiple stemmed (McIntyre 1936; McQuilkin 1975; Gould et al. 2007). The frequent survival of double or triple stems into maturity has led silviculturists from this region to recommend thinning sprouts to a single stem to improve stand growth rates (Lamson 1976). Sprout survivorship studies validate interpreting witness tree stem form as an indication of sprout origin (Keyser and Zarnoch 2014). However, this leaves the important question of why sprout-origin trees were less common in pre-European settlement forests. In present-day, harvest-origin forests, sprout-origin trees comprise

Table 4. Proportion (%) of sprout-origin trees used in land survey records from 13 counties between 1734 and 1830 in the southern Appalachian Mountains.

	Physiographic province			
Common name	Piedmont	Blue Ridge	Ridge and Valley	Cumberland Plateau
Ash	1.4	8.1	2.1	2.3
Basswood	9.1	20.0	10.8	11.8
Beech	1.6	4.4	1.8	0.8
Black gum	1.5	0.7	0.8	0.0
Black oak	2.2	2.6	0.9	0.0
Black walnut	0.0	0.0	4.3	0.0
Buckeye	0.0	1.8	3.7	1.7
Chestnut	2.3	4.6	4.3	5.1
Chestnut oak	0.8	4.2	1.8	7.3
Dogwood	1.2	16.3	4.1	1.2
Elm	0.0	0.0	5.4	0.9
Hickory	2.3	2.8	2.4	0.3
Locust	0.0	0.9	0.8	0.0
Pine	0.3	2.0	1.0	1.4
Post oak	1.9	0.0	0.0	0.0
Red maple	0.8	19.2	3.2	3.6
Red oak	0.8	2.4	1.0	2.5
Scarlet oak	0.8	2.4	1.0	3.1
Sourwood	1.1	0.0	3.5	3.1
Sugar maple	0.0	1.5	3.6	0.7
Sycamore	0.0	4.3	11.2	4.6
Yellow poplar	1.7	4.5	1.6	2.3
White oak	1.4	3.0	1.6	1.1

Note: The 13 counties spanned four physiographic provinces, and results are shown by province.

75% of the individuals and 50% of the basal area (Ebinger 1973). However, in pre-European settlement forests, only 2% of oaks recorded as witness trees had double or multiple stems, meaning the vast majority of oak trees were of seedling rather than sprout origin. Given the inverse relationship between tree diameter and probability of stump sprouting (Keyser and Loftis 2015), it may be possible that pre-European settlement forests had a greater proportion of larger diameter trees and this stand structure reduced the likelihood of regeneration from sprouts after damage to the original stem. Additionally, natural disturbance events such as wind storms resulted in fewer trees sprouting after stem damage (Peterson 2000) than occurred when trees were felled during harvesting. Unfortunately, metes-and-bounds witness trees do not include stem diameter, and therefore, it is not possible to reconstruct diameter distributions of historical stands.

Fewer sprout-origin trees in pre-European settlement forests could result from either more trees regenerating from seed (resulting in a higher frequency of single-stem trees) or a lower survivorship of sprouts (resulting in a higher frequency of single-stem trees). In Chinese forests, multi-stemmed snakebark maple (*Acer tegmentosum*) decrease in frequency in stands with higher basal area because of self-thinning of sprouts induced by competition for light (Ye et al. 2014). Silvicultural studies on oak stump sprouts have reported a decline in survivorship with reduced light availability in the understory (Dey et al. 2008). Disturbances caused by allogenic events that create high-light conditions in the understory, e.g., hurricanes, insect outbreaks, ice storms, timber harvesting, and sustained periods of drought (Butler et al. 2014), may be more common in present-day forests and may have resulted in both an increase in the frequency of sprouting and a higher survival of sprouts because of high-light conditions caused by extensive canopy damage.

We had hoped that examining stem form in witness tree records would reveal species-level differences in regeneration patterns under environmental conditions that predate European-style land uses. Basswood has long been identified as a species that has benefitted from the introduced of European-style forest harvesting because of its unequaled ability to sprout from cut stumps (Scholz 1958), and it has been theorized that with regular disturbance, basswood "seems to be capable of perpetuating itself indefinitely by basal sprouts" (Daubenmire 1936). The witness tree records (Table 2) show that the ability to sprout also benefitted basswood in pre-European settlement forests, and based on landscape differences in stem form (Table 4), it is likely that the disturbance that benefitted basswood during this era was fire. Basswood had its highest proportion of sprout-origin trees (20%; Table 4) in the Blue Ridge physiographic province, and other proxy records show that because of longer periods of dry weather, fire was more frequent in the Blue Ridge than in the Ridge and Valley or the Cumberland Plateau (Aldrich et al. 2014). Thus, basswood has retained a similar pattern of regenerating largely through sprouts; however, the cause of disturbance has shifted from fire during pre-European settlement conditions to harvesting in present-day forests.

Sprout-origin stem form is not always an indication of disturbance; it can also reflect a species' silvics and (or) abiotic growing conditions. In temperate forests in China, 27% of snakebark maple trees have multiple stems, but only 3% of painted maple (*Acer mono*) trees have multiple stems, and individuals growing at high elevations are more likely to have multiple stems than those growing at lower elevations (Ye et al. 2014). In this study, sycamore was a species with a relatively high proportion (6%) of sprout-origin witness trees (Table 2). In open-grown conditions, sycamore takes on the spreading, multi-stemmed shape (Wells and Schmidtling 1990) described by the surveyors. A vast majority of the surveys that used sycamore as witness trees included a description of a riparian location that would have favored the spreading crown associated in this species under open growing conditions, e.g., "crossing a part of the river to a sycamore near the upper end of an island" (Giles County, Virginia Deed Book A, page 33); "to three sycamores on the bank at the mouth of the creek" (Giles County, Virginia Deed Book A, page 55); and "at a double sycamore on the bank of the river" (Giles County, Virginia Deed Book A, page 120). Therefore, interpretation of stem form in the witness tree record must include the possibility that the stem form may be a result of the silvics of the species and the growing condition of the tree.

The introduction of extensive harvesting to the forests of the southern Appalachian Mountains has caused a shift in regeneration patterns from seedling germination and release of understory saplings in small canopy gaps to large-scale disturbances that favor sprouting and rapid revegetation (Shure et al. 2006). Studies from other forest types that have experienced a similar increase in the frequency of multi-stemmed trees have noted that these individuals occupy a larger proportion of the canopy, and therefore, stem form directly impacts canopy structure and indirectly impacts photosynthetic and growth rates of forests (Taylor et al. 2016). The witness tree records provide a historical baseline to document a decrease in the importance of seed germination as the primary source of tree establishment in pre-European settlement forests of the southern Appalachian Mountains.

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