# **Competition and Climate Affects US Hardwood-Forest Tree Mortality**

Daniel A. Yaussy, Louis R. Iverson, and Stephen N. Matthews

**Abstract:** Individual-tree measurements have been collected periodically on sites established in Kentucky, New York, Ohio, and Pennsylvania to investigate the effects of thinning on the growth and yield of valuable hardwood species. These plots were installed between 1959 and 1985. The long-term characteristics of this data set of 47,853 trees allowed us to investigate potential climatic effects on the mortality of individual trees. Stand and tree measures of competition, monthly and annual temperatures, and precipitation were statistically assessed against mortality through proportional hazards survival analysis for 21 species groups. Competitive factors entered the models more consistently than climatic factors. However, some of the climate factors were of higher importance than some of the competitive factors. The models produced were then run using future climate predictions from conservative and extreme general circulation model scenarios to estimate possible future hazard rates of mortality. These rates varied greatly based on species group and future climate scenario because of the highly variable climate. The high variability of future climate projections make it difficult to estimate changes in future risks of tree mortality because of climate change. However, the study reiterates that managing for more resilient forests by reducing competitive stress will help mitigate the effects of climatic stress as well as many other stresses such as those caused by insects and pathogens. FOR. SCI. 59(4):416–430.

Keywords: climate change, survival analysis, general circulation models, hazard rate

**T** REE MORTALITY IS CAUSED BY AN ACCUMULATION OF STRESS. The stress may take the form of catastrophic events such as windthrow, intense fire, or damaging insect infestation in which a single stress event of high intensity may cause healthy trees to die or stress may accumulate through several sources, each weakening the tree's defenses to the point that it eventually dies (Mannion 1991, Das et al. 2011). These stresses can take the form of competition for light, nutrients, or water; defoliation from insects or fungi; loss of cambial function from insects or fungi; or other sources. Root structure, bark thickness, water use efficiency, or other ecophysiological characteristics of tree species may cause differential mortality in reaction to certain stresses (Hilt 1985b).

Climate change has been shown to affect an increasing number of species around the world (Cotton 2002, Fitter and Fitter 2002, Laliberte and Ripple 2004, Parmesan and Galbraith 2004, Wilson et al. 2004). Evidence is mounting that these changes are accelerating (Chen et al. 2011). This evidence has motivated many studies that use a modeling approach to predict the effects of future climatic change on ecological systems (e.g., Guisan and Thuerillat 2000, Yates et al. 2000, Hansen et al. 2001, National Assessment Synthesis Team 2001, Retuerto and Carballeira 2004, Lovejoy and Hannah 2005, Ibáńez et al. 2006, Rehfeldt et al. 2006, Thuiller et al. 2006, Iverson et al. 2011). One recent study of the boreal forests of Siberia, Canada, and Alaska reported that many of the modeled predictions of forest change are now occurring: a northern and upslope migration of certain trees, death or dieback of certain species, and increased outbreaks of insects and fire (Soja et al. 2007). Van Mantgem et al. (2009) conducted a regional analysis on long-term data from the western United States and modeled increases in tree mortality attributed to climate change. The projected increases in atmospheric  $CO_2$  concentration and changes in temperature and precipitation patterns have the potential to alter ecosystem functions, species interactions, population biology, and plant distributions (Melillo et al. 1990, Kirschbaum 2000).

Detecting climate-induced effects in forest ecosystems is not possible under traditional methods of modeling tree mortality, which are often constructed from measurements taken at only two time periods, one before and another after a treatment or natural event. When treated sites are compared with untreated sites over the same time period, changes in mortality rate are attributed to the treatment or event. This analysis often uses logistic regression to model the influence of treatment, tree species, size, or other characteristics on mortality (Ryan et al. 1988, Beverly and Martell 2003, Zhao et al. 2007, Chen et al. 2008, Fan et al. 2008, Greenwood and Weisberg 2008, Crecente-Campo et al. 2009, Kiernan et al. 2009, Rathburn et al. 2010). A less-used modeling method for assessing mortality and its potential causal agents is classification and regression tree analysis (Dobbertin and Biging 1998, Kabrick et al. 2004, Shifley et al. 2006), which bifurcates the data into successively more homogeneous groups based on threshold values of explanatory variables.

In contrast with mortality analysis using paired data from two points of time, survival analysis using proportional

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Daniel A. Yaussy (dyaussy@fs.fed.us), USDA Forest Service, Delaware, OH. Louis R. Iverson (liverson@fs.fed.us), USDA Forest Service. Stephen N. Matthews (matthews.204@osu.edu), The Ohio State University.

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hazards models may be used when individual-tree data are collected with several measurements over a long time period (Volney 1998, Wyckoff and Clark 2000, Woodall et al. 2005, Rose et al. 2006, Roy et al. 2006, McPherson et al. 2010). Fan et al. (2006) combined the classification and regression tree and proportional hazards methods to model mortality in oak-dominated forests of Missouri. Their study indicated that tree species, crown class, dbh, and basal area of larger trees were closely associated with differences in tree survival rates.

Climate often provides drivers that affect forests, both over large areas and over long periods of time. Thus, many years of data collection over large regions may be needed to evaluate the quite subtle effects that climate has on mortality rate. This article uses proportional hazards regression methods on data collected over a 45-year period and with time-dependent covariates to explore the interaction of species group, competitive stress, and moisture deficit caused by climatic conditions on individual-tree mortality in the central and northern hardwoods of the eastern United States. We then postulate how this mortality might be affected by the future climate as predicted by a range of outputs from several general circulation models (GCMs).

#### Methods

#### Data

The tree data were originally collected to evaluate the effects of thinning levels on the growth of the residual trees (Hilt 1985a, Marquis and Ernst 1991, Nowak 1996). The forests of the six stand density studies, installed in even-

aged upland oak stands of southeastern Kentucky and southern Ohio (studies 11–24), were dominated by *Quercus alba* (see Table 1 for common names and scientific nomenclature), *Quercus coccinea*, *Quercus prinus*, and *Quercus velutina*, with a small amount of *Carya* species (Figure 1). Stands ranged from 30 to 80 years of age at study installation in the early 1960s with a *Q. velutina* 50-year-old site index range of 18 to 23 m (60–77 ft.) These studies and others were used to calculate upland oak stocking guides (Gingrich 1967). Studies 25 and 27 were installed in 110-year-old unmanaged upland oak stands in Ohio in the late 1970s (Appendix 1). Residual stocking after thinning ranged from 15 to 100%.

The 11 sites in the unglaciated region of the Allegheny Plateau in northwestern Pennsylvania and southwestern New York (studies 76-1 to 76-13) were installed in evenaged stands dominated by *Prunus serotina, Acer rubrum, Acer saccharum,* and *Fagus grandifolia* ranging in age from 30 to 120 years (Figure 1). Many of these studies were used to calculate northern hardwood stocking guides (Roach 1977). Residual stocking after thinning ranged from 25 to 80%. All but one site retained plots of unthinned controls, also used in this analysis (Appendix 1).

All stands were in secondary forests; therefore, a stand origination date was determined by dating cores of several trees with dominant or codominant crown positions during study installation (Appendix 1). Plot sizes are uniform within a study except for study 25, in which two plots are 0.2023 ha and one plot is 0.0405 ha. Data were collected at each study site 3–27 times. Each tree in the studies was individually identified and measured at least twice. The

 Table 1.
 List of species and species groups, number of trees by state, percent mortality over the course of the study, and mean dbh and SD.

		No. of trees by state					dbh (cm)		
Scientific name	Common name	KY	NY	OH	PA	Total	% Mortality	Mean	SD
Acer pensylvanicum L.	Striped maple	0	339	0	2,567	2,906	13.7	7.0	2.8
Acer rubrum L.	Red maple	2,152	618	2,469	1,537	6,776	13.2	8.9	5.7
Acer saccharum Marsh.	Sugar maple	27	695	102	8,272	9,096	45.5	10.3	6.8
Betula L. spp.	Birch spp.	14	43	0	1,685	1,742	17.2	5.1	5.2
Carya Nutt. spp.	Hickory spp.	315	8	744	1	1,068	32.7	10.1	7.5
Cornus florida L.	Flowering dogwood	472	0	1,392	0	1,864	60.7	6.2	3.5
Fagus grandifolia Ehrh.	American beech	95	138	17	3,765	4,015	13.2	5.0	4.5
Fraxinus L. spp.	Ash spp.	43	27	243	99	412	20.6	12.7	12.4
Liriodendron tulipifera L.	Yellow-poplar	535	1	186	28	750	23.1	11.2	7.8
Magnolia acuminata (L.) L.	Cucumber-tree	0	344	0	45	389	20.3	6.2	7.1
Nyssa sylvatica Marsh.	Blackgum	100	1	893	10	1,004	8.5	6.2	5.4
Oxydendrum arboreum (L.) DC.	Sourwood	659	0	894	0	1,553	33.5	3.1	0.9
Prunus serotina Ehrh.	Black cherry	60	1,045	40	2,314	3,459	16.7	13.5	13.2
Quercus alba L.	White oak	5,121	225	1,229	29	6,604	38.9	15.4	9.0
Quercus coccinea Münchh.	Scarlet oak	168	0	1,535	45	1,748	50.7	15.9	7.4
Quercus prinus L.	Chestnut oak	95	0	1,075	0	1,170	26.2	14.6	9.7
Quercus rubra L.	Northern red oak	15	39	60	363	477	26.4	29.8	11.6
Quercus velutina Lam.	Black oak	398	1	820	0	1,219	47.6	16.7	9.3
Sassafras albidum (Nutt.) Nees	Sassafras	47	0	494	0	541	42.5	4.9	1.3
Tsuga canadensis (L.) Carrière	Eastern hemlock	272	1	1	10	284	22.9	11.1	4.4
Other species <sup>a</sup>		302	60	322	92	776	44.8	8.4	6.0
Total		10,890	3,585	12,516	20,862	47,853			

<sup>a</sup> Other species include Aralia spinosa L., Amelanchier Medik. spp., Carpinus caroliniana Walter, Castanea dentata (Marsh.) Borkh., Celtis occidentalis L., Cercis canadensis L., Crataegus L. sp., Corylus americana Walter, Diospyros virginiana L., Ilex opaca Aiton, Juglans cinerea L., Juglans nigra L., Liquidambar styraciflua L., Magnolia L. spp., Nyssa aquatica L., Nyssa biflora Walter, Ostrya virginiana (Mill.) K. Koch, Pinus L. spp., Platanus occidentalis L., Populus grandidentata Michx., Prunus pensylvanica L. f., Quercus muehlenbergii Engelm., Quercus stellata Wangenh., Robinia pseudoacacia L., and Ulmus L. spp.



Figure 1. Map of study and weather station locations, NCDC climatic divisions, and ecological divisions (Dyer 2006).

minimum individual-tree measurements collected during each visit at each site included species, diameter at 1.37 m (dbh), and STATUS (living or dead). In most cases, when a site was revisited and a tree was found to be dead, no dbh was recorded for that tree. In these cases, the dbh and annual diameter growth (DGROW) from the previous measurement were assigned to the tree for the year in which it was found dead. From these individual-tree measurements, plotlevel variables were calculated, as well as relative diameter (RD) indicating each tree's competitive position in the plot, for each measurement period (Appendix 2). RD accounts for the relatively higher mortality found in small stems. Measurement periods ranged from 1 to 7 years. Basal area per ha (BAH) and trees per ha (TPH) of all trees on the plot greater than 10 cm were calculated as stand-level indicators of competitive stress. Species groups consisting of at least 250 individuals measured across all studies are listed in Table 1. DGROW and RD were the two variables with the highest correlation to changes in STATUS for the majority of species groups. Dbh, cross-sectional area at 1.37 m (basal area), basal area growth, and BAH of all trees larger than the individual were highly correlated to DGROW and RD (r > 0.5) and were not used in the analysis. RD is an indicator of a tree's comparative size, which translates into access to resources. DGROW is a measure of the tree's ability to use resources. BAH and TPH quantify the local demand for resources.

Historical climate data were downloaded from the National Climate Data Center (NCDC) for weather stations closest to the study sites and with the most complete sets of monthly precipitation and temperature, covering the period from stand establishment through 2009 for individual sites (Appendix 3; Figure 1). A single, nearby station was used for each state because of the unavailability of continuous data near each study site (Figure 1). If small lapses in the records occurred, these gaps were filled with summarized data from the NCDC divisional climate data. Data were assembled into ecological years beginning in October and ending in September to capture growing season effects. Tree measurements were taken in the dormant season and associated with the previous growing season climate variables. A cold January day in Kentucky could be considered quite moderate in New York and vice versa for warm July days. The climate variables were, therefore, centralized by subtracting the 110-year mean station value of each variable to minimize latitudinal bias. Standardization of the data would have resulted in the loss of interpretable units of measurement that aid in the understanding of the model results (i.e., how does an increase in temperature of 10°C affect the hazard rate for mortality?). The climate variables investigated in this article were average annual temperature (AVGT), average July temperature (JULT), and average annual precipitation (PCP). A 5-year running average of PCP (PCP5) was calculated to investigate the effects of long-term moisture stress on mortality. Average growing season (May-September) potential evapotranspiration (MSPET) was calculated according to equations in Willmott and Rowe (1985). Climate variables should affect the risk of tree mortality through changes in available moisture: directly from precipitation (PCP and PCP5) and indirectly through evaporation or transpiration (AVGT, JULT, and MSPET). Several climate variables were considered; however, only those most correlated with STATUS that were not correlated with each other (r < 0.5) were used for modeling.

Two GCMs, the parallel climate model (PCM) and the Hadley CM3 model (HAD) (Hayhoe et al. 2006), were used for future climate scenarios as described by the Intergovernmental Panel on Climate Change (IPCC) (2007). In addition, two emission scenarios were used in conjunction with the GCM model outputs: high (current carbon emissions trajectory [A1fi]) and low (reasonable conservation of energy implemented [B1]) (Nakicenovic and Swart 2000). These climate models and scenarios represent a broad range of climate predictions and incorporate both the mild (PCM) and harsh (HAD) models and explore how the high versus low emission scenarios might affect the future mortality hazard rate of the species group. Use of this mix, therefore, represents a sensitivity analysis of possible future climate scenarios. Departures from AVGT, JULT, MSPET, PCP, and PCP5 were calculated using mean outputs from PCM/high emissions (PCMhi), PCM/low emissions (PCMlo), HAD/high emissions (HADhi), and HAD/low emissions (HADlo) trajectories for each  $20 \times 20$  km grid cell that contained a study site in 2010-2039, 2040-2069, and 2070-2099 (Iverson et al. 2008). Figure 2 illustrates the variability among the models and scenarios across a latitudinal gradient from north to south for AVGT, JULT, MSPET, and for the 2070-2099 time period. To obtain conservative estimates of future predicted PCP5, the historical standard deviation (SD) of annual precipitation (PCP) was added to and subtracted from the future predictions of PCP to estimate a range of model outputs.

Unfortunately, integrated metrics shown useful for assessing mortality, such as the Palmer Drought Severity index, have not been projected into the future through the GCMs and were not included in this analysis.

#### Analysis

The change in hazard rate due to each explanatory variable was estimated using Cox proportional hazards regression with the time-dependent methods of the PHREG procedure provided by SAS/STAT1 software (version 9.3 of the SAS System for Windows, Copyright ©2002-2007). Readers may be familiar with the use of this type of survival analysis in clinical trials that estimate the change in hazard rates for mortality or for contracting a disease due to smoking or other behaviors (Hanaoka et al. 2005). Tree, plot, and climate variables were assigned to each tree for each year from stand origination (year 0, Appendix 1) to the last measurement. Because there was no way to determine age for each individual tree, all trees in each stand were assumed to be established at year 0 (obviously an assumption known to be false). The interdependency of trees within plots was accounted for by declaring each plot as a random variable. Tree and plot values for years without measurements were treated as null (missing). At each time step, tree status and the explanatory variables were updated with data appropriate for that time period, if available.

Ten percent of the data set (4,759 of the 47,859 trees) was randomly set aside for validation of the models developed with the remainder of the data. After validation, the data sets were combined, and the models were recalculated with the full data set.

The survival analysis was first conducted with species groups as the only explanatory variable to contrast the



Figure 2. Departures from average for (A) centralized mean AVGT, (B) mean JULT, (C) mean MSPET, and (D) PCP (Table 2) for four future 2070–2099 climate scenarios: HADhi; HADlo; PCMhi; and PCMlo for the six study locations.

hazard rates for mortality among the groups. The hazard rate is the probability of dying in a given year divided by the probability of dying in a later year. The hazard ratio (HR) calculated with this form of analysis estimates the increase or decrease in hazard rates for mortality, proportional to a reference condition (i.e., one of the species groups), due to explanatory variables. For the model comparing the hazard rates among species groups, the groups are compared with the "Other species" group. The Other species group consists of trees from 28 (Table 1) different species with diverse mean sizes, growth rates, and, presumably, rates of mortality. This group is assigned an HR of exactly 1 and serves as a baseline representing any unspecified tree from which to compare the known tree species groups. An HR >1 indicates that a species group has a higher hazard rate for mortality than the Other species group. An HR <1 indicates a lower hazard rate for mortality. In this article, we present the HR axis using a  $\log_{10}$  scale to better illustrate the values <1. For example: a HR of 2 is represented as the same distance from the baseline value of 1 as a HR of 0.5.

Models also were calculated for each individual species group. For these, the explanatory variables selected were intended to minimize correlation among variables, and they include surrogates for competitive stress and heat or moisture stress (Appendix 2).

## **Results and Discussion**

#### **Comparisons Among Species Groups**

Analysis of the development data set indicated that the parameter estimates for Oxydendrum arboreum, Q. coc-

cinea, and Q. velutina were not statistically different from 0, i.e., HR = 1, the HR of the Other species group. Over the length of the study, 27% of the trees in the validation data set died for species groups with HR <1, 43% died for the Other species group and the three groups that did not differ from the Other species group, and 56% died for species groups with HR > 1, indicating that this modeling method was appropriate for these data. Because the Other species group was composed of unique species with various life history characteristics, it provided a stable comparison of HRs across species groups. It should be pointed out that the preponderance of species showing low risk of mortality relative to the Other species was expected, given that conglomeration of unique species on the whole would probably have a higher risk of mortality than species that are largely dominant or at least consistently found in sites. The consistent occurrence of a species implies the ability to successfully grow and reproduce at a higher rate than one of the Other species.

The model was refit using the entire data set. Figure 3 illustrates the hazard rates for mortality of the species groups compared with the Other species group with no consideration of competition or climate. *Cornus florida*, and *Sassafras albidum* are at relatively higher hazard rates for mortality (e.g., a *C. florida* tree has a hazard rate nearly 1.5 times the hazard rate of the Other species group) (Figure 3). This reflects the occurrence of dogwood anthracnose (*Discula destructive*), which was first detected in Ohio in 1993 (Oswalt and Oswalt 2010).

In contrast, 15 of the 18 species groups had relatively



Figure 3. HRs and SDs calculated for species groups in the study with no consideration of competitive or climatic stress.

lower hazard rates for mortality (Figure 3). The low hazard rate for mortality calculated for F. grandifolia reflects the species' shade tolerance that allows it to persist in the understory. Nyssa sylvatica has life history characteristics that make it the longest lived hardwood species in the eastern United States (Abrams 2007). Low risks of mortality do not bode well for these two species according to Kuparinen et al. (2010), who found that species with increased mortality rates or forests experiencing frequent disturbances are more likely to adapt to warming temperatures. With a similar tolerance for shade, A. saccharum would be expected to exhibit an HR similar to that of F. grandifolia. A. saccharum experienced a decline in the 1990s (Hallett et al. 2006, Roy et al. 2006) in the Pennsylvania and New York areas in which many of these data were collected. The mortality has been attributed to low nutrient levels exacerbated by several years of defoliation (Hallett et al. 2006). The low mortality hazard rates for Fraxinus spp., Tsuga canadensis, and F. grandifolia do not reflect the introductions of the non-native emerald ash borer (Agrilus planipennis (Cook and McCullough 2009), hemlock woolly adelgid (Adelges tsugae) (Townsend and Rieske-Kinney 2006), or beech scale insect (Cryptococcus fagisuga) (Houston et al. 1979) to some of these areas.

#### Individual Species Group Models

Survival analysis provides an opportunity to relate the potential factors associated with the hazard rates for mortality to each species group. Preliminary models were calculated for each of the 21 species groups using the development data set. These models were applied to the validation data set, and the distribution of HRs for trees that died compared with living trees are shown in Figure 4 for each species group. Except for four species groups (*Betula, Fraxinus, N. sylvatica, and S. albidum*), the median HR value of dead trees was higher than that of living trees. Thus, proportional hazards regression appears adequate for the modeling of hazard of mortality.

Table 2 lists the time-dependent survival analysis estimated coefficients and associated HRs attributed to each significant predictor variable calculated using the entire data set for each species group. These results provide great insight into the individual species group models. When a model is applied to the average tree on an average site in an average year, the HR is equal to 1. For example, if a *Q. alba* tree is average in all respects except for a DGROW 1 mm/year above average, the HR drops to 0.778 (Table 2). Thus, for this species group (and most others), an increased growth rate logically results in decreased risk of mortality as well.

DGROW occurred in all but the *P. serotina* and *Quercus rubra* models. Except for *Acer pensylvanicum* and *Magno-lia acuminata*, the coefficients for DGROW for each species group were all <0 and the HRs were <1, indicating that an increase in DGROW decreases the overall HR for mortality for most species, as found in other studies (e.g., Dwyer et al. 1995, Wyckoff and Clark 2000, 2002). Dwyer et al. (1995) and Pedersen (1998) have shown that *Q. velutina* and *Q. coccinea* may show reduced diameter growth for several decades after a drought. DGROW was the only significant



Figure 4. Boxplot comparisons of hazard rates calculated for live or dead trees in the validation data set from models created using the development data set for each of the 21 species groups.

Scientific name	DGROW	RD	TPH	BAH	PCP	PCP5	MSPET	AVGT	JULT
Acer pensylvanicum	0.164	-15.188	0.006	a					
1	1 178	2536E - 07	1.006 <sup>b</sup>						
	86.010	136 503	30.871						
A a an multimum	-0.217	-2 517	0.005	0.044	-0.007	0.028			-0.182
Acer rubrum	-0.217	-5.517	0.005	0.044	-0.007	0.028			-0.162
	0.804	0.030	1.005	1.045	0.993	1.022			0.833
	/6.883	199.736	32.776	4.020	4.605	6.242			11.639
Acer saccharum	-0.288	-2.624	0.003	-0.041	—	-0.049	0.118	-0.816	
	0.750	0.073	1.003	0.960		0.952	1.125	0.442	
	128.991	909.349	51.176	19.365		7.062	25.124	53.642	
Betula spp.	-0.206	-1.651	0.007	0.126					
**	0.814	0.192	1.007	1.134					
	27.818	25.930	33.042	11.563					
Carva spp.	-0.407	-1.290	0.003	_	0.012				_
earja spp.	0.666	0.275	1 003		1.012				
	51 288	24 508	11.610		6.878				
Comus florida	_0.251	-4.545	11.010	0.110	0.070	0.040		0.000	-0.267
Cornus fiorida	-0.551	-4.545		0.110		0.040		0.900	-0.307
	0.704	0.011		1.117		1.040		2.457	0.693
	101.165	46.871		36.950		19.233		66.154	42.130
Fagus grandifolia	-0.323	-1.474	0.005	_	-0.086	0.210	_	_	_
	0.724	0.229	1.005		0.917	1.234			
	39.05	20.051	48.289		12.354	5.433			
Fraxinus spp.	-0.625	_		0.120		_		_	
	0.535			1.128					
	33.064			9.377					
Liriodendron tulinifera	-0.380	-1.865	0.003	0.093				0 947	-0.536
Zintodeniai ont ninipijera	0.684	0.155	1.003	1 097				2 578	0.585
	55 175	10 124	1.005	6 3 4 9				10 470	11 127
Manualia anuninata	0.260	2 904	4.155	0.549				19.479	11.127
magnotia acuminata	0.200	-2.800							
	1.296	0.060							
	28.463	14.992							
Nyssa sylvatica	-0.539	-4.739					-0.352		0.680
	0.583	0.009					0.704		1.973
	19.117	7.680					7.294		6.095
Oxydendrum arboreum	-0.420	-3.605	0.002	0.119	0.0145	0.021		0.712	-0.367
-	0.65	0.027	1.002	1.127	1.015	1.021		2.038	0.693
	164.531	46.288	9.050	31.784	10.900	5.288		39.146	34.356
Prunus serotina	_	-4.616	0.007	0.091		-0.093			_
		0.010	1 007	1 095		0.911			
		3/2 610	18 83/	11 740		1 831			
Quaraus alba	-0.250	-3 553	0.004	0.074		4.051		0.364	
Quercus uibu	0.230	0.020	1.004	1.077				1 420	
	0.778	0.029	1.004	1.077				1.439	
	5/4.554	1127.380	80.628	17.672				52.011	
Quercus coccinea	-0.095	-2.660	0.002	0.0882				0.278	
	0.909	0.070	1.002	1.092				1.320	
	50.649	327.078	15.330	13.562				9.699	
Quercus prinus	-0.558	-0.991	_	_		0.0695	_	0.350	_
	0.572	0.371				1.072		1.419	
	164.306	22.302				16.095		4.621	
Ouercus rubra		-1.971							
~		0.139							
		41.691							
Quercus velutina	-0.421	-2 633	0.002	0.097		-0.025		0 393	
Quereus venunu	0.656	0.072	1.002	1 102		0.025		1 / 81	
	105 868	181 723	11 424	21 208		4.036		16 307	
Sassafras alleiden	_0.404	-6 005	11.424	21.270		T.730		10.307	-0.457
Sassajras aibiaum	-0.490	-0.003			_				-0.437
	0.609	0.002							0.633
<i>—</i> • •	38.030	11.659							1.112
Isuga canadensis	-0.274	_	_	_	_		_		_
	0.760								
	13.300								
Other species	-0.319	-0.894	0.004			—		—	
	0.727	0.409	1.004						
	54.886	9.070	13.618						

Table 2. Time-dependent survival analysis estimated coefficients, hazard ratios (below coefficients), and  $\chi^2$  statistic (below hazard ratios) by species.

<sup>a</sup> Only variables significantly different from zero (P < 0.05) are presented. <sup>b</sup> Hazard ratios >1 indicate a relatively increased level of mortality risk, whereas ratios <1 indicate a lesser risk.

variable in estimating the hazard rates for mortality for *T. canadensis*. Decreased diameter growth may result from an inability to compete for light, water, and nutrient resources due to shade, small root systems, poor soils, and/or cambial conductance inhibited by bole damage, insects, pathogens, or other disturbances.

The larger a tree is relative to others in the stand (RD) also reflects a tree's ability to compete for resources, because root and crown size are directly proportional to dbh (Yaussy et al. 2004, Tobin et al. 2007, Chen et al. 2008). Therefore, for trees in the majority of species groups investigated, the larger the dbh of the tree, the more likely it was to have reduced hazard rates for mortality (Tables 1 and 2).

The stand competition variables of tree density (TPH) or total basal area (BAH) also played a significant role in 15 of the 21 species groups (Table 2). For 14 species groups, increases in the stand-level stressors of TPH and BAH led to overstocking and concomitant increased hazard rates for mortality. The exception was A. saccharum, which appears to be at less risk of mortality in stands with high BAH. One possible explanation for this phenomenon is that many closed canopy stands at these sites are filled with saplings of this species due to its highly shade-tolerant characteristics (Burns and Honkala 1990). A. saccharum responds well to decreases in BAH by thinning or gap formation. Although the decrease in BAH may decrease competition in the overstory, the increased growth response in the midstory and understory increases competitive stress within the sapling and pole size class, thereby increasing the hazard rates for mortality in this species. This explanation may also account for the positive coefficient for DGROW in the A. pensylvanicum model.

No clear trends could be associated with annual or multiyear precipitation (PCP and PCP5). *A. rubrum* and *F. grandifolia* had negative coefficients for PCP, indicating that increases in annual precipitation reduced the hazard of mortality. *Carya* and *O. arboreum* had positive coefficients reflecting a decreased hazard of mortality in drought years. Three species groups had negative coefficients for PCP5, and five had positive coefficients. In the *A. rubrum* and *F. grandifolia* models, both precipitation variables were present but opposite in sign. This opposite pattern may indicate that the effects of an annual drought may be offset by previous years of ample precipitation or vice versa. Neither PCP nor PCP5 accounts for the seasonality of precipitation, which could also play a role in survival and mortality.

HRs >1 for PCP and PCP5 would appear to be counterintuitive (Stringer et al. 1989, Jenkins and Pallardy 1995, Allen et al. 2010) and seem to indicate that these species groups have higher probabilities of survival after a multiyear drought. This trend could be partially related to the dominant size classes of the species. For example, He et al. (2005) found that *A. rubrum* and *Betula papyrifera* saplings did not experience decreased radial growth after a drought event as did mature trees of those species. Four of the five species groups, including *A. rubrum* and *Betula* spp., were dominated by small size classes (Table 1).

Increases in MSPET would increase the risk of mortality for *A. saccharum* while decreasing it for *N. sylvatica*, according to the models. A decrease in AVGT decreased the hazard rates for mortality for the species group models in which the variable was significant, except for *A. saccharum* (Table 2). The indications are reversed, however, for JULT; five species groups had negative coefficients and *N. sylvatica* was the only species with a positive coefficient.

Comparing  $\chi^2$  significance values for each variable within a species group model (Table 2) illustrates the relative importance of the variable in estimating risk of mortality. Each of the variables linked to competition appeared in more species group models than in any of the climate variables. However, of the 21 species group models, 7 groups did not include any significant climate variables, 5 groups had no climate variables with  $\chi^2$  values above those of the competition variables, and 9 species group models had at least one climate variable of higher relative importance in estimating risk of mortality than at least one of the competition variables. Even though the competition variables occurred more often, they were not always of more relative importance than the climate variables.

### Application of Models with Future Climate

Coefficients of the model for *A. rubrum* that occurred in significant numbers in the four states of this study (Table 1) were applied to the mean climate predictions from the four future scenarios (HADhi, HADlo, PCMhi, and PCMlo) at the McKee, KY, and Kane, PA, sites to demonstrate the possible changes in hazard rates for mortality over space and time. These sites were chosen because they had the greatest differences in predicted future temperatures. The tree and stand competition variables were kept at mean values throughout the predicted future scenarios; therefore, the graphs show changes in HR due to predicted climate change. To obtain a conservative estimate of the range of possible outcomes of HR, a surrogate for PCP5 was calculated by adding or subtracting the historical SD of PCP to the future prediction of PCP.

The variability in climate is projected to increase in the future, with generally more precipitation, longer droughts, colder winters, and hotter summers (IPCC 2007). Therefore, historical climate SDs (Appendix 3) also were applied to each of the climate variables included in the model of *A. rubrum*, under current and future GCM projections, resulting in relatively large increases or decreases in the predicted hazard rates for mortality (Figure 5). Depending on site and whether negative or positive SDs are applied, the future climate scenarios could produce a hazard rate for mortality 7 times greater than the current average for *A. rubrum* (Figure 5A), or the hazard rate could decrease to less than one-tenth (Figure 5D).

A. saccharum and Q. alba are represented with large numbers of observations but are not as even at all sites as A. rubrum (Table 1). We applied the same techniques to the models for these species as we did for A. rubrum in Figure 5, for the HADhi and PCMlo scenarios (Figure 6). The survival model developed for A. saccharum contains coefficients for AVGT, PCP5, and MSPET (Table 2). The HADhi scenario predicts future increases in these variables (Figure 2; future PCP5 being a function of PCP) for both



Figure 5. Predicted change in hazard rate for *A. rubrum*. A and B. Hazard rate minimized by appropriately adding or subtracting the historical SDs of climate variables (Appendix 3) to departures estimated by each of the four future climate scenarios. C and D. Hazard rate maximized by appropriately adding or subtracting the historical SDs of climate variables to departures estimated by each of the four future climate scenarios. A and C represent McKee, KY; B and D represent Kane, PA.



Figure 6. Minimized and maximized predicted change in hazard rate for *A. saccharum* (A and C) and *Q. alba* (B and D) for HADhi and PCMlo climate scenarios. A and B represent McKee, KY; C and D represent Kane, PA.



Figure 7. Historical (1896–2009) departures from climate means and future (2010–2099) departures from climate means predicted by HADhi for the sites in the four states in the study and for (A) centralized PCP and (B) centralized AVGT.

sites and similarly for the PCMlo at the Kane, PA, site. AVGT and MSPET departed little from current for the future predictions of the PCMlo scenario at McKee, KY. PCP and PCP5 are predicted to increase significantly at the McKee site. Increases in AVGT and PCP5 decrease the predicted risk of mortality based on this model, whereas an increase in MSPET increases this risk. These confounding effects, in addition to the effect of current SDs, result in predictions of risk of mortality that are more than a magnitude above or below the current risk for McKee, KY, and close to two magnitudes above and below current for Kane, PA (Figure 6A and C). The minimized SD values applied to the HADhi scenario resulted in a prediction of a risk of mortality so low that if these conditions were to exist in a future year, few if any trees would die. On the other hand, the maximized SD values applied to the same scenario resulted in predicted risk of mortality so high that if these conditions were to exist in a future year, nearly all *A. saccharum* would perish.

AVGT is the only climate variable that proved significant to the prediction of risk of mortality for *Q. alba*. This variable is predicted to change slightly in the future by the PCMIo scenario at the McKee site, which is reflected in the stable prediction of future risk of mortality for *Q. alba* at this site (Figure 6B). A significant increase in AVGT predicted by the HADhi scenario resulted in a similar increase in the predicted risk of mortality at both sites for this species (Figure 6B and D).

The historical climate data from the weather stations were averaged over 30-year periods similar to those of the future projections. Figure 7 uses the HADhi projections to illustrate how the predicted future climate differs from the



Figure 8. Historical (1896–2009) extreme departures from climate means and future (2010–2099) departures from climate means predicted by HADhi for the sites in Kentucky and Pennsylvania for (A) centralized PCP and (B) centralized AVGT.

past. Because there are two sites in Kentucky and Ohio for which future climate data were calculated and only a single weather station used for historical climate data, the future climate data were averaged for the two pixels associated with the study locations within each state and time period. The New York and Pennsylvania sites experienced more change in average PCP over the last 110 years than is predicted for the future, whereas average PCP on the Ohio sites increases only slightly. The Kentucky sites are predicted to experience the largest increase in average PCP (Figure 7A).

The three temperature-related variables (AVGT, JULT, and MSPET) all indicate a large and rapid increase in future compared with past records (Figure 2A, B, and C). Both the rising means and associated increases in extreme climatic events would be expected to cause periodic increases and decreases in mortality. In Figure 8, we show the past extreme events for PCP in Kentucky and for AVGT in Pennsylvania (the states with the most extreme changes in PCP and AVGT in the HADhi projections) (Figure 7). Past extreme PCP years exceed the amount of average increase projected for the future in Kentucky, whereas temperature extremes in Pennsylvania almost equal the projected increase in average AVGT. Surviving trees in this study have weathered extremes larger than the mean values projected in the future; however, extreme events for PCP, AVGT, and JULT are expected to increase above those seen in these records (IPCC 2007).

### Conclusions

Using data from a total of 47,853 trees, we have investigated the effects of competitive and climatic stress on the mortality of 21 tree species groups common to the Allegheny and/or Cumberland Plateaus in the eastern United States. Over the sampling span of 45 years and a large geographic range, species groups demonstrated widely divergent mortality hazard rates. Some of the differences can be accounted for through various levels of attack from insects and pathogens, low nutrient levels, and differences in relative age.

Models of the effects of competitive and climatic stress on individual species groups revealed that decreased diameter growth, reduced relative size, high numbers of trees, and high basal area were significant factors in predicting increased hazard rates for mortality. This result indicates that managers would do well to manage forests to reduce competitive stress (e.g., manage density and/or basal area), so that the trees are in a better position to withstand the extra stresses associated with climate change and invasions of exotic organisms.

The HR analysis conducted here was shown to be effective at both comparing mortality hazard rates among species groups and evaluating the influences of competitive and climate covariates on tree species group mortality hazard rates. Although not intended to be used in simulations to predict future mortality hazard rates, the outputs provide the significantly important variables and the strength of the variables, affecting projected outcomes. The effects of climate variables on hazard rates for mortality were not always as intuitive as those variables representing competitive stress. For many species groups, the results do clearly point to consistent trends in future climate-induced mortality. For six of the eight species group models with annual temperature entering significantly into the model (P < 0.05), the hazard rates for mortality were substantially increased with increasing temperatures. These trends match those projected both by species group change models (e.g., Iverson et al. 2008) and independent data (e.g., Woodall et al. 2009). Although these other studies do not address mortality per se, they do suggest the potential for changes in forest composition over time.

However, caution is needed in the HR analysis and interpretation because sometimes the sampling period, even though long, did not capture much of the variability in climate conditions relative to the future changes projected by GCMs. The variations presented by the different GCM scenarios, coupled with the conservative application of current SDs in the climate variables, produced results that scatter across the range from little or no change in hazard rates for mortality to greatly increased or decreased hazard, depending on the species group. This is not an indication of imprecision in the models, but of the highly variable nature of climate. With the prediction that changes in the variation of future precipitation and temperature will be greater than the future means (i.e., more extreme events), it follows that the hazard rates for mortality will increase over the current hazard for every species group during some time period in the next 100 years. Although there will also be periods of decreased hazard due to climate extremes in the opposite direction, these times of respite may not be able to compensate for the greater accumulation of stress that can increase overall hazard.

In sum, we present a data-rich case for mortality hazard rate being subject first to the competitive factors associated with it, followed by climatic factors. Projecting to the future is always difficult and dangerous, but indications from these analyses show that, in general, the projected increases in temperature will probably translate to higher tree mortality hazard rates. Projected slight increases in precipitation may moderate these increased hazard rates to some degree but not sufficiently to avoid increased mortality due to extreme climate events. Forest managers have little ability to affect the extremes of weather or the mortality that might follow its occurrence. Luckily, competitive stress affects the risk of mortality much more than the changing climate, and managers are quite capable of reducing competitive stress. The removal of smaller stems through partial harvesting, the use of prescribed fire or herbicide would result in the reduction of numbers of trees and stand basal area, thereby decreasing the risk of mortality for the residual trees.

Based on history though, we may witness increases in mortality primarily from other factors (e.g., invasive insects, pathogens, plants, and increased fire), with the climate changes providing additional stress, which predisposes the trees to greater susceptibility to these other causal agents. Management to reduce competitive stress will increase the ability of trees to withstand these and other future stresses. These invasive agents and the effects they have on the risk of mortality were not able to be directly studied here, but such studies are needed to further unravel the big questions associated with forecasting and managing our forest resource.

#### Endnote

1. SAS and all other SAS Institute, Inc., product or service names are registered trademarks or trademarks of SAS Institute, Inc., Cary, NC.

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## Appendix 1

#### Descriptions of study sites.

Location	Study no.	Measurement year	No. of measurements	Year of stand origination	No. of Plots	Plot size (ha)	No. of trees	Stocking % treatments <sup>a</sup>
Baldrock. KY	13	1959-2006	23	1882	16	0.4047	5,761	20-75
McKee, KY	11	1961-2006	22	1928	15	0.2023	4,327	15-85
	12	1962-2006	20	1928	6	0.1012	802	35
Lucasville, OH	24	1962-2005	20	1900	16	0.2023	4,989	40-100
McArthur, OH	21	1961-2009	21	1929	16	0.2023	6,147	40-100
	22	1963-2009	18	1912	6	0.1349	430	50
	25	1978-2009	27	1868	3	0.2023	269	Unthinned
	27	1977-2009	25	1868	3	0.4047	681	Unthinned
Kane, PA	76-1	1972-1998	10	1925	11	0.2428	3,674	25-unthinned
	76-2	1974-2004	11	1925	10	0.2428	4,050	35-unthinned
	76-3	1975-2000	11	1925	11	0.2428	7,601	50-unthinned
Marienville, PA	76-4	1979–1984	4	1910	1	0.2428	184	70
	76-5	1979–1999	7	1900	3	0.2428	570	60-unthinned
Coudersport, PA	76-6	1984-1999	4	1910	2	0.2428	586	80-unthinned
	76-7	1984–1999	4	1920	5	0.2428	1,667	45-unthinned
	76-8	1984-1999	4	1925	5	0.2428	1,462	35-unthinned
Warren, PA	76-13	1985-1990	2	1920	5	0.2428	1,068	40-unthinned
Sinclairville, NY	76-9	1984–1999	4	1865	3	0.2428	1,280	40-unthinned
	76-12	1985-2001	4	1885	5	0.2428	2,305	60-unthinned

<sup>a</sup> Nominal stocking percent values were calculated using formulae found in Gingrich (1967) for studies in Kentucky and Ohio and in Roach (1977) for studies in New York and Pennsylvania.

# Appendix 2

Variables measured or calculated for use in the modeling of individual-tree survival.

Variable	Definition				
Individual-tree					
STATUS	Mortal status at time of measurement: living or dead				
DGROW	Annual diameter growth calculated by subtraction of diameter at 1.37 m height (dbh) of the previous measurement period from current dbh divided by number of years in the measurement period (mm)				
RD	Tree dbh divided by the quadratic mean diameter (QMD) of the plot: $QMD = SQRT(BAH/TPH/3.1416) \cdot 200$				
Stand					
BAH	Summation of individual-tree cross-sectional area of live trees at 1.37 m height for all living trees $>10$ cm on the plot (m <sup>2</sup> /ha)				
TPH	Number of living trees $> 10$ cm on the plot converted to number/ha (trees/ha)				
AGE	Age of stand at each measurement period based on age recorded at the initiation of each study				
Climate					
AVGT	Mean annual temperature centralized by station				
JULT	Mean July temperature centralized by station				
MSPET	Mean May through September potential evapotranspiration calculated from equations based on mean monthly temperatures and day length, presented in Willmott and Rowe (1985) centralized by station				
PCP	Annual precipitation centralized by station				
PCP5	5-yr running average of PCP				

## Appendix 3

Location	110-yr average (SD)									
Latitude Longitude Weather station	AVGT JULT MSF		MSPET (mm) <sup>a</sup>	PCP (cm)						
°C										
London Corbin Airport, KY 37.083 84.083 COOPID 154898	13.2 (0.7)	24.1 (1.1)	118.9 (5.5)	118.0 (17.8)						
Jackson 3 NW, OH 39.083 82.700 COOPID 334004	11.5 (0.9)	23.3 (1.2)	113.4 (5.1)	106.7 (15.9)						
Kane 1NNE, PA 41.683 78.800 COOPID 364432	7.8 (2.1)	19.8 (2.3)	99.5 (9.6)	110.8 (16.6)						
Jamestown 4ENE, NY 42.117 79.167 COOPID 304207	8.5 (1.2)	20.9 (1.6)	103.2 (5.6)	102.4 (18.1)						

Weather station locations, 110-year average, and standard deviation for the four climate variables used in the survival analysis.

<sup>a</sup> Growing season (May-September) potential evapotranspiration calculated with equations found in Willmott and Rowe (1985).