

Long-term drought sensitivity of trees in second-growth forests in a humid region

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Abstract: Classical field methods of reconstructing drought using tree rings in humid, temperate regions typically target old trees from drought-prone sites. This approach limits investigators to a handful of species and excludes large amounts of data that might be useful, especially for coverage gaps in large-scale networks. By sampling in more “typical” forests, network density and species diversity would increase in ways that could potentially improve reconstructions. Ten nonclassical tree-ring chronologies derived from randomly selected trees, trees from logged forests, or both were compared to more classical chronologies and an independent regional drought reconstruction to determine their usefulness for dendrohydroclimatic research. We find that nonclassical chronologies are significantly correlated to classical chronologies and reconstructed drought over the last 2–3 centuries. While nonclassical chronologies have spectral properties similar to those from classical dendroclimatic collections, they do lack spectral power at lower frequencies that are present in the drought reconstruction. Importantly, our results show that tree growth is strongly dependent on moisture availability, even for small, randomly selected trees in cut forests. These results indicate that there could be more data available in areas with few current tree-ring collections for studying climate history and that drought plays an important role in humid forests.

Résumé : Les méthodes de terrain classiques pour reconstituer les périodes de sécheresse à l'aide des cernes des arbres dans les régions tempérées humides ciblent typiquement les vieux arbres dans les stations sujettes à la sécheresse. Cette approche limite les chercheurs à une poignée d'espèces et exclut de grandes quantités de données qui pourraient être utiles, particulièrement pour les bris de couverture dans les réseaux à grande échelle. En échantillonnant dans des forêts plus typiques, la densité des réseaux et la diversité des espèces augmenteraient, ce qui pourrait améliorer les reconstitutions. Dix séries dendrochronologiques non classiques dérivées d'arbres choisis au hasard, d'arbres provenant de forêts coupées, ou des deux, ont été comparées à des séries dendrochronologiques plus classiques et à une reconstitution indépendante des périodes de sécheresse régionale pour déterminer leur utilité pour la recherche en dendrohydroclimatologie. Nous avons trouvé que les séries dendrochronologiques non classiques sont significativement corrélées avec les séries dendrochronologiques classiques et avec les périodes de sécheresse reconstituées au cours des derniers deux à trois siècles. Alors que les séries dendrochronologiques non classiques ont des propriétés spectrales semblables à celles des collections dendroclimatiques classiques, elles n'ont pas la puissance spectrale aux fréquences plus faibles qui est présente dans la reconstitution des périodes de sécheresse. Nos résultats montrent surtout que la croissance des arbres est fortement dépendante de l'humidité disponible, même celle des petits arbres choisis au hasard dans les forêts coupées. Ces résultats indiquent que plus de données pourraient être disponibles dans les régions qui comptent actuellement peu de collections dendrochronologiques pour l'étude du climat passé et que la sécheresse joue un rôle important dans les forêts humides.

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Introduction

Many classical, tree-ring based drought reconstructions target trees from old-growth forests or forests that are largely undisturbed by human land use. However, the amount of old-growth forest in humid regions is low. As one example, the amount of old-growth forest (defined here

as forests with no logging history) in the eastern United States represents approximately 0.5% of the forested landscape (Davis 1996). Regions with productive soils, low topographical relief, and a relatively high amount of rainfall have even less old-growth forest. For the North American Drought Atlas (NADA) (Cook et al. 2010), this results in gaps of the underlying tree-ring network. Although the awareness

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and discovery of old-growth forest increased during the 1990s (Davis 1996), there is little guarantee that old-growth forests will remain intact, i.e., retain the natural integrity of structure and function in old, uncut forests. In addition to the threat of future pests and diseases, old-growth forest is still being lost due to logging. Therefore, when following the classical approach of relying upon old-growth forests, the amount of land that can be used for climatic reconstructions is extremely limited.

Another classical approach for reconstructing drought in humid to perhumid environments is to target trees growing on dry sites with low water-holding capacity or high evaporative demand. This has many benefits. First, dry sites have lower productivity and are less likely to have been extensively logged. In fact, low productivity sites are some of the better places to search for old-growth forests in humid regions (Stahle and Chaney 1994). Second, because drier sites tend to be lower in productivity, they tend to have lower tree density and less tree-to-tree competition. Because of this, ring width patterns of trees from more xeric sites in humid region are more likely to be driven by climatic variation than by disturbance. Third, trees on dry sites tend to be mostly drought sensitive (e.g., Cook and Jacoby 1977; Stahle and Cleaveland 1988), although there exceptions such as baldcypress (*Taxodium distichum* (L.) Rich.) growing in wetlands (Stahle and Cleaveland 1992). Finally, recent evidence suggests that trees growing on adverse sites or experiencing suppression or negative climatic conditions tend to have greater longevity (e.g., Black et al. 2008; Di Filippo et al. 2012). Thus, the targeting of trees on drought-prone sites in humid environments often results in older trees with stronger drought signals than disturbance signals embedded in their rings.

There is an important limitation, however, to targeting drier sites in humid environments. Sampling only dry sites can limit investigators to a handful of species. In eastern North America, this roughly translates to <10% of the 300+ canopy tree species. This is an important limitation because recent work indicates that a multispecies network improves climate reconstructions (García-Suárez et al. 2009; Cook and Pederson 2011; Maxwell et al. 2011; Pederson et al. 2012b). And, considering the increased rate of species extinction, new sources of dendroclimatic material are needed. Hemlock (eastern hemlock (*Tsuga canadensis* (L.) Carrière) and Carolina hemlock (*Tsuga caroliniana* Engelm.)), a commonly used dendroclimatic species (Hessl and Pederson 2013), is becoming functionally extinct over much of its range. The discovery of new dendroclimatically sensitive species is important for future studies.

Fortunately, the number of scientists using tree rings to study past environments over the past two decades has increased. Many of these scientists are collecting samples for reasons other than reconstructing climate history and, sometimes, in forests with a significant amount of human disturbance (e.g., Druckenbrod and Shugart 2004; Davis et al. 2009; Hart et al. 2012). If some of these data are useful for paleoclimatic investigations, there can be an increase in the spatial density and species diversity of chronologies for paleoclimatic research.

Here, we explore a new approach to dendropaleoclimatic research in two ways. First, we examine the long-term radial growth patterns of trees from second-growth forests. Second, Cook (1982) suggested that site selection for dendrohydroclimatic research does not matter as one might suppose in the temperate forests of humid, eastern North America — tree age is more important. Here, we test the conjecture by using tree-ring collections from forests with different land-use histories and site types. The exploration of data from different forest types gives us the opportunity to investigate the usefulness of new species as possible replacements for hemlock. Finally, some of the new collections used here also allow us to compare radial growth of “typical” trees (trees from randomly placed plots in logged forests) versus targeted trees. This analysis will give insight to the long-term climatic sensitivity of much of today’s forests.

Eastern Kentucky is a good region to conduct this investigation, as (1) there are currently only two chronologies in NADA for eastern Kentucky and (2) the long and heavy land-use history in this region has created at least one anthropogenic ecosystem (McEwan and McCarthy 2008); forests thought to be old-growth turn out to have much anthropogenic disturbance (Cooper 2011). Additionally, the considerable topographical variation in eastern Kentucky could play a role in tree growth across our network. If coherency between these records is found at short and long time scales, it suggests that climate influences radial growth across contrasting land uses and site types. Therefore, our investigation will provide insight into the usefulness of tree-ring records from nonclassical sites for regions with little old-growth forest.

Methodology

Study region and sites

Our 10 new chronologies are distributed over three physiographic provinces and span approximately 4200 km². Collections were made in 10 areas (Fig. 1; Table 1; Supplemental Material: Additional Site History Information, Fig. S1).¹ Five of these areas are in the London Ranger District of the Daniel Boone National Forest, while the remaining collections are from forest preserves. In this region, average total annual precipitation is 1194.3 mm, while average temperature is 1.6 °C in January and 24.0 °C in July (NOAA’s National Climatic Data Center: <http://www.ncdc.noaa.gov/temp-and-precip/time-series/>).

The London Forest tulip-poplar (*Liriodendron tulipifera* L.) was derived from the 2706 ha Cane Creek Wildlife Management Area in the Daniel Boone National Forest, a multiaged, mature second-growth ravine forest comprised of hemlock and mixed-mesophytic species (Tackett 2012), and the nearby Angel Hollow forest, an old forest with evidence of anthropogenic disturbance (Cooper 2011; Supplemental Material Fig. S1c). The proximity of the two sites and high correlation between both sites ($r = 0.607$ for the common period with at least four cores, 1780–2007, $p < 0.0001$) allowed for the combination of the *L. tulipifera* collections. Collections of white oak (*Quercus alba* L.), chestnut oak (*Quercus montana* Willd.), and *T. canadensis* were made in the old-growth forest at Blanton Forest, a 1264 ha preserve where approximately

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/x2012-130>.

Fig. 1. Map of the eastern Kentucky tree-ring network used here. Three chronologies were collected in Blanton Forest, while two were collected from Griffith Woods. Chronologies were created from cores at Rock Creek and Cane Creek (see Fig. 2d) and Rock Creek and Angel Hollow (see Fig. 2i). Lilley Cornett Woods and Mammoth Cave, chronologies collected in the 1980s, are a part of the North American Drought Atlas.

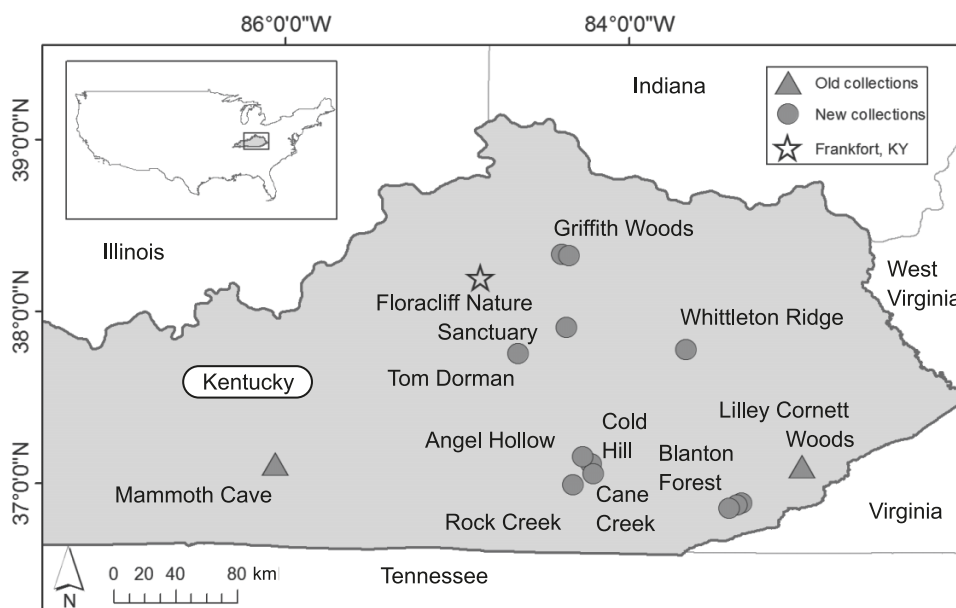


Table 1. Chronology statistics for new chronologies from the eastern Kentucky network.

Site	Chronology species	Trees (series)	Interval	Mean segment length (years)	Series intercorrelation	% series gap-filled	EPS	rbar	Forest status	Sampling strategy
London Forest	<i>Liriodendron tulipifera</i>	13 (24)	1633–2007	224	0.577	17	0.938	0.379	Man	Random ^a
Blanton Forest	<i>Quercus alba</i>	12 (29)	1673–2005	260	0.543	0	0.916	0.327	OG	Targeted
Blanton Forest	<i>Quercus montana</i>	16 (32)	1670–2005	240	0.504	21	0.917	0.267	OG	Targeted
Blanton Forest	<i>Tsuga canadensis</i>	16 (31)	1684–2006	180	0.579	13	0.942	0.337	OG	Targeted
London Forest	<i>Tsuga canadensis</i>	23 (38)	1725–2006	107	0.467	0	0.880	0.254	Man	Random ^a
Cold Hill, DBNF	<i>Quercus</i> subgenus <i>Leucobalanus</i>	26 (28)	1731–2005	83	0.483	0	0.761	0.268	Man	Random
Floracliff	<i>Quercus muehlenbergii</i>	29 (56)	1612–2008	239	0.538	0	0.948	0.336	Man	Targeted
Griffith Woods	<i>Fraxinus quadrangulata</i>	18 (19)	1752–2008	147	0.542	5	0.823	0.367	Man	Targeted
Griffith Woods	<i>Quercus muehlenbergii</i>	35 (35)	1683–2008	168	0.517	0	0.904	0.331	Man	Targeted
Whittleton Ridge	<i>Quercus montana</i>	16 (32)	1695–2007	173	0.504	0	0.896	0.295	Man	Targeted
Average		20.4 (32.4)	1752–2005 ^b	182.1	0.525	5.2	0.893	0.316		

Note: DBNF, Daniel Boone National Forest. See the Methodology section for descriptions for EPS and rbar. % series gap-filled, percentage of series in each collection with gaps that were filled via the program ARSTAN. Man, managed forest; OG, old-growth forest; random, trees from randomly selected plots; targeted, trees collected through targeted sampling. See text for more details.

^aA few trees in this collection were targeted for age. See text for more details.

^bCommon interval.

67% is old-growth forest. The London Forest *T. canadensis* was composed of trees from Cane Creek and Wildlife Management Area and Rock Creek Research Natural Area, a 430 ha mixed-mesophytic forest with a mix of old-growth forest and patches of selective cutting (Tackett 2012; Supplemental Material Fig. S1b). Proximity and high correlation ($r = 0.609$ from 1780 to 2006, $p < 0.0001$) allowed for the com-

bination of these collections. The Cold Hill *Quercus* subgenus *Leucobalanus* chronology is composed of *Q. alba* and *Q. montana*. Cold Hill, on the plateau above Cane Creek, is a second-growth forest that has been logged and burned from the late 19th century to approximately the 1970s. Because replication back in time was low for both species on Cold Hill, both have a similar climatic response (Pederson et al. 2004),

and they correlate well ($r = 0.653$ from 1910 to 2005, $p < 0.0001$), samples were combined into one chronology. The Floracliff chinkapin oak (*Quercus muehlenbergii* Engelm.) is a combination of cores from Floracliff Nature Sanctuary, a 116 ha second-growth forest with abandoned agricultural land and scattered old, remnant trees, and Tom Dorman State Nature preserve, a 300 ha preserve with a similar forest structure and land-use history as Floracliff. Being geographically and ecologically similar and having high correlation between trees from both forests ($r = 0.640$ from 1710 to 2007, $p < 0.0001$) allowed for improved replication through the combination of both collections. Chronologies of blue ash (*Fraxinus quadrangulata* Michx.) and *Q. muehlenbergii* were made at Griffith Woods, a 301 ha preserve with open-grown trees in a savanna-woodland ecosystem (Supplemental Material Fig. S1a). While initially hypothesized to be a pre-European settlement ecosystem, Griffith Woods is likely anthropogenic in origin (McEwan and McCarthy 2008). Finally, the Whittleton Ridge *Q. montana* chronology was collected from a forest that was heavily cut during the 20th century (Supplemental Material Fig. S1d). Two additional chronologies were downloaded from the International Tree-Ring Databank (ITRDB). Collections of *Q. alba* were made in Mammoth Cave National Park in 1966 by E.T. Estes and in 1986 by E.R. Cook, while a collection of *Q. alba* was made from Lilley Cornett Woods in 1983 by E.R. Cook and others. Both collections targeted trees from old-growth forest. Species nomenclature follows Jones (2005).

Field methods

Standard dendroclimatological techniques were used when possible. While the oldest-looking individuals were targeted (Stahle and Chaney 1994; Pederson 2010), collections made in second-growth forest make the final chronologies a hybrid of classical and nonclassical approaches. For example, the number of old *F. quadrangulata* at Griffith Woods forest was limited. Therefore, chronology length and replication were boosted by samples from remnant forests within 20 km of Griffith Woods (see McEwan and McCarthy 2008).

Even less classical dendroclimatic sampling was employed at Angel Hollow, Cane Creek, Cold Hill, and Rock Creek. At Angel Hollow, trees >10 cm diameter at breast height (DBH) were selected using the point-center quarter transect method along 100 m transects (Cooper 2011). At Cane Creek and Rock Creek, plots were randomly located prior to field sampling and all in-plot trees ≥ 10 cm DBH were cored (Tackett 2012). Similarly, all *Q. alba* and *Q. montana* in the Cold Hill District ≥ 10 cm DBH were cored in plots placed systematically within six random locations (Schweitzer et al. 2008). The youngest *Q. alba* and *Q. montana* cored at Cold Hill, <50 years, were not used, as they would not typically be used for dendroclimatic research. To boost sample depth of older trees at Angel Hollow, Cane Creek, and Rock Creek, a few old-looking *T. canadensis* and *L. tulipifera* were cored outside the designated plots or transects (Cooper 2011; Tackett 2012). Most trees cored in these forests were collected through random selection sampling.

Project goals and collection restrictions resulted in other deviations from classical dendroclimatological methods. Sampling protocol dictated the collection of one core per tree from the Cold Hill *Q. alba* and *Q. montana* and the Griffith Woods *F. quad-*

rangulata and *Q. muehlenbergii*. Three cores per *T. canadensis* and *L. tulipifera* tree were removed at Cane Creek and Rock Creek, although only two cores per tree were used here.

Laboratory methods

All core samples were prepared using standard techniques (Cook and Kairiukstis 1990). Each core was visually cross-dated using marker rings and then measured to the nearest 0.001 mm. Visual crossdating was verified using the program COFECHA (Holmes 1983).

Raw ring width measurements for each collection were processed into separate tree-ring chronologies using the program ARSTAN (Cook 1985; Cook and Krusic 2011). A small number of cores required “gap-filling” because of sections with distorted ring widths, areas of rot, or missing sections of wood; an average of 5.2% of all series were gap-filled, although series from six collections required no gap-filling (Table 1). Gaps were modeled and filled to reduce the “segment length curse” (Cook et al. 1995; Pederson et al. 2004). Variance of all series was stabilized using the adaptive power transformation, rbar-weighted, or spline stabilization procedures (Cook and Kairiukstis 1990). Tree-ring widths were detrended to retain as much low-frequency information as possible while removing step-changes in ring width that likely arise from canopy disturbance (Cook and Peters 1981; Pederson et al. 2004). The first step of this process uses negative exponential or negative linear curves to remove trends that likely are related to decline in ring widths as the stem expands. For series lacking a negative trend in ring widths, ARSTAN automatically fit a horizontal line through the mean of the series. The second step was to go through all series following the first detrending to remove abrupt changes in ring width related to canopy disturbance using the Friedman Super Smoother (Friedman 1984). For series with no obvious change in ring width resembling a growth release, a horizontal straight line was fit through the mean. The detrended time series were combined into an annual mean for each population using a biweight robust mean function (Cook 1985). rbar, the mean correlation of all time series in a sample collection, and the expressed population signal (EPS) were used to quantify chronology quality (Cook and Kairiukstis 1990); a chronology with an EPS of 0.85 is generally considered sufficient for climatic reconstructions. The ARSTAN chronology of each collection is used in these analyses, as this chronology type is partially composed of common lower-frequency variation within a collection that is suspected to derive from outside the sampled forest and more likely to be regional climate (Cook 1985).

Principal component analysis (PCA) and varimax rotated principal component analysis (RPCA) were used to identify common patterns of growth between chronologies and to combine time series from different collections. Eigenvector rotation helps preserve factor-loading orthogonality so that each variable typically loads onto one eigenvector, which results in an increase in interpretation of retained eigenvectors (Richman 1986). The Monte Carlo “Rule-N” technique was used to determine the number of eigenvectors to retain (Preisendorfer et al. 1981). Time series of PCA scores were used to examine patterns of common variance through time.

We used multitaper spectral analysis following Mann and Lees (1996) to investigate the range of periodicities retained in

all time series. Spectral analysis identifies significant periodicities (or cycles) in a time series and can estimate the strength of the signal (or power) that resides in each periodicity. One goal in dendroclimatic research is to preserve and reconstruct changes in ring widths at low frequencies (periodicities >10 years, for example), so that long-term changes in climate can be identified. The multitaper spectral analysis method allows us to compare the power spectra of time series among series created from different field methods or forest conditions to determine their value for dendroclimatic research. Chronologies lacking power in low frequency or having spectral properties dissimilar from reconstructed drought or classical dendroclimatic chronologies could be seen as not useful for dendroclimatic research.

The final test to determine the potential usefulness of non-classical tree-ring collections for dendroclimatic research was to compare the new collections with (1) each other, (2) the classical collections at Lilley Cornett and Mammoth Cave records, and (3) reconstructed drought from the NADA covering our study region in eastern Kentucky (Cook et al. 2010) using correlation analysis and comparison of spectral properties for each record.

Results

General network characteristics

The new chronologies have a common interval from 1752 to 2005 (Table 1; Fig. 2). The longest chronology, Floracliff Nature Sanctuary *Q. muehlenbergii*, spans 1612–2007. The London Forest *L. tulipifera*, Floracliff *Q. muehlenbergii*, and Blanton Forest *T. canadensis* collections have the strongest chronology statistics, while the Cold Hill *Quercus* subgenus *Leucobalanus* and London Forest *T. canadensis* chronologies are weaker (Table 1). EPS for Cold Hill is above 0.85 for most of the 1900s, drops to 0.60 in the 1890s, and stays below 0.70 into the 1700s. Excepting the low EPS of Cold Hill *Quercus* subgenus *Leucobalanus* and Griffith Woods *F. quadrangulata* chronologies, chronology statistics are generally acceptable for tree-ring analysis (Cook and Kairiukstis 1990).

Despite relatively low replication in some chronologies during the 1800s (Fig. 2), series intercorrelation, correlation, and PCA indicate good coherency among most records (Tables 1, 2, and 3). Series intercorrelation for the 1752–2005 common period is 0.525 ($p < 0.0001$) (Table 1). One of the more striking differences is the sudden and extended drop in ring index during the 1790s of the Inner Bluegrass Province chronologies (Floracliff Nature Sanctuary and Griffith Woods). The remaining records generally show strong and extended above-average ring index during this time (Fig. 2). Because of this and some low replication before 1790, further analyses are limited to 1796–2005 where appropriate.

All chronologies load positively onto the first PCA principal component and RPCA eigenvector (Table 2). The first unrotated principal component accounts for 40.9% of the common variance among all 12 chronologies. Factor loadings on the first RPCA varimax factor (VF1), accounting for 38.8% of the common variance, are most heavily weighted by *Quercus* and the southern chronologies in our network. The second varimax factor (VF2) accounts for 14% of the variation and is composed primarily of the two *T. canadensis* chronologies. Chronologies from the northern end of the new network load most strongly on the third varimax factor (VF3) (10.2% of the

annual variance). Conspicuously, Whittleton Ridge, the northernmost collection not in the Inner Bluegrass Province, loaded almost evenly between VF1 and VF3 (Fig. 1; Table 2).

Genera and radial increment patterns within the new network

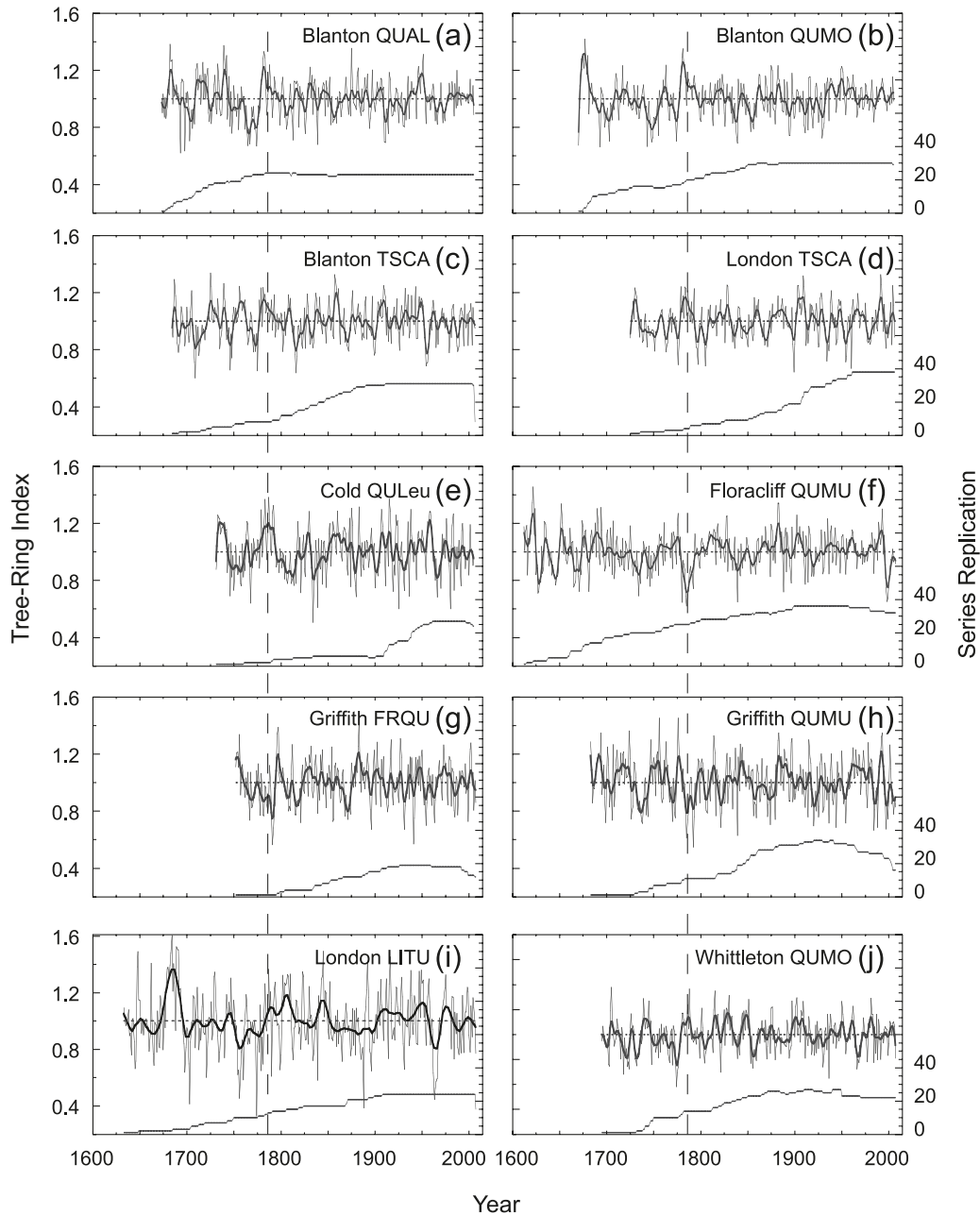
Correlation and PCA suggest that genetics matters more than geographic proximity for ring width variation (Tables 2 and 3). Four pieces of evidence indicate that the two *T. canadensis* chronologies are the most dissimilar from the network. First, these series have the lowest correlations compared with the remaining chronologies in the network (Table 3). Second, removing the *T. canadensis* chronology improves the network series intercorrelation to 0.604. Third, the second component of PCA and RPCA is primarily composed of the *T. canadensis* series. Fourth, the *Q. alba* and *Q. montana* chronologies are more highly correlated with collections of the same species from more than 90 km away than the *T. canadensis* chronologies from the same forest. In addition, genetic differences appear to be important among the angiosperms. The Griffith Woods *Q. muehlenbergii* chronology was more strongly correlated with the Floracliff Nature Sanctuary *Q. muehlenbergii* chronology than the Griffith Woods *F. quadrangulata* chronology ($r = 0.545$ versus $r = 0.460$, respectively).

Differences in genetics and radial increment can be seen in the loadings on the first unrotated principal component (Table 2). While all species load positively onto this component, the *T. canadensis* collections are the lowest loadings followed by the singleton *F. quadrangulata* and *L. tulipifera* chronologies. All *Quercus* chronologies, save the Cold Hill *Quercus* subgenus *Leucobalanus* chronology (low replication and randomly selected trees from a cut forest), load ≥ 0.308 . However, even this Cold Hill chronology loads higher (0.295) than the other genera.

Comparisons of chronologies from different treatments

In this ad hoc analysis, it is not possible to clearly separate the potential additive effects between sampling strategies and forest conditions. Despite this limitation, we make comparisons to determine if there are substantial differences in radial growth between various combinations of “treatments” (previously cut forests, old-growth forests, randomly selected trees, targeted trees) (Fig. 3). Chronologies from previously cut forests, including some records from randomly selected trees in cut forests, show strong annual correlation with and generally have multiannual coherency with chronologies from old-growth forests. Focusing on *Quercus* and *Tsuga* chronologies, significant correlation is found between the classic old-growth forest chronologies (Mammoth Caves, Lilley Cornett Woods, and three Blanton Forest collections) and logged forest chronologies (Cold Hill *Leucobalanus*, London Forest *T. canadensis*, London Forest *Liriodendron*, Whittleton Ridge, Floracliff, and Griffith Woods) (Figs. 3a and 3b; Table 3). Of note: correlation analysis and PCA both suggest that there is a potential geographic interaction within our network (Tables 2 and 3). Correlations are weaker when comparing chronologies in southern and southeastern Kentucky with collections at the northern end of our network. A similar drop in correlation is apparent from the western portion of our study area versus the eastern portion. Despite this limitation, we find significant

Fig. 2. New tree-ring chronologies in eastern Kentucky. (a) Blanton Forest *Quercus alba*, (b) Blanton Forest *Quercus montana*, (c) Blanton Forest *Tsuga canadensis*, (d) London Forest *T. canadensis*, (e) Cold Hill *Quercus* subgenus *Leucobalanus*, (f) Floracliff Nature Sanctuary *Quercus muehlenbergii*, (g) Griffith Woods *Fraxinus quadrangulata*, (h) Griffith Woods *Q. muehlenbergii*, (i) London Forest *Liriodendron tulipifera*, and (j) Whittleton Ridge *Q. montana*. Each curve has a 9 year spline to reveal multiannual variation in ring index. Dashed horizontal lines represent the mean. The two dashed vertical lines highlight the sudden and extended downturn in ring index during the 1790s that is only seen in the Inner Bluegrass Region records (Figs. 2f, 2g, and 2h).



similarities in ring width variation between trees from logged and old-growth forests. Finally, when we combine chronologies from old-growth ($n = 5$) and second-growth forests ($n = 7$) into a single time series of the first unrotated principal component of PCA for each forest condition, we find a very strong relation in annual variation over the 1796–1982 common period ($r = 0.809$, $p < 0.0001$) (Fig. 3c).

Comparisons between targeted and random sampling methods gave further insight into the usefulness of the nonclassical

tree-ring collections for dendroclimatic purposes. For a fairer comparison with the Cold Hill *Leucobalanus* chronology, the targeted classical Blanton Forest *Q. alba* and *Q. montana* collections were combined in ARSTAN using the methods above. Targeted and randomly sampled chronologies are positive and significantly correlated (London Forest *T. canadensis* versus Blanton Forest *T. canadensis*, $r = 0.472$, $p < 0.0001$; combined Blanton versus Cold Hill *Leucobalanus*, $r = 0.441$, $p < 0.0001$). Despite low replication in the Cold Hill *Leuco-*

Table 2. Varimax factor scores for rotated principal component analysis for the new chronologies from eastern Kentucky for the 1796–2005 common period.

Chronology	VF1	VF2	VF3	Loading on first unrotated principal component
Blanton Forest <i>Quercus alba</i>	0.750	–0.041	0.335	0.343
Blanton Forest <i>Quercus montana</i>	0.784	0.109	0.272	0.339
Blanton Forest <i>Tsuga canadensis</i>	0.113	0.862	0.080	0.150
London Forest <i>Liriodendron tulipifera</i>	0.705	0.087	–0.104	0.223
London Forest <i>Tsuga canadensis</i>	0.066	0.841	0.153	0.134
Cold Hill <i>Quercus</i> subgenus <i>Leucobalanus</i>	0.637	0.151	0.204	0.295
Floracliff Sanctuary <i>Quercus meuhlenbergii</i>	0.023	0.138	0.732	0.341
Griffith Woods <i>Fraxinus quadrangulata</i>	0.469	0.113	0.607	0.219
Griffith Woods <i>Quercus meuhlenbergii</i>	0.210	0.123	0.813	0.308
Whittleton Ridge <i>Quercus montana</i>	0.536	–0.040	0.522	0.320
Lilley Cornett <i>Quercus alba</i>	na	na	na	0.350
Mammoth Cave <i>Quercus alba</i>	na	na	na	0.326

Note: Scores >0.600 are in bold to emphasize the species level and geographic aspect of the network. The last column shows the loadings of all site chronologies used in this study onto the first unrotated principal component for the 1796–1982 common period. The first unrotated principal component accounts for 40.9% of the common variance among all 12 chronologies. na, not applicable.

Table 3. Correlations between the ARSTAN chronologies of tree-ring collections in eastern Kentucky.

Chronology	<u>London LITU</u>	Blanton QUAL	Blanton QUMO	Blanton TSCA	<u>London TSCA</u>	<u>Cold Hill Leuc.</u>	Floracliff QUMU	Griffith FRQU	Griffith QUMU	Whittleton QUMO	Mammoth QUAL
Blanton QUAL	0.359**	—									
Blanton QUMO	0.380**	0.691**	—								
Blanton TSCA	<i>0.143</i>	0.092	<i>0.172</i>	—							
<u>London TSCA</u>	0.047	0.116	0.214	0.513**	—						
<u>Cold Hill Leuc.</u>	0.310**	0.408**	0.458**	0.193	<i>0.156</i>	—					
<u>Floracliff QUMU</u>	0.225*	0.469**	0.553**	0.189	0.225*	0.364**	—				
<u>Griffith FRQU</u>	0.192	0.259*	0.216	<i>0.152</i>	<i>0.152</i>	0.198	0.292**	—			
<u>Griffith QUMU</u>	<i>0.148</i>	0.403**	0.384**	0.182	0.232*	0.342**	0.545**	0.460**	—		
<u>Whittleton QUMO</u>	0.260*	0.531**	0.440**	0.118	0.113	0.407**	0.517**	0.291**	0.424**	—	
Mammoth QUAL	0.287**	0.477**	0.389**	0.237	<i>0.148</i>	0.402**	0.410**	0.254*	0.392**	0.390**	—
Lilley QUAL	0.271**	0.573**	0.469**	0.238	0.231	0.459**	0.387**	0.197	0.298**	0.568**	0.540**

Note: Correlations are for the 1796–2005 period except for comparisons with Mammoth Cave and Lilley Cornett Woods. The latter chronologies are the only classical dendroclimatic collections in eastern Kentucky and are correlated for the 1796–1985 and 1796–1982 common periods, respectively. See Table 1 for site names. Underlined site names represents randomly sampled trees. See Table 1 and text for more details. Species: LITU, *Liriodendron tulipifera*; QUAL, *Quercus alba*; QUMO, *Quercus montana*; TSCA, *Tsuga canadensis*; Leuc., *Quercus* subgenus *Leucobalanus* and is comprised of QUAL and QUMO; QUMU, *Quercus meuhlenbergii*; FRQU, *Fraxinus quadrangulata*. Italics, significant at $p < 0.05$; bold, significant at $p < 0.01$; *significant at $p < 0.001$; **significant at $p < 0.0001$.

balanus and London Forest *T. canadensis* chronologies, there is some temporal coherence in ring width at multiannual to decadal time scales (Figs. 3a and 3b). *Tsuga canadensis* chronologies are visually coherent in the latter half of the 1700s and from the mid-1800s through the 1970s, while the *Quercus* chronologies generally show less coherence. The period of low agreement between the *Quercus* chronologies coincides with the lowest Cold Hill EPS values. Finally, correlating the Blanton Forest *Leucobalanus* record with the Lilley Cornett and Mammoth Cave *Quercus* chronologies indicates that, while classical records retain more of the regional signal, differences are small enough to suggest that even records of randomly selected trees in cut forests with low replication over roughly half of their record retain a significant portion of the larger signal. The Blanton Forest *Leucobalanus* combined record correlates slightly greater than Cold Hill *Leucobalanus* record versus the Lilley Cornett ($r = 0.476$ versus 0.459) and

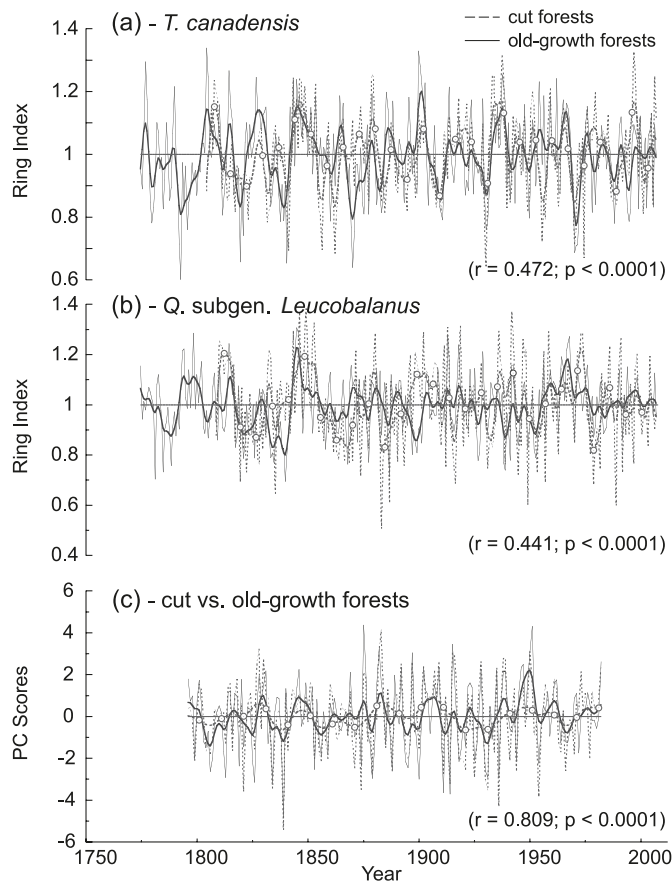
Mammoth Cave ($r = 0.453$ versus 0.402) classical collections over the 1796–1982 common period.

Spectral analysis

Spectral analysis indicates a range of retained power at various frequencies in all 12 chronologies (Fig. 4). Most records have significant spectral power at frequencies of 2.2–9.4 years and less power beyond 10 years. Collections from intensively logged forests, Cold Hill *Leucobalanus* and Whittleton Ridge *Q. montana* (Figs. 4f and 4j, respectively), have an absence of power at 3–6 year frequencies. Unexpectedly, the two classical collections, Lilley Cornett Woods *Q. alba* and Mammoth Cave National Park *Q. alba* (Figs. 4k and 4l, respectively), do not have statistically significant power at low frequency, while two logged forests have significant power at periodicities >10 years, Floracliff *Q. meuhlenbergii* and Whittleton Ridge *Q. montana* (Figs. 4i and 4j, respec-

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Fig. 3. Comparison of smoothed curves of (a) *Tsuga canadensis*, (b) *Quercus* subgenus *Leucobalanus* from Cold Hill (dashed line) and Blanton Forest (solid line), and (c) chronologies from previously cut (dashed line) versus old-growth forests (solid line). The common period for comparison in Fig. 3c is limited because two collections were made during the 1980s. Each curve was smoothed with a 9 year spline to emphasize multiannual- to decadal-scale variability. Solid horizontal lines represent the mean. The curves in Figs. 3a and 3b contain not only trees from cut forests but also randomly selected trees. See text for more details.



tively). Interestingly, Floracliff *Q. meulenbergi* has a significant peak at 38 years as well as a long-term (or secular) trend at multicentennial periodicities (actual power = 7.668 versus 90% confidence limit (CL) criteria = 6.73 and 95% CL criteria = 7.67). Similarly, the London Forest *L. tulipifera* has a peak at 22.8 years, just below the 90% CL (actual power = 28.532 versus 90% CL criteria = 28.9). The Mammoth Cave *Q. alba* also has a peak just below the 90% CL at 10.8 years (actual = 6.44 versus 90% CL criteria = 6.51).

The first principal component of the new tree-ring collections in eastern Kentucky has significant power at 2.6–7.3 years (Fig. 5a). Comparing the spectral properties of the first principal component from previously cut forests and old-growth forest collections indicates similar spectral properties (Figs. 5b and 5c). While the time series from previously cut forest has less power at 6–7 years compared with the old-growth forest series, it has power at 3.4 years that is absent in the old-growth forest series.

Comparison with the North American Drought Atlas

When comparing these series of (1) all new chronologies, (2) previously cut forests, and (3) old-growth forests with eastern Kentucky drought, we see less spectral power at lower frequencies than the frequencies in the NADA series but more power at middle frequencies (3–7 years) (Figs. 5a–5d). To extend this analysis over a longer time period to test if the shorter period is causing differences in retained periodicity, nested reconstruction techniques (Meko 1997) were employed on the new chronologies and normalized to create z -scores from 1633 to 2005 (Supplemental Material). Replication is low for all records in Kentucky prior to 1650, so comparison of the z -scores is limited to 1650–2005. The new long record is significantly correlated with drought ($r = 0.723, p = 0.0001$). Even though spectral analysis indicates that new records have no power at lower frequencies like the NADA drought record, the two series are generally in phase at multiannual periods from 1660 to 2005 (Fig. 6a).

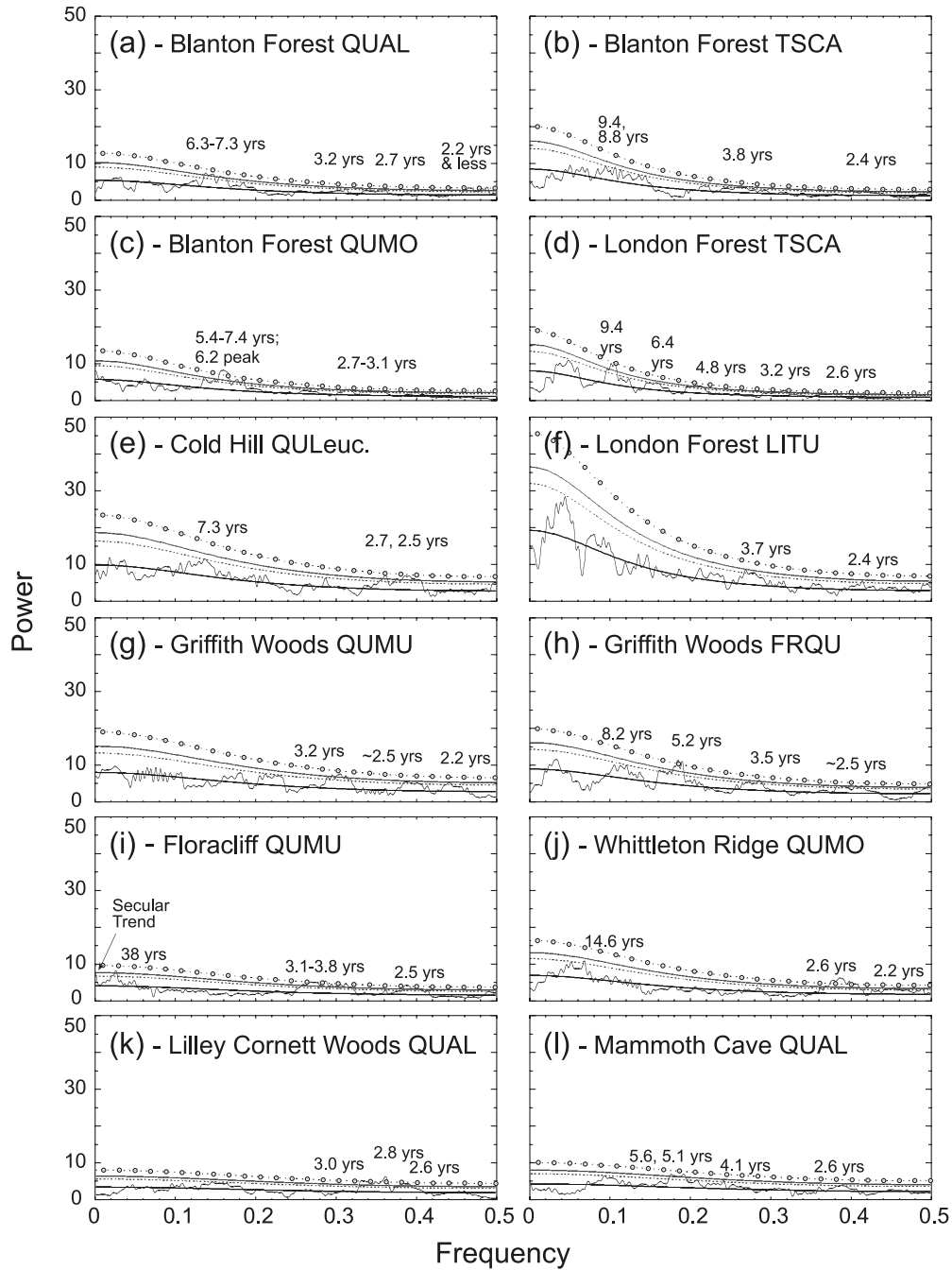
Finally, PCA was used to create a time series of new or rarely used species for dendroclimatology (*F. quadrangulata*, *L. tulipifera*, and *Q. muehlenbergii*) to examine their potential for paleoclimatic research. The “new species” chronology correlates at 0.679 ($p = 0.0001$) against eastern Kentucky drought from 1796 to 2005 (Fig. 6b). Like most of the new records here, spectral analysis of this series reveals several peaks of spectral power at periodicities between 2.5 and 5.6 years (Supplemental Material Fig. S2).

Discussion

Using a new, independent, and more spatially dense network of eastern Kentucky tree-ring records, we find that composite records drawn from nonclassical records could be useful for reconstructions. Despite the potential that additive impacts from different forest conditions and sampling methods could make a final chronology noisier, our analysis indicates that combinations of trees from previously cut forests (including randomly selected trees) generally match ring width variation from more classical dendroclimatic collections, chronologies from old-growth forests, and reconstructed drought at 1–7 year time scales. These results suggest that nonclassical records can be useful for reconstructing drought in areas with little old-growth forest. These results support the postulation that site selection might not be the most critical aspect of field methods in humid eastern North America (Cook 1982). In fact, these results extend that postulation by showing that trees in heavily cut forests can be of value for reconstructing climate.

Importantly for dendroclimatology, the similarities in annual- to decadal-scale variations in radial growth are encouraging, if not somewhat surprising, given the differing types of field methodologies, forest histories, complex topography, and low replication of some collections between populations nearly 90 km apart (Fig. 3). If this kind of data is to be used for dendroclimatic studies, it should be combined with data from older trees outside randomly selected plots to ensure better replication in the earlier portions of a chronology. Individual chronologies from nonclassical collections do not appear sufficient enough to retain the larger regional signal on their own (Fig. 3; Tables 2 and 3). Therefore, by utilizing nonclassical records with more classical records, network gaps can be filled to enhance understanding of regional climatic variation (see fig. 5 in Cook et al. 2010).

Fig. 4. Spectral analysis for all eastern Kentucky tree-ring records. (a) Blanton Forest *Quercus alba*, (b) Blanton Forest *Tsuga canadensis*, (c) Blanton Forest *Quercus montana*, (d) London Forest *T. canadensis*, (e) Cold Hill *Quercus* subgenus *Leucobalanus*, (f) London Forest *Lirodendron tulipifera*, (g) Griffith Woods *Quercus muehlenbergii*, (h) Griffith Woods *Fraxinus quadrangulata*, (i) Floracliff Nature Sanctuary *Q. muehlenbergii*, (j) Whittleton Ridge *Q. montana*, (k) Lilley Cornett Woods *Q. alba*, and (l) Mammoth Cave National Park *Q. alba*. The lower smooth and solid curve on each graph represents the null hypothesis. The dotted smooth curve represents the 90% confidence limit (CL). The thinner smooth curve above the 90% CL is the 95% CL. The dashed line with circles represents the 99% CL. Graphs are arranged so spectral frequencies can be compared by species. Spectral analysis was conducted on ring index from 1796 to 2005 except for Lilley Cornett Woods (1796–1982) and Mammoth Cave National Park (1796–1985). Numbers on each panel represent significant periodicities in ring width variation ($\geq 90\%$ CL).

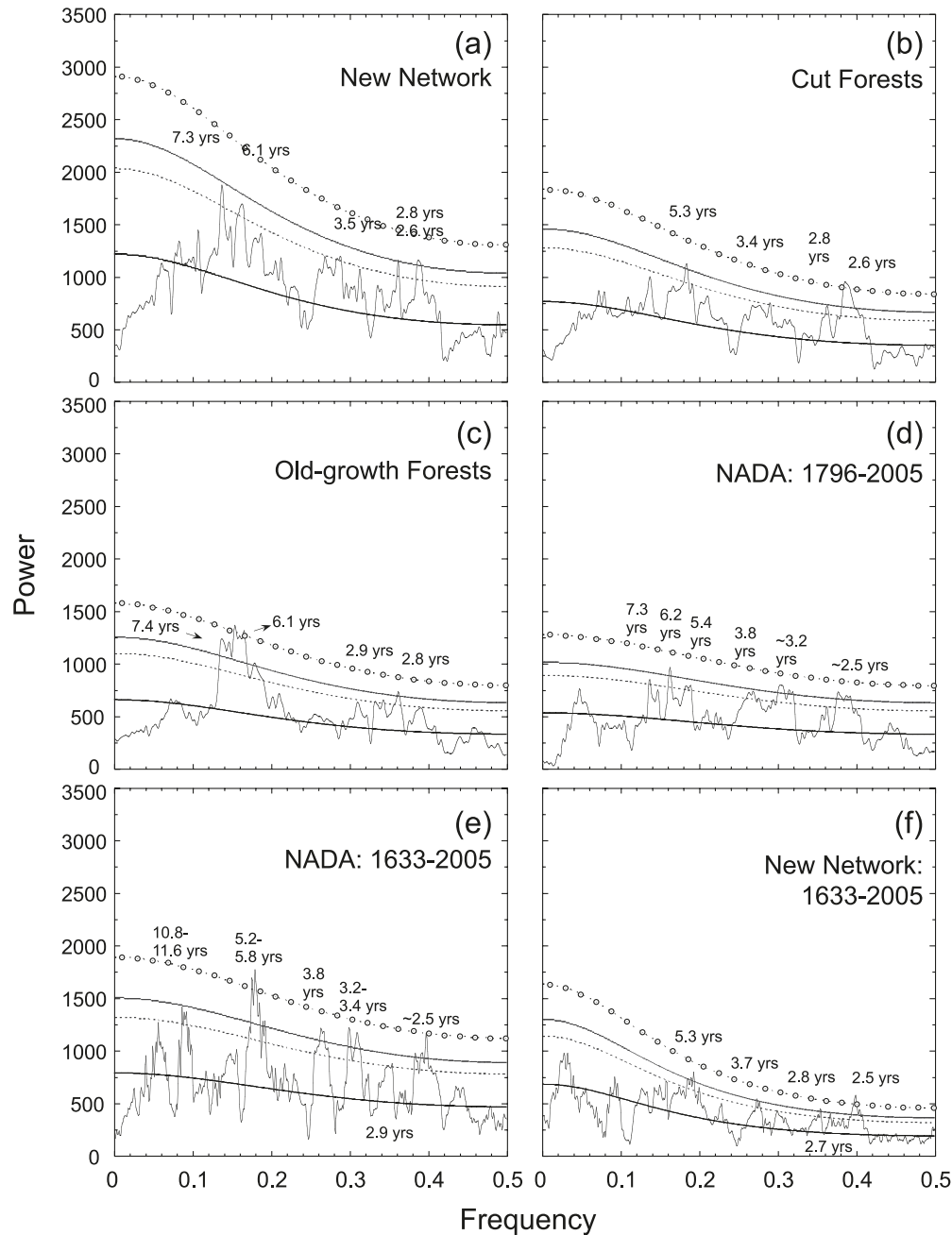


Limitations: longevity, disturbance, and low-frequency information

One potential limitation for using records from nonclassical dendroclimatic species is that some of these species are

perceived to be shorter-lived than traditional species. This is important in at least two ways. First, series composed of shorter segments will limit the maximum wavelength of ring variation, which results in the “segment length curse” (Cook et

Fig. 5. Spectral analysis for differing types of tree-ring records and drought history in eastern Kentucky. (a) Spectral analysis of the first principal component of the 10 new tree-ring records from 1796 to 2005, (b) spectral analysis of tree-ring records from previously cut forests from 1796 to 1982, (c) spectral analysis of tree-ring records from old-growth forests from 1796 to 1982, (d) spectral analysis of the eastern Kentucky North American Drought Atlas from 1796 to 2005, (e) spectral analysis of the average North American Drought Atlas grid points in eastern Kentucky from 1633 to 2005, and (f) spectral analysis of z-scores of the new tree-ring records from eastern Kentucky from 1633 to 2005. Confidence limits and significant periodicities are the same as in Fig. 4.

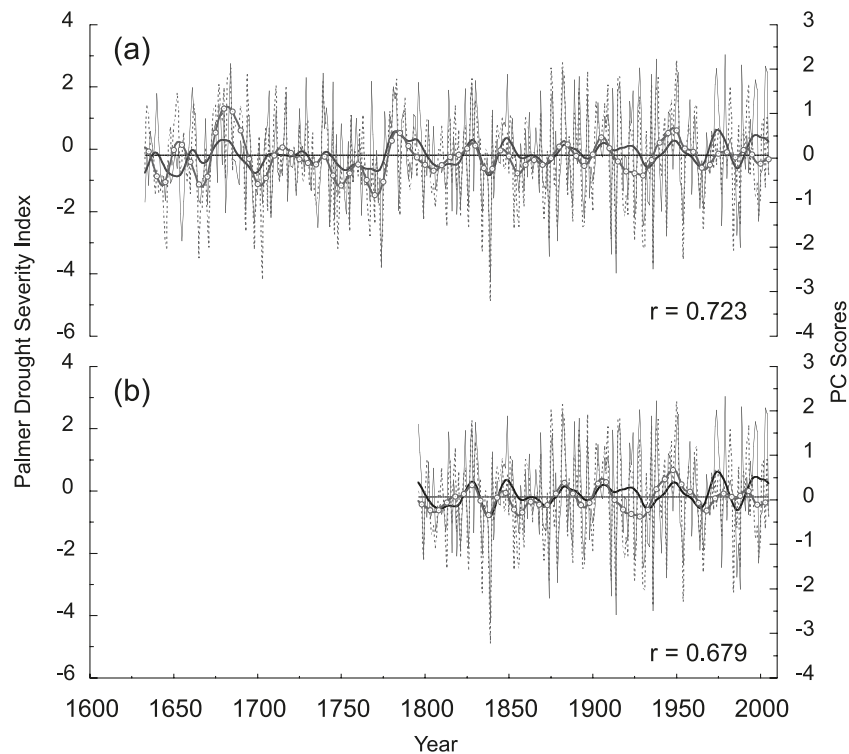


al. 1995). Climatic reconstructions composed of records biased with this “curse” would have less recoverable low-frequency information. Second, the length of the shortest chronology can limit the final length of a climatic reconstruction. The nested methodology used here, however, makes it possible to include shorter records in the development of climatic reconstructions (Cook et al. 2003). Just as important, recent evidence indicates that some short-lived species live longer than previously

thought (Pederson et al. 2007; Pederson 2010). A good example of this is *L. tulipifera*, where trees >400 years not too unusual, the current maximum age is at 509 years, and a maximum age of 600 years seems likely (Pederson 2010; Pederson et al. 2012a). If greater longevities are found in more species, then species longevities will be much less of a problem.

Another problem related to tree age is the perception that forests disturbed by logging do not have old trees. Our inves-

Fig. 6. Comparison of eastern Kentucky drought from the North American Drought Atlas (solid line with a black line highlighting multiannual- to decadal-scale variability) and (a) z-scores of the new tree-ring records from eastern Kentucky (dashed line and a gray line with dotted circles) from 1633 to 2005 and (b) z-scores derived from tree-ring records of rarely used species for hydroclimatic studies (dashed line and a gray line with dotted circles) from 1796 to 2005. All curves were smoothed with a 9 year spline. The horizontal line represents the mean.



tigations in eastern Kentucky have revealed the presence of old trees in previously cut forests, including forests that have been likely cut at least twice since the late 19th century. Many forests in the eastern United States were high-graded, or cut without using professional forest management techniques (i.e., cut without regard for future regeneration and sustainability), to gain short-term economical returns (Frothingham 1931). Often, the least valuable trees (e.g., hollow, poor stem form, undesirable timber species) were left in the forest. Some of these trees can be quite old (Pederson 2010). The heavily cut Cold Hill forest, characterized by a predominance of trees dating between 1880 and 1940, had several *Q. alba* dating to the 1700s. Given that *Q. alba* is a highly valued timber species, this discovery was surprising. Similarly, the forest below Cold Hill, Cane Creek Wildlife Management Area, contains many trees dating to the 1600s and 1700s despite evidence of logging (Tackett 2012). In fact, in all of the previously cut forests, we found older trees without spending an inordinate amount of time searching for old trees. The best example might be the approximately 400 year old yellow buckeye (*Aesculus flava* Sol.) in the cut forests near Whittleton Ridge (Cooper 2011). A thorough investigation using search images of old trees (Stahle and Chaney 1994; Pederson 2010) in regions with little old-growth forest could have a significant payoff for dendroclimatic research.

Disturbance frequency in nonclassical forests, however, could be a less surmountable limitation. Land-use legacies could degrade the climatic signal in surviving trees (Gunnarson et al. 2012). We see some indication of this here. The

Quercus chronology that loaded the lowest on the first unrotated principal component is composed of trees from the midst of one of the most repeatedly cut forests in our study (Table 2). Teasing out confounding effects, such as randomly selected trees or canopy status, in our study here, however, is impossible. A study on the impact of single-tree selection, however, suggests that surviving trees >5 m from a stump generally contain the larger-scale climate signal (Esper et al. 2012). We also note that collections in our study from the most repeatedly and intensively logged forests generally have an absence of power at low frequencies (Fig. 4e), although there are exceptions (Figs. 4i and 4j). Low-frequency signals in tree-ring records from heavily cut forests could be lost due to the greater frequency of changes in competitive pressure compared with old-growth forests (although age structure of these forests can revive the segment length curse, too). Trees from old-growth forests experience substantial changes in competitive pressure that are not dissimilar to trees left in forests during logging (Rentch et al. 2002). What is dissimilar between these land-use histories is most often the frequency and spatial scale of disturbance since the 19th century. Logging rotations often occurred every 30–50 years at a spatial scale that impacts most of the forest. The frequency and spatial intensity of wide-scale logging that occurred around the turn of the 19th century do not match the typical gap-dynamics disturbance regime of closed-canopy forests. Thus, logged forests originated from this era would have more stand-wide changes in competitive pressure. In this scenario, the frequent and spatially pervasive change in competitive pressure could override decadal to

multidecadal changes in climate and force the detrending of tree rings from these forests to reduce the influence of changes in competition in such a way that it reduces the low-frequency signal.

Differences in the retention of low-frequency signals between reconstructed drought and chronologies in our network could be the result of standardization. To test this, we experimented with restandardizing the entire network using the signal-free method (Melvin and Briffa 2008; Supplemental Material). The signal-free method was developed to help retain spectral power lost through standardization methods that employ varying lengths of bandpass filters or splines. While a spectral analysis of the new network using some chronologies developed through the signal-free method improved the spectral power at lower frequencies, none of these lower frequencies were statistically significant (Supplemental Material Fig. S3). This analysis indicates that tree-ring data from nonclassical locations might have limitations at retaining low-frequency information. Therefore, there is a great need to develop new standardization techniques for trees with shorter segments from frequently disturbed, high-density forests.

Genera and patterns of radial increment

Through correlation and spectral analysis, we found that genera matter in long-term ring width variation. *Quercus* and *Tsuga* chronologies correlated better with chronologies of the same species or subgenus across the region than chronologies of different species in the same forest. This finding supports tree-ring investigations of phylogenetic signals (Graumlich 1993; Cook et al. 2001). *Tsuga canadensis* appears to have the most unique pattern of ring width variation in our network. The impending functional extinction of *T. canadensis* due to the hemlock adelgid will bring about the loss of a strong and specific dendroclimatic signal because *T. canadensis* is one of the more important species for the NADA.

While we did not sample a species that could completely replace *T. canadensis* for dendroclimatic research, we did find three underutilized species that contain hydroclimatic information (Fig. 6b). It is not surprising that a drought-deciduous species like *L. tulipifera* tracks hydroclimate. This climatic sensitivity allows it to contribute to reconstructions of hydroclimatic, including three recent reconstructions (Maxwell et al. 2011; Pederson et al. 2012a, 2012b). Two other species, *F. quadrangulata* (for which this seems to be the first tree-ring chronology of this species) and *Q. muehlenbergii* (a species not present in the ITRDB), significantly contribute to the “new species chronology” that is significantly correlated with reconstructed drought from 1796 to 2005 (Fig. 6b). That the Griffith Woods *F. quadrangulata* and *Q. muehlenbergii* collections are drought sensitive is important because both chronologies are drawn from open-grown forests growing on relatively rich soils in a humid region (Supplemental Material). The finding that the radial increment of trees in a humid environment and low-density forests varied with drought for over 200 years is not expected given that trees in thinned forests are less water stressed (e.g., Martín-Benito et al. 2010). Combined with our findings here, results indicating that low-density forests are less water stressed suggest that these species would hypothetically have an even stronger relationship to drought in denser forests.

Drought as a strong factor of stem growth

Our findings that trees in nonclassical forests have strong drought signals, even in low-density forests, have broad implications. Because a substantial proportion of the annual to multiannual variation in tree growth from trees across canopy strata is controlled by drought over the last 210–346 years (once important factors like competition are reduced), we conclude that the growth of most trees is strongly related to drought variation. These results support evidence since 1920 indicating that water stress is an important limiting factor for trees from a range of species not growing on classic dendroclimatic sites (e.g., Douglass 1920; Schumacher and Day 1939; Graumlich 1993; Orwig and Abrams 1997; Cook et al. 2001; LeBlanc and Terrel 2001; Takahashi et al. 2003; Piovesan et al. 2005; Tardif et al. 2006). This is important because it is often perceived that drought is not important to tree growth in humid environments (e.g., McMahon et al. 2010). Our evidence extends this knowledge beyond most tree-ring collections: even trees growing in open woodlands or randomly selected trees ≥ 10 cm DBH in moist ravines or “typical” upland forests have a significant relationship to drought (Fig. 6; Supplemental Material). These results indicate that drought is not only an important factor of forests on dry or more classic dendrohydroclimatic sites, but that it is a significant, long-term factor in humid regions.

Summary

Results here indicate that nonclassical tree-ring data from previously cut forests or tree-ring records collected using nontraditional field methods could have some utilization for reconstructing climate. We found striking similarity in radial growth across a topographically diverse region between classical and nonclassical collections and nonclassical tree-ring records and reconstructed drought at annual to decadal time scales. Such data will be most valuable in areas with little old-growth forest. If these patterns are replicated in other regions, the next phase of paleoclimatic research could utilize existing or future dendroecological tree-ring data sets to build networks with greater spatial network density and species diversity for areas with exiguous old-growth forest. Perhaps most importantly, our results indicate that drought is an important driver of radial growth of forest interior trees in humid environments.

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