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Modeling transient response of forests to climate change

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ABSTRACT

Our hypothesis is that a high diversity of dominant life forms in Tennessee forests conveys resilience to disturbance such as climate change. Because of uncertainty in climate change and their effects, three climate change scenarios for 2030 and 2080 from three General Circulation Models (GCMs) were used to simulate a range of potential climate conditions for the state. These climate changes derive from the Intergovernmental Panel on Climate Change (IPCC) "A1B" storyline that assumes rapid global economic growth. The precipitation and temperature projections from the three GCMs for 2030 and 2080 were related to changes in five ecological provinces using the monthly record of temperature and precipitation from 1980 to 1997 for each 1 km cell across the state as aggregated into the provinces. Temperatures are projected to increase in all ecological provinces in all months for all three GCMs for both 2030 and 2080. Precipitation differences from the long-term average are more complex but less striking. The forest ecosystem model LINKAGES was used to simulate conditions for five ecological provinces from 1989 to 2300. Average output projects changes in tree diversity and species composition in all ecological provinces in Tennessee with the greatest changes in the Southern Mixed Forest province. Projected declines in total tree biomass are followed by biomass recovery as species replacement occurs in stands. The Southern Mixed Forest province results in less diversity in dominant trees as well as lower overall biomass than projections for the other four provinces. The biomass and composition changes projected in this study differ from forest dynamics expected without climate change. These results suggest that biomass recovery following climate change is linked to dominant tree diversity in the southeastern forest of the US. The generality of this observation warrants further investigation, for it relates to ways that forest management may influence climate change effects.

1. Introduction

Great attention is now focused on climate change and its impacts (Walther et al., 2002; IPCC 2007). Forests are highly vulnerable to climate change and significant forest dieback can occur (Chapter 4 in Working Groups II Report for the IPCC, 2007). Impacts of global warming on plants have already been documented (Root et al., 2003). Climate change is anticipated to affect forests by altering both forest processes (Aber et al., 2001) and biodiversity (Hansen et al., 2001; Hansen and Dale 2001) and in doing so change forest location, composition, and productivity (Shugart et al., 2003). Most models based on the IPCC A2 scenarios show significant forest dieback towards the end of this century and beyond in tropical, boreal, and mountain areas with a concomitant loss in key services (Fischlin et al., 2007). Changes in productivity, carbon sequestration, forest water resources and the way people relate to the forests (such as recreation) may be less resilient to change than economic responses (Irland et al., 2001). All of these impacts are moderated by interactions between climate, disturbances, land-use change, and forests (Dale et al., 2000). Key forest disturbances are fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, wind storms, and ice storms. However, to understand how this suite of factors can influence forest systems, we need to have a clear understanding of how projected climate changes are likely to affect the structure and composition of forests.

Most analyses of the effects of climate change on forests have been at large scales, ranging from the globe, to national, and occasionally to key regions. Yet effects of climate change are likely to be driven by site-specific characteristics including soil depth, soil water holding capacity, and species sensitivity to drought and temperature. Projected climate changes can thus be expected to differ by location, and those effects on forests are largely determined by local conditions such as existing forest composition and structure and prevailing environmental conditions (Iverson and Prasad, 1998). Therefore, it is important to consider location specific effects of climate change.

The southeastern portion of the United States has been identified as a critical region in which it is necessary to understand potential effects of climate change because most of the forest industry in the US occurs

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there, the region is anticipated to undergo severe climate changes, forest diversity is high, and hence predictions of potential effects are a challenge (Joyce et al., 2001). Studies using the satellite-sensed normalized difference vegetation index (NDVI) as a measure of the biotic response to climate change documented a persistent increase in NDVI from 1981 to 1999 for needle forests of the southeast US (Zhou et al., 2001).

Watson et al. (1996) analyze how different models project forest growth and decline in the face of climate change in the southeastern US. Simulations with the MAPSS and BIOME3 biogeochemical models project temperate mixed forest in the US undergoing a loss of leaf area (e.g., biomass decrease) of 12% to 76% for the SAR scenarios without CO_2 effects. However a comparison of six different ecological models to a doubling of atmospheric CO_2 and several different climate change scenarios for the conterminous US shows different results (VEMAP 1995; Malcolm and Pitelka, 2000). Shugart et al. (2003) suggest that these differences are not unexpected, given differences in model formulation and resolution. For example, two of the seven projections with MAPSS show forests in Tennessee being replaced by savanna/woodland vegetation (Neilson, 1995). These results suggest that Tennessee is in a tension zone with respect to effects on forests of projected climate change and thus warrants further investigation. The longevity of the trees in the southeastern forests and diversity of these systems make it unclear what the long-term forest composition and productivity might be.

This study focuses on long-term changes in forests within Tennessee, a state within this important forest region and which, because of its altitudinal gradient, contains several ecological and climate zones. Tennessee forests were chosen as the focus of this study for several reasons. Tennessee is expected to experience dramatic changes in climate in ensuing decades. Forestry is a critical part of the economy of the state. Direct benefits from forestry include 73,400 jobs and annual wages of $2.4 billion, and supplier industries provide an additional 184,300 jobs and $5.6 billion in wages with a total economic contribution exceeding $33.7 billion (English et al., 2004). Furthermore, the more than 71 species that comprise Tennessee's natural forests support great diversity in plants and animals across the state. Tennessee has one of the highest species diversity of inland states in the United States (Stein et al., 2000), which is partially related to variability in topography, climate regimes, and hence vegetation types.

By considering the transient response over three centuries to three scenarios of climate changes in temperature and precipitation on Tennessee forests, this study examines the long-term effects of temperature and precipitation at a spatial resolution that has importance both ecologically and in the many ways that people interface with forest systems. The key question that this study addresses is how a highly diverse and complex forest system responds to projected change in temperature and precipitation. Such responses are quite complex (Cao and Woodward, 1998) and can induce a variety of changes (Joyce et al., 2001) and must be considered at local scales as well as globally (Woodward and Williams, 1987). Because Tennessee has such high ecological diversity, its five ecological provinces are considered separately. The projections of changes in forest biomass and composition reported in this study lay the groundwork for assessing potential effects on a variety of ecological services provided by Tennessee forests.

2. Methods

2.1. Ecological provinces and forested lands of Tennessee

This study focuses on the five ecological provinces in Bailey's ecoregions analysis (Bailey, 1995) that occur in Tennessee (Fig. 1). We used Bailey's province descriptions but have modified the names of these provinces to better describe the conditions in Tennessee to be the *Southern Mixed Forest, Mississippi (MS) Riverine Forest, Central Tennessee (TN) Broadleaf Forest, East TN Broadleaf Forest,* and *Appalachian Forest* (Table 1).

The amount of forested land in Tennessee has been on the rise since the last century when many of the trees were harvested for railroads and the land was put temporarily into agriculture. Today, most of the forested areas are natural second growth stands, with less than 4% of Tennessee forests being plantations. In the early part of the twenty-first century, about 69% was in private ownership by individuals, 10% was owned by the forestry industry, and 13% was under federal or state government. However these numbers have been rapidly changing. A widespread outbreak of the native pine bark beetle destroyed many pine stands and combined with the pressure for land development for residential use, the number of landowners is increasing dramatically. As a result average tract size is declining.

2.2. Climate projections

This study simulates transient response of forests to projected climate change from 1989 to 2300 as described in detail below. The monthly temperature and precipitation data used in the forest simulation are a piecewise continuous curve for each ecological province beginning with average conditions for 1989 (derived from average conditions from 1980 to 1997), a linear extrapolation from 1989 to the 2030 climate projections from three General Circulation Models (GCMs), a linear extrapolation from 2030 to the 2080 GCM projections,

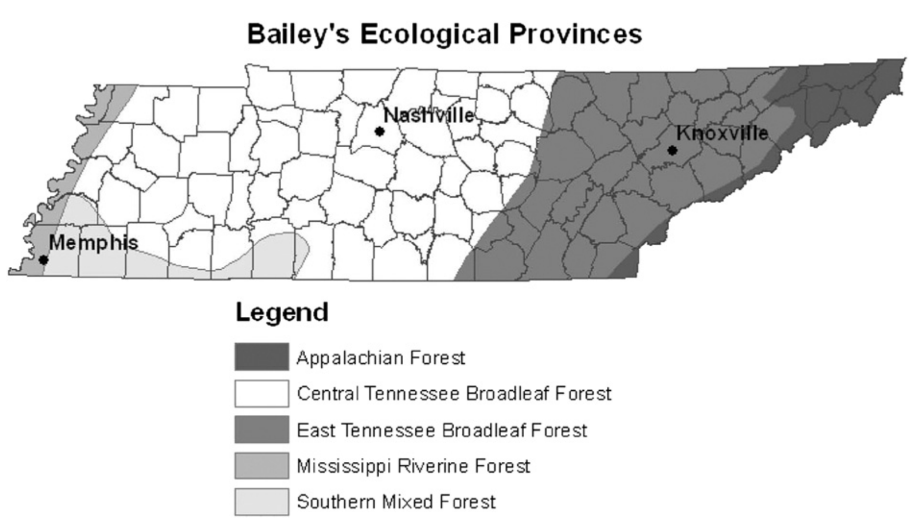

Fig. 1. Map of the ecological provinces in Tennessee used in this analysis.

Table 1
Description of Bailey's provinces as they occur in Tennessee forests.

Tennessee forest type	Bailey's province	Land surface form	Temperature	Vegetation	Dominant soils
Southern Mixed Forest	Southern Mixed Forest Province	Gentle slopes and local relief	Mild winters and hot, humid summers	Broadleaf deciduous and pine trees	Ultisols dominate with inceptisols on floodplains
Mississippi Riverine Forest	Lower Mississippi Riverine Forest Province	Flat to gently sloping broad floodplain and low terraces	Warm winters, hot summers	Bottom-land deciduous forest	A mosaic of inceptisols, alfisols, and mollisols
Central Tennessee Broadleaf Forest	Eastern Broadleaf Forest (Continental) Province	Low rolling hills, dissected plateaus, and basins	Hot summers and cold winters	Temperate deciduous oak-hickory forest	Alfisols with ultisols on plains and plateaus
East Tennessee Broadleaf Forest	Eastern Broadleaf Forest (Oceanic) Province	Plateaus, hilly and mountainous	Strong annual temperature cycle, with cold winters and hot summers	Temperate deciduous forest consisting of mixed mesophytic species	Alfisols, ultisols, and inceptisols
Appalachian Forest	Central Appalachian Broadleaf Forest–Coniferous Forest–Meadow Province	Mountainous	Distinct summer and winter	Mixed oak–pine forest, northern hardwood forest, and spruce–fir forest	Ultisols in gentle topography, and inceptisols on steep landforms

and the constant value of the 2080 GCM projections out to 2300 (see example in Fig. 2). The challenge in performing such simulation is choosing how to define the scenarios. We selected to simulate a "no change" scenario because we do not know how the conditions will change from 2080 to 2300. We do know that availability of fossil fuels will be severely reduced over time, and thus the major input of CO_2 into the atmosphere will be much less. Therefore, it is very likely that the changes in climate will greatly diminish as well. The effects of the 2080 climate conditions are immediately apparent, and the simulation was carried forward an additional 220 years to allow assessment of the long-term implications.

These GCM runs were from the A1B storyline, as developed by the IPCC, that was designed to build from an underlying consistency in the social and physical relationships driving greenhouse gas (GHG) emissions (Nakićenovic et al., 2000) and is a midline estimate of changes. The A1B scenario focuses on global solutions to economic, social and environmental sustainability, particularly targeting economic growth under a mix of fossil intensive and non-fossil fuel energy sources (Nakićenovic et al., 2000). It assumes that CO_2 concentrations would be about 700 ppm by 2100. The A1B storyline assumes rapid global economic growth (3%) and liberal globalization as characterized by low population growth, very high GDP growth, high-to-very high energy use, low-to-medium changes in land use, medium-to-high resource availability, and rapid technological advancement. Under this storyline, personal wealth is emphasized over environmental quality, and there would be reduced differences in regional incomes. This storyline emphasizes market-based solutions; high savings and investment, especially in education and technology; and international mobility of people, ideas, and technology.

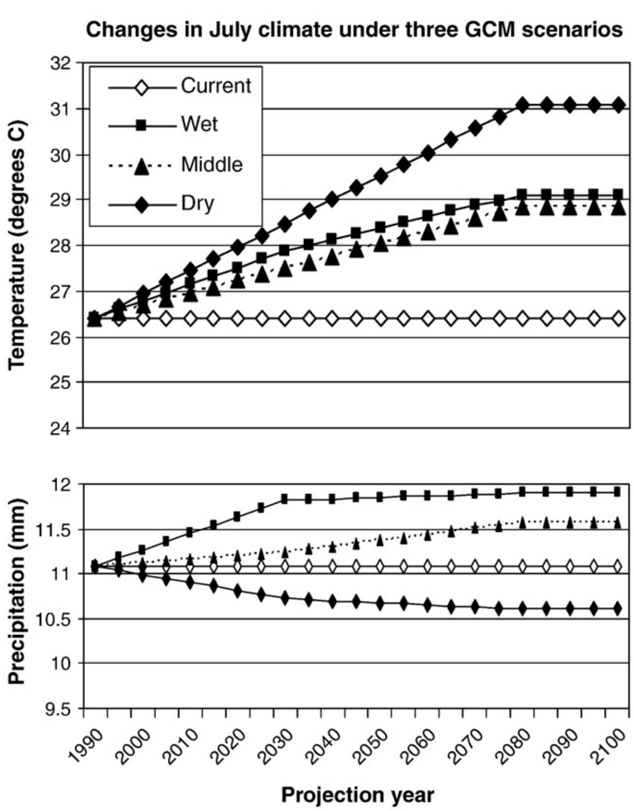

Fig. 2. Example of how climate changes were implemented in LINKAGES. July temperature and precipitation changes for 1990 to 2100 for the Southern Mixed Forest.

Climate change projections from three GCMs were used to adjust the temperature and precipitation in 2030 and 2080 in each ecological province. The temperature and precipitation change projections for 2030 and 2080 for Tennessee were provided by the National Center for Atmospheric Research (NCAR) from three GCMs (selected from 18 possible GCMs) that provide a moderate range of potential climate conditions for Tennessee (the most extreme emissions scenario is not considered here) (personal communication, August 1, 2006, J.B. Smith and C. Wagner, Stratus Consulting Inc., Boulder, CO) (see Tables 2 and 3). The "2030" projections are model simulations of the years 2020–2039, and the "2080" projections are model simulations of the years 2070–2089. NCAR provided climate data for an area from 35°N to 38°N in latitude and 81°W to 91°W in longitude that slightly exceeds the state boundaries (since the climate region for the GCMs is very large — approximately 480 km across). The models' grids were interpolated by NCAR to a "T42" grid, which represents the median resolution among the models contributing to the Program for Climate Model Diagnosis and Intercomparison (PCMDI) archive (for further information, see Tebaldi et al., 2004, 2005). The GCM output is a monthly average and does not indicate how daily or inter-annual variability can change. The selected GCM outputs represent three conditions:

- Wet [National Center for Atmospheric Research's Community Climate System Model (ccsm3) (Collins et al., 2006; and http://www.ccsm.ucar.edu/models/ccsm3.0/)]
- Middle [National Center for Atmospheric Research's Parallel Climate Model (PPM) (Washington et al., 2000; and http://www.cgd.ucar.edu/pcm/)]
- Dry [Center Climate System Research (The University of Tokyo), National Institute for Environmental Studies, and Frontier Research Center for Global Change (JAMSTEC) Model for Interdisciplinary Research on Climate, medium resolution] (Watanabe et al., 2008).

Table 2
Differences in projected mean monthly temperature and precipitation for Tennessee from the three General Circulation Models. "Wet" comes from the National Center for Atmospheric Research's Community Climate System Model (ccsm3) (Collins et al., 2006), "Middle" from the National Center for Atmospheric Research's Parallel Climate Model (PPM) (Washington et al., 2000), and "Dry" from the Center Climate System Research (The University of Tokyo), National Institute for Environmental Studies, and Frontier Research Center for Global Change (JAMSTEC) Model for Interdisciplinary Research on Climate, medium resolution. The models were run under the A1B storyline of IPCC that assumes rapid global economic growth (3%) and liberal globalization as characterized by low population growth, very high GDP growth, high-to-very high energy use, low-to-medium changes in land use, medium-to-high resource availability, and rapid technological advancement.

Month	Temperature (°C)						Precipitation (mm)					
	2030 difference			2080 difference			2030 difference			2080 difference		
	Wet	Middle	Dry	Wet	Middle	Dry	Wet	Middle	Dry	Wet	Middle	Dry
January	1.20	0.05	1.85	2.63	1.23	3.92	0.176	0.005	0.174	0.319	−0.075	0.24
February	1.50	0.70	2.10	2.61	1.54	4.54	0.007	0.456	−0.053	0.143	−0.055	-0.13
March	1.74	0.76	1.85	2.70	1.84	4.53	0.228	0.236	0.108	0.467	0.423	−0.12
April	1.22	0.33	1.97	2.57	1.77	4.19	0.017	0.13	−0.042	0.131	−0.053	−0.384
May	1.73	0.90	1.61	3.05	2.58	4.40	0.128	0.082	−0.652	0.475	0.139	−0.909
June	2.01	1.15	2.05	3.26	2.25	4.39	0.286	−0.14	−0.69	0.405	0.336	−0.681
July	1.46	1.09	2.07	2.70	2.44	4.67	0.736	0.153	−0.357	0.816	0.492	−0.476
August	0.83	1.28	2.03	2.04	2.42	5.58	0.773	0.028	0.173	1.125	0.354	−0.699
September	1.93	1.33	2.75	3.17	2.80	6.33	0.279	0	−0.612	0.389	−0.099	−1.143
October	1.81	1.72	1.77	3.72	2.74	4.77	0.032	−0.058	−0.183	0.108	0.032	−0.392
November	1.74	0.74	1.68	3.12	1.77	4.65	0.079	0.077	0.025	0.046	0.016	−0.221
December	1.57	0.64	1.25	2.51	0.78	4.37	0.123	0.03	−0.113	0.191	0.11	0.108

The GCMs and global climate modeling approaches are described in IPCC (2007).

An appropriate way to apply the GCM output of projected climate change is to combine it with an observed weather database. Therefore, the precipitation and temperature change projections from the three climate change models for 2030 and 2080 were related to changes in the five ecological provinces of Tennessee by using the monthly record from 1980 to 1997 for each 1 km cell across the state that is available from the Daily Surface Weather and Climatalogical Summaries (DAYMET http://www.daymet.org/). The DAYMET data were derived by using a digital elevation model based on daily observations of minimum and maximum temperatures and precipitation from ground-based meteorological stations over an 18 year period (1980–1997). The data consist of temperature, precipitation, humidity, and radiation at a 1 km resolution and are complete for our study area (Thornton et al., 1997; Kimball et al., 1997; Thornton and Running, 1999). We averaged the observed 1 km climate data for the five provinces and combined them with the monthly GCM output of temperature and precipitation to produce monthly climate projections for 2030 and 2080. Climate data from the years 1980 to 1997 were used in this analysis because that is the summary period of the DAYMET project. There was an extreme drought in Tennessee from 1985 to 1988; yet 1989 was an extremely wet year with precipitation being about 130% of normal. The period from 1980 to 1997 experienced both warmer and cooler years than the long-term trend (NOAA, 2006).

2.3. Projecting changes in forest stand structure and composition in Tennessee

Changes in forest conditions for the five ecological provinces in Tennessee were projected by using the LINKAGES forest ecosystem model (see model documentation by Pastor and Post, 1985). LINKAGES simulates changes in forest composition and structure based on changing biogeochemistry for a 1/12 ha plot (Post and Pastor, 1996). It was developed from the family of gap models known as JABOWA (Botkin et al., 1972) and FORET (Shugart and West, 1980) that simulates changes over time in size and species of individual trees as influenced by competition for light and soil moisture and as determined by prevailing temperature. The unique features of LINKAGES are that it models (1) the direct effects that climate change can have on forest ecosystem production and hence carbon storage through temperature and water limitations and (2) the indirect effect through the nitrogen cycle by affecting species composition (Post and Pastor, 1996). In the model, monthly mean and standard deviations of temperature and precipitation determine growing degree days, soil moisture, and annual evapotranspiration. Availability of light for each tree is determined by sunlight (as influenced by latitude) as well as by the accumulated height of all taller trees in the plot. Growing degree days and light and water availability constrain species reproduction. These environmental factors along with soil nitrogen availability affect tree growth and mortality and hence biomass and carbon accumulation.

A variety of models exist to examine effects of climate change on forest ecosystems (Dale and Rauscher, 1994; He et al., 1999; Iverson et al., 1999; Luxmoore et al., 2000; Moisen and Frescino, 2002; Porte and Bartelink, 2002; He et al., 2005). LINKAGES was selected for this study because it can model climate change effects on the forest ecosystem that includes the full diversity of tree species found in Tennessee forests. LINKAGES simulates effects of temperature on a species based on its geographic distribution rather than empirical physiological measures, which Loehle and LeBlanc (1996) argue can overestimate the influence of climate. Indeed, an examination of a gap model and a physiology model for Scots pine (*Pinus sylvestris*) showed that the gap model was not unduly sensitive to climate under prevailing conditions in Finland but might be at the northern or southern extent of the species range (Talkkari et al., 1999). This result makes the restriction of the LINKAGES application to Tennessee appropriate since the state lies in the central portion of the range of many eastern deciduous forest species (Burns and Honkala, 1990). Furthermore, individual tree growth in LINKAGES is determined by the single factor most restrictive to each tree among several potential constraints including light, soil moisture, soil nitrogen, and temperature as influenced by prevailing environmental conditions and other trees in the model stand. Pastor and Post (1988) earlier demonstrated that it was important to include both soil moisture and nitrogen availability in simulations of climate change. Many applications of this type of gap model have demonstrated its utility in understanding how climate change can affect forest composition and structure (e.g., Solomon, 1986; Pastor and Post, 1986; Dale and Franklin, 1989; Shugart et al., 1992; Shugart and Smith, 1996; Bugmann et al., 2001; Hanson et al., 2005; He et al., 2005; Yan and Shugart, 2005). Nevertheless, we recognize that these types of models are most useful to improve understanding of key influences in the ecological system and to project features of forest composition and structure that may change; they are not meant to be predictions of the future (Dale and Van Winkle, 1998).

LINKAGES was used to project changes over time from 1989 to 2300 in total stand biomass and biomass of tree species following the approach developed by Solomon (1986). Output is based on 100 stochastic model runs that are averaged for each ecological province. All 71 species native to Tennessee forests were available for reproduction in any year in all provinces. Monthly mean and standard deviations of temperature and precipitation climate conditions used by LINKAGES were from a piecewise curve for each ecological province, as described above. The average monthly conditions for the 1980 to 1997 period provided the base case for the 200 year LINKAGES model runs up to 1989 that allowed the model to equilibrate. Thereafter, the temperature and precipitation increased linearly to 2030, continued to increase linearly to 2080, and thereafter remained stable.

3. Results

3.1. Projected climate change

Projected climate changes for the five ecological provinces in Tennessee for 2030 and 2080 show strong trends (Table 2). Temperatures are projected to increase from the 1980-to-1997 average (Table 3) for all months for all provinces for all three GCMs, with warmer temperature projected for 2080 than for 2030 (Table 2). By 2030, the "dry" scenario for September is projected to have the greatest increase (2.75 °C) over the 18-year average, and the "middle" scenario for January the lowest increase (0.05 °C). By 2080, the greatest increase is projected for the "dry" scenario in September (6.33 °C), and the lowest for the "middle" scenario in December (0.78 °C).

Precipitation patterns are more complex but less striking. The "wet" GCM tends to have wetter summer months than the "middle" GCM, and both experience more annual precipitation than the1980-to-1997 average. The "dry" GCM projects drier months than the 18-year average except for January, March, August, and November in 2030 and January and December in 2080. These changes in precipitation are generally within the monthly standard deviation from the long-term record from 1980 to 1997 (compare Tables 2 and 3B).

3.2. Projected changes in forest stand biomass

Total forest biomass projections over the 311 year period show similarities in initial trends for the "dry" scenario for all five ecological provinces (Fig. 3). These trends can be compared to an approximate constant biomass level that would be maintained by the forest after reaching the 1989 stand structure if not exposed to climate changes. The Southern Mixed Forest, MS Riverine Forest, Central TN Broadleaf Forest, East TN Broadleaf Forest, and Appalachian Forest all display a distinct decline in total forest biomass from 2000 to 2080 for the "dry" scenario, with the biomass gradually increasing back to the 1989 level in all but the Southern Mixed Forest. The "dry" scenario of the Southern Mixed Forest recovers only about one third of the forest biomass by year 2300.

The "wet" scenarios of the MS Riverine Forest, East TN Broadleaf Forest, Appalachian Forest, and Southern Mixed Forest all experience a decline in total forest biomass before 2100, but the timing of the initiation of the decline, of the low point, and of the recovery period are each unique. The "wet" scenario of the Central TN Broadleaf Forest undergoes a slight decline in biomass beginning in 2000 but recovers by 2080 and then experiences another decline from about 2090 to 2150 before initiating recovery again.

The "middle" scenario has a unique projection of total forest biomass for all five ecological provinces. The MS Riverine Forest experiences a dip in biomass between 2080 and 2125. The Central TN Broadleaf Forest biomass decline begins in 2030, reaches a low at about 2050, increases to 2080, experiences a small drop, then increases to its initial value by year 2125, and thereafter experiences gentle decline. The East TN Broadleaf Forest, in contrast to the other provinces, increases in total biomass to about year 2050, then declines to 2080, after which it increases gradually during the rest of the simulation period. The Southern Mixed Forest case has a gradual decline to about year 2100 and then a gradual increase. The Appalachian Forest "middle" scenario undergoes a sharp decrease to about year 2050, then a sharp increase to reach a new high by year 2200, after which it slightly declines. New highs in total biomass are achieved for all three cases for the East TN Broadleaf and Appalachian Forests, which exceed values expected with no climate changes.

The variability in projected biomass over time is low for all provinces and all climate change scenarios. The 95% confidence intervals for total biomass calculated from the 100 replications never exceed 16 Mg/ha for any one year.

Most of the climate change scenarios and forest types show a decline and then recovery of total forest biomass over time, with the dry scenarios taking the longest time to reestablish initial levels of biomass.

Table 3
Climate conditions for the five ecological provinces based on the DAYMET 1 km data from 1980 to 1997for the five ecological provinces based on the DAYMET 1 km data from 1980 to 1997.

Month	Appalachian Forest	Central Tennessee Broadleaf Forest	East Tennessee Forest	Lower Mississippi Riverine Forest	Southeastern Mixed Forest
A. Monthly temperature mean (and standard deviation) (°C)					
Jan	1.21 (1.21)	2.37 (.55)	2.08 (.89)	2.59 (.84)	3.26 (.33)
Feb	3.29 (1.31)	4.86 (.54)	4.34 (.93)	5.26 (.83)	5.80 (.37)
March	7.38 (1.44)	9.51 (.52)	8.62 (.93)	10.18 (.73)	10.44 (.46)
April	11.66 (1.54)	14.15 (.53)	13.07 (.87)	15.20 (.57)	15.02 (.57)
May	16.24 (1.55)	18.96 (.61)	17.71 (.85)	20.39 (.49)	19.88 (.74)
June	20.58 (1.69)	23.44 (.65)	22.12 (.9)	25.05 (.41)	24.26 (.8)
July	22.79 (1.7)	25.73 (.6)	24.40 (.89)	27.17 (.34)	26.41 (.75)
August	21.90 (1.72)	24.94 (.56)	23.60 (.91)	26.12 (.37)	25.61 (.66)
September	18.42 (1.64)	21.03 (.5)	19.95 (.91)	22.06 (.5)	21.79 (.58)
October	12.63 (1.46)	14.83 (.47)	13.88 (.82)	15.93 (.54)	15.62 (.6)
November	7.43 (1.29)	9.27 (.44)	8.43 (.76)	9.92 (.6)	10.05 (.45)
December	2.96 (1.2)	4.42 (.49)	3.87 (.81)	4.76 (.75)	5.25 (.36)
B. Monthly precipitation mean (and standard deviation) (cm)					
Jan	10.81 (2.57)	10.30 (1.21)	12.41 (1.29)	9.31 (.64)	10.35 (.8)
Feb	11.82 (2.19)	12.13 (.75)	12.94 (1.12)	11.04 (.41)	12.26 (.73)
March	12.37 (2.82)	14.26 (1.22)	14.27 (1.75)	12.57 (.94)	14.45 (.88)
April	10.10 (1.84)	11.43 (1.02)	10.85 (.99)	13.38 (.67)	13.71 (.46)
May	12.90 (1.47)	14.16 (1.19)	12.79 (1.37)	12.98 (.64)	15.05 (1.51)
June	11.11 (1.86)	11.56 (.75)	11.17 (.94)	11.56 (.38)	12.02 (.49)
July	12.65 (1.2)	11.27 (.77)	11.68 (.95)	9.15 (.47)	11.08 (.74)
August	10.86 (1.93)	8.01 (1.29)	10.39 (1.01)	5.81 (.45)	7.33 (1.19)
September	9.37 (1.49)	10.21 (.75)	9.82 (1.3)	8.62 (.55)	9.58 (.77)
October	7.90 (1.67)	9.50 (.55)	8.73 (1.23)	10.32 (.28)	10.07 (.37)
November	10.31 (2.19)	13.87 (.59)	12.63 (1.71)	14.07 (.53)	14.51 (.48)
December	10.77 (2.36)	14.62 (.86)	13.48 (1.54)	14.08 (.78)	15.65 (.71)

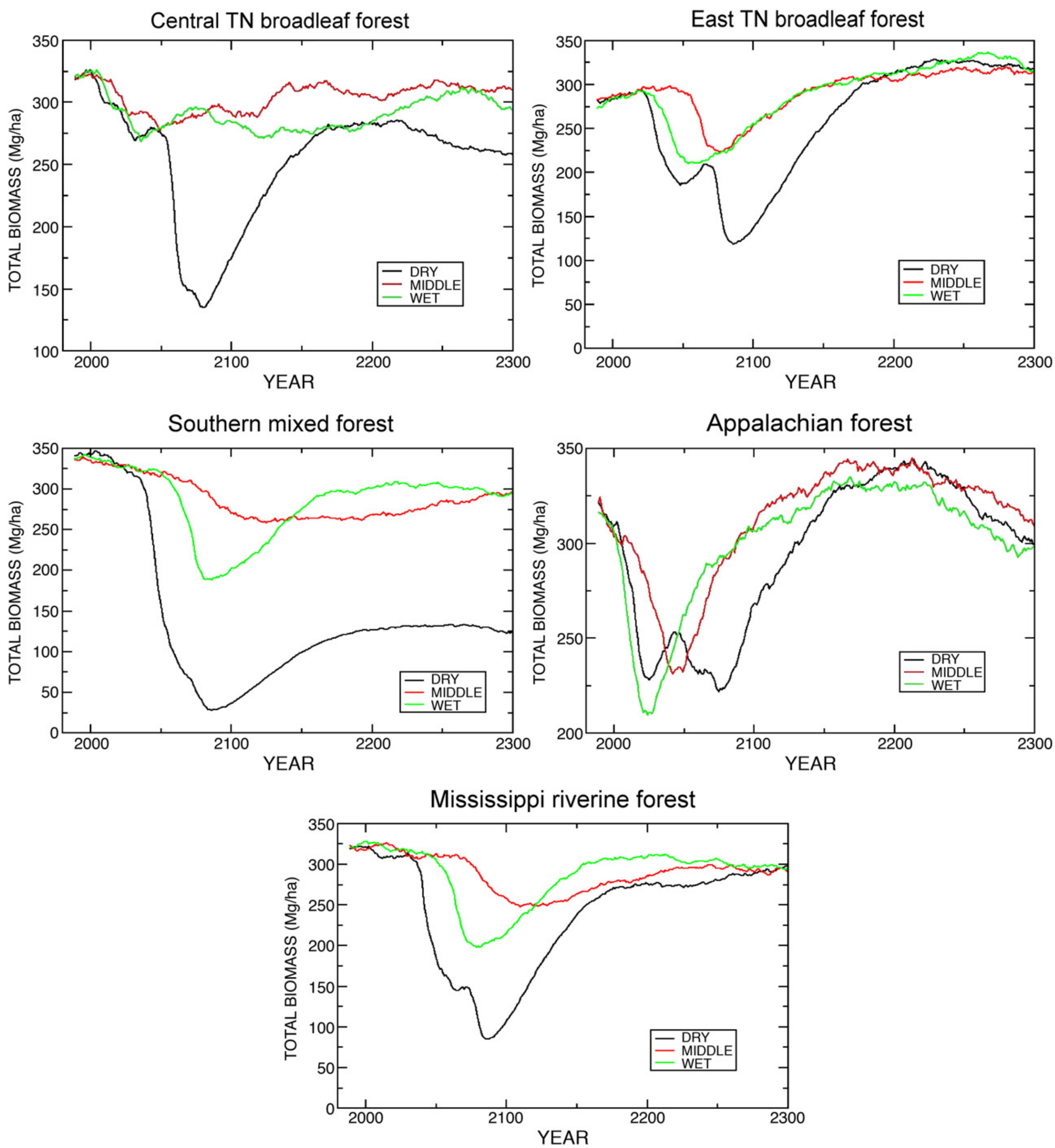

Fig. 3. Projected changes over time in total forest biomass of five ecological provinces in Tennessee.

3.3. Projected forest composition

In all cases there is some shift of forest species composition. The hickories (*Carya* species) and hackberry (*Celtis laevigata*) tend to become more dominant. Basswood (*Tilia heterophylla*) attains greater biomass in some scenarios and declines in others. Both chestnut oak (*Quercus prinus*) and black oak (*Q. velutina*) decline in their biomass contribution to the forest. The least effects on total forest biomass occur for the middle and wet scenarios for the Central Tennessee Broadleaf Forest.

There are changes in the contribution of tree species to total biomass for all forest provinces for all scenarios as compared to the 1989 stand structure. The Southern Mixed Forest experiences the greatest alteration in forest composition among the provinces considered (Fig. 4). Under the "dry" scenario, the Southern Mixed Forest that was once rich in species diversity becomes dominated by only four species [loblolly pine (*Pinus taeda*) and three oaks]. The "middle" and "wet" scenarios both result in greater dominance of hackberry and less biomass of white basswood but retain their high species diversity.

The East TN Broadleaf Forest maintains its high diversity under all cases but experiences great shifts in species composition (Fig. 5). The "dry" scenario shows responses to both the 2030 and the 2080 climate conditions as evidenced by dramatic changes in forest composition subsequent to those climate changes being initiated in the model in those years. Dominance by white basswood, chestnut oak, black oak, and yellow buckeye (*Aesculus octandra*) shifts to dominance by five hickory species, white oak (*Q. alba*), southern red oak (*Q. falcata*) and white ash ((*Fraxinus americana*). Under both the "middle" and; the

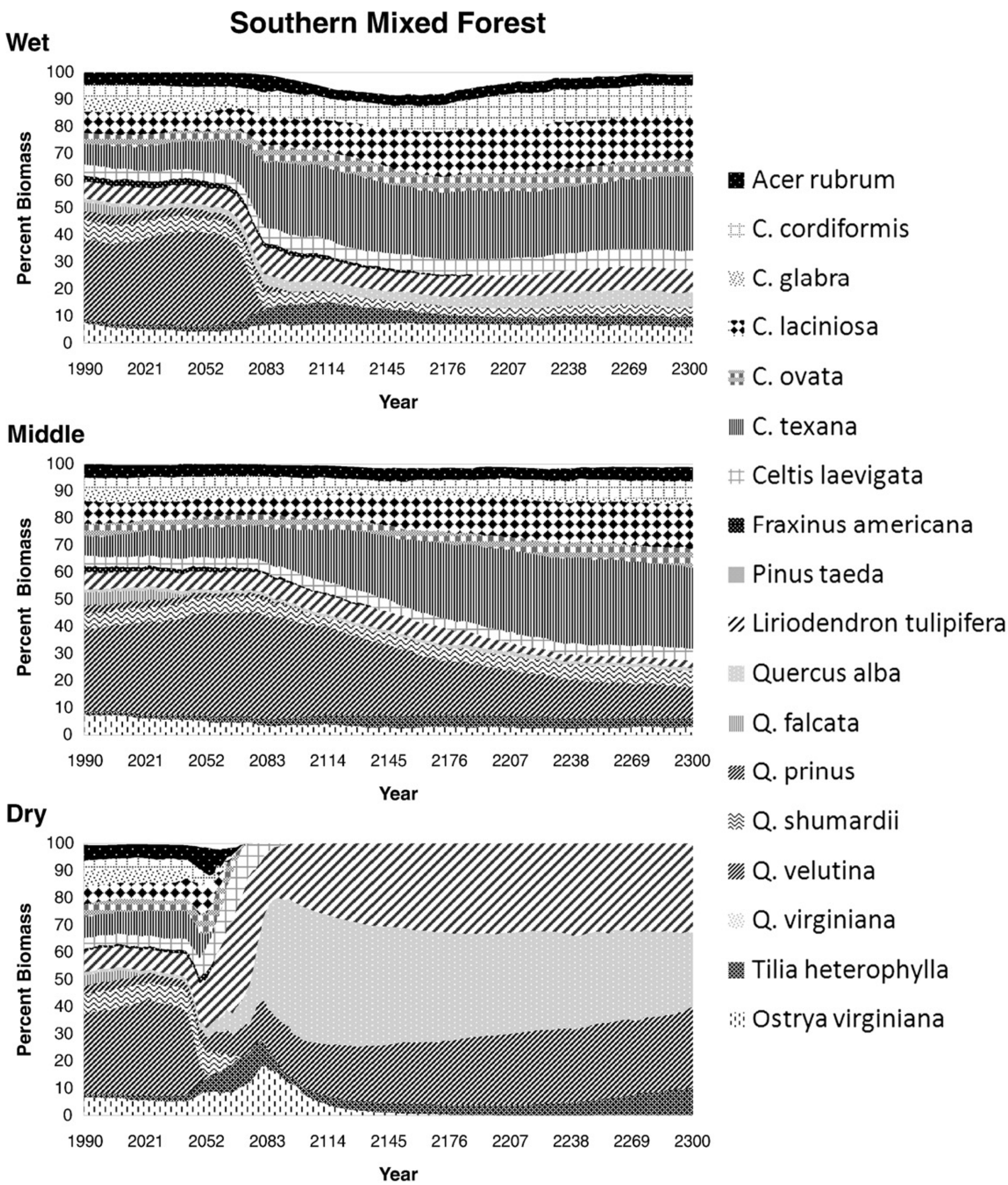

Fig. 4. Projected changes over time in biomass of major species for the Southern Mixed Forest in Tennessee.

"wet" scenarios, biomass increases for white basswood and decreases for chestnut oak, black oak, and yellow buckeye.

The Appalachian Forest experiences both an increase in diversity and a shift in dominance with the simulated climate changes (Fig. 6). Under all scenarios, chestnut oak displays an initial increase and then decline in terms of its contribution to stand biomass; white basswood increases in biomass; and hickory diversity and biomass also increase.

Strong changes occur in the Central TN Broadleaf Forest under projected climate changes (Fig. 7). For the "middle" and "wet" scenarios, the stands become dominated by six hickory species, hackberry, and white basswood. For the "dry" case, the forest stands consists mostly of four hickory species, white oak, southern red oak, and white ash; and white basswood is greatly diminished over time. In this case the importance of chestnut oak, black oak, and yellow buckeye is greatly reduced.

Projected biomasses for the MS Riverine Forest all have a decline in chestnut oak, black oak, basswood , and Shumard oak (*Q. shumardii*) (Fig. 8). For the "dry" scenario, red maple (*Acer rubrum*), hickory species, southern red oak, loblolly pine, and ash assume dominance. For the "middle" and "wet" scenarios, hickory species attain about 40% of the stand biomass and hackberry about 30%.

4. Discussion

The model projections suggest that under future climate change the forests in Tennessee will experience quantifiable changes. The projected decline in biomass is consistent with both the IPCC (2007) and many previous modeling studies [as reviewed by Watson et al. (1996) and recent analyses by Lischke et al. (2006)]. Furthermore, mortality rates of forest tress have doubled in forest stands in the western US (van Mantgem et al., 2009). What is unique about this study is that, when the model runs extend out for three centuries, after the decline there is a recovery of biomass as a new composition of the regional forest is established. The set of dominant tree species is

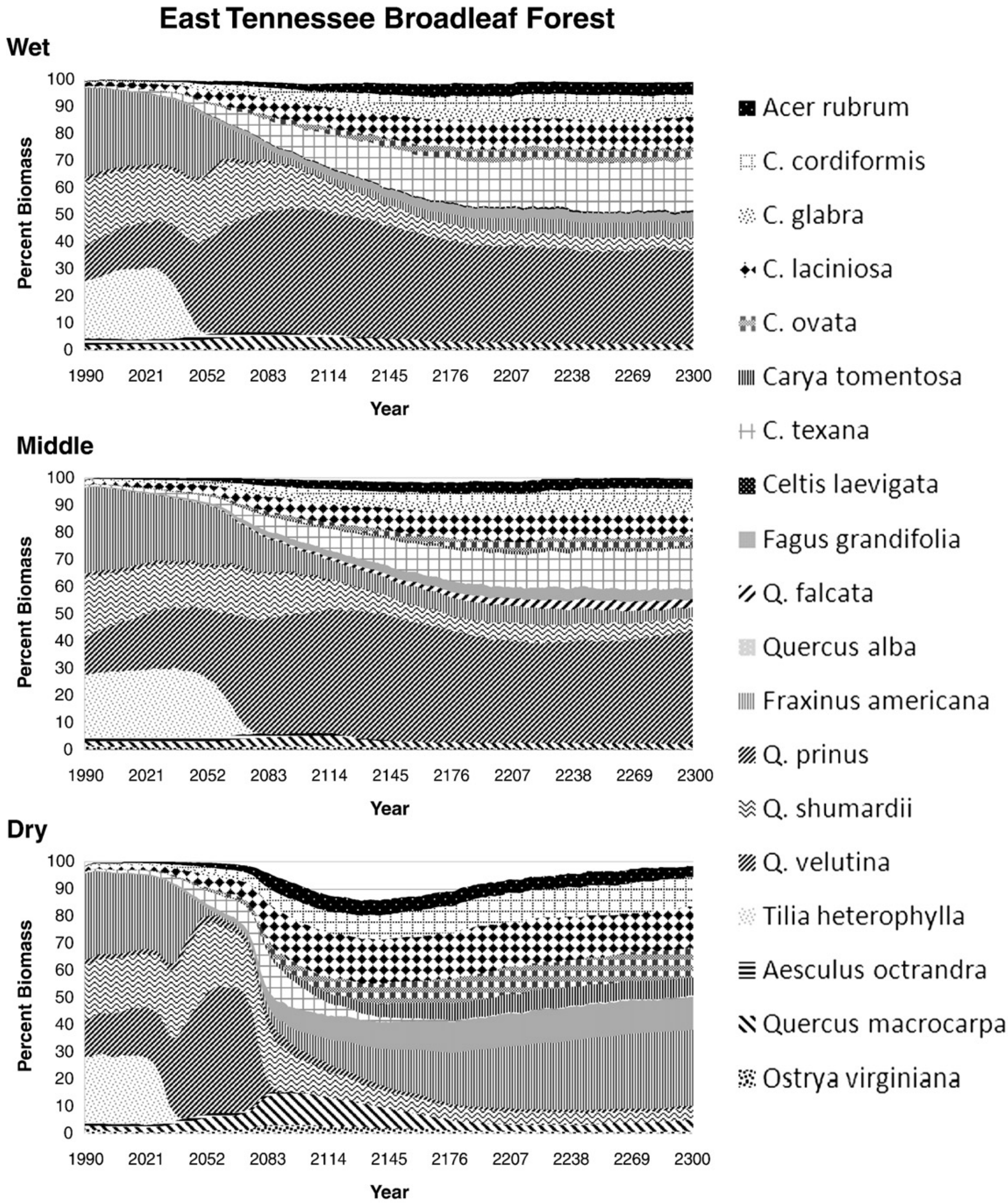

Fig. 5. Projected changes over time in biomass of major species for the East TN Broadleaf Forest.

unique for each region and each climate scenario. The model projects a mix of species that are common to the southeastern US and that are a part of the LINKAGES model; yet the forest composition is altered under the climate change scenarios.

The IPCC (2007) notes that the potential for forest dieback in the southeastern US as a result of climate change is supported by many kinds of model simulations. The key question seems to be how severe these diebacks actually are. The IPCC (2007) report discusses how gap models using the FAR GCM results show potential for forest dieback under the higher temperatures (Solomon, 1986; Pastor and Post, 1988; Urban and Shugart, 1989). With cooler SAR scenarios and improved GAP model technology, these diebacks are not as severe (Loehle and LeBlanc, 1996; Shugart and Smith, 1996). Studies using a regional forest growth model suggest that forest in the southeastern US could experience significant dieback (using a model that incorporates a direct CO_2 effect but does not consider vegetation redistribution). The major instigator of such increased mortality is unclear but may likely be warming, which increases evaporative loss. However, such an analysis has not yet been done for the southeastern US.

The model projections in this study are for a longer time period than the IPCC (2007) because the longevity of southern trees means it is useful to understand the long-term effects of climate change. Model projections for all of the ecological provinces under all climate change scenarios show a recovery in forest biomass as new combinations of tree species gain dominance, although the amount of biomass reestablishment varies. These results suggest that Tennessee will remain a forested region, but the dominance of tree species will change.

The changes in forest composition are consistent with other studies. Projections of Iverson and Prasad (1998) showed that as many as 30 species could expand their range and up to 30 species could retract their range in their studies of how individual species relate to prevailing environmental conditions the eastern US. In contrast to that study, the

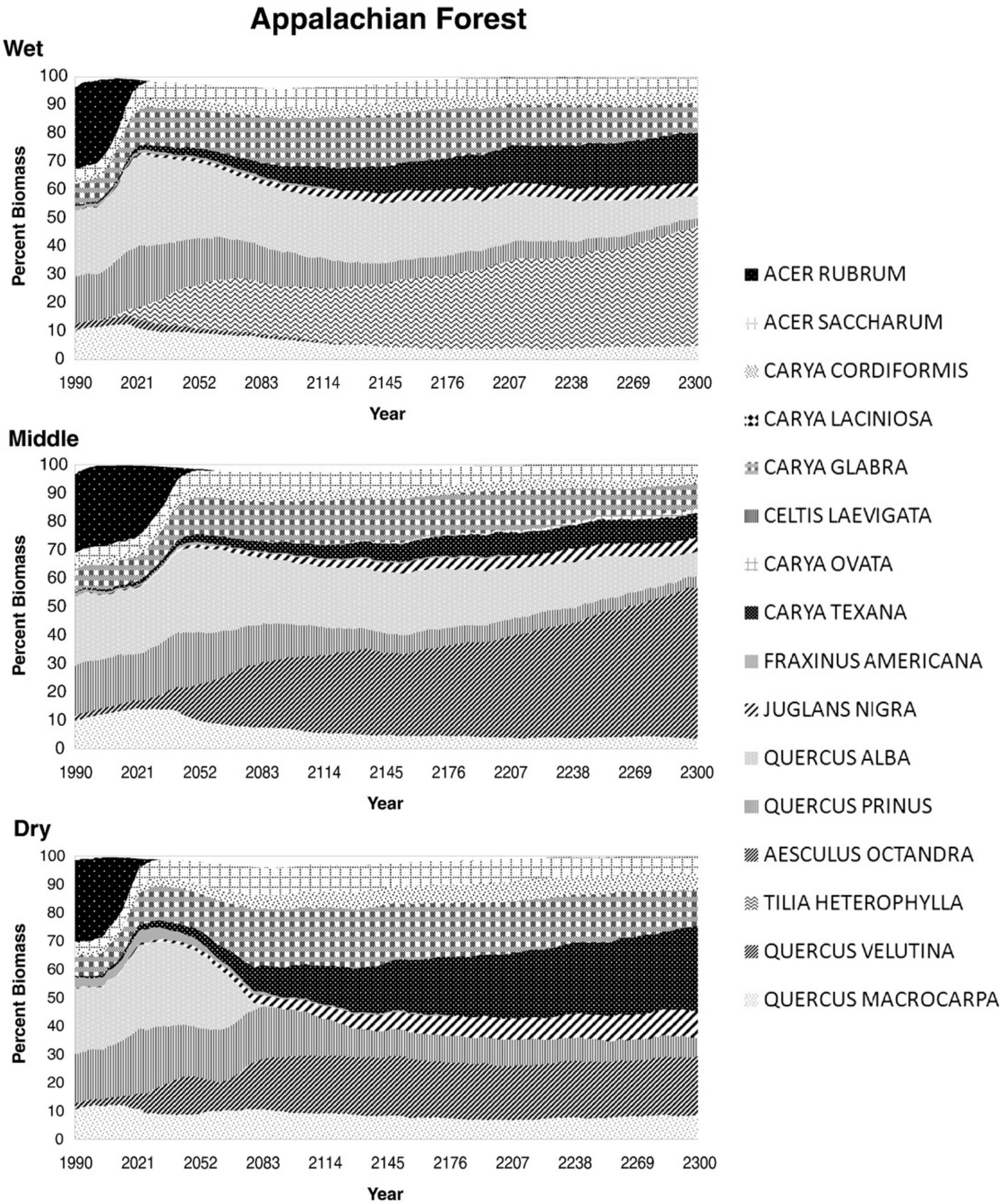

Fig. 6. Projected changes over time in biomass of major species for the Appalachian Forest in Tennessee.

LINKAGES model allows us to examine how forest composition changes within the competitive forces of the forest system. Thus this study focuses on the changing composition within a region rather than the extent of species ranges. These model projections are also consistent with the paleoecological studies of Delcourt and Delcourt (1998), who found that climate changes during the Quaternary influenced changes in species and landscape diversity in this region.

The strongest effects of projected climate change occur under the dry scenario and in the Southern Mixed Forest. The dry scenario projects both warmer year-round temperatures and drier summers. These changes result in a decline in total biomass, which does not fully recover to its original biomass levels over the projection period. The diverse Southern Mixed Forests are replaced by forests dominated largely by only three species: loblolly pine (*P. taeda*), southern red oak (*Q. falcata*), and Shumard oak (*Q. shumardii*). This decline in diversity may be a reason for the decline in stand biomass. The new simplified forest may change overall susceptibility to insects and pathogens as well as affect the native diversity of flora and fauna, which depend on these forest habitats.

The climate projections used in this analysis were selected from the medium levels in the PCMDI archive and under the A1B storyline of the IPCC that assumes rapid global economic growth (3%) and liberal globalization as characterized by low population growth, very high GDP growth, high-to-very high energy use, low-to-medium changes in land use, medium-to-high resource availability, and rapid technological advancement (Nakićenovic et al., 2000). More extreme climate projections or the inclusion of natural disturbances would likely have produced even stronger effects on the forest systems.

Abrupt biomass declines or even tree mortality are common under droughts (Webb, 1987; Breshears and Allen, 2002; Bigler et al., 2007; Nepstad et al., 2007). Gitlin et al. (2006) found three patterns of plant mortality with droughts: death of dominant species from diverse habitat types; average mortality differing among dominant species; and all dominant species showing localized patterns of very high mortality

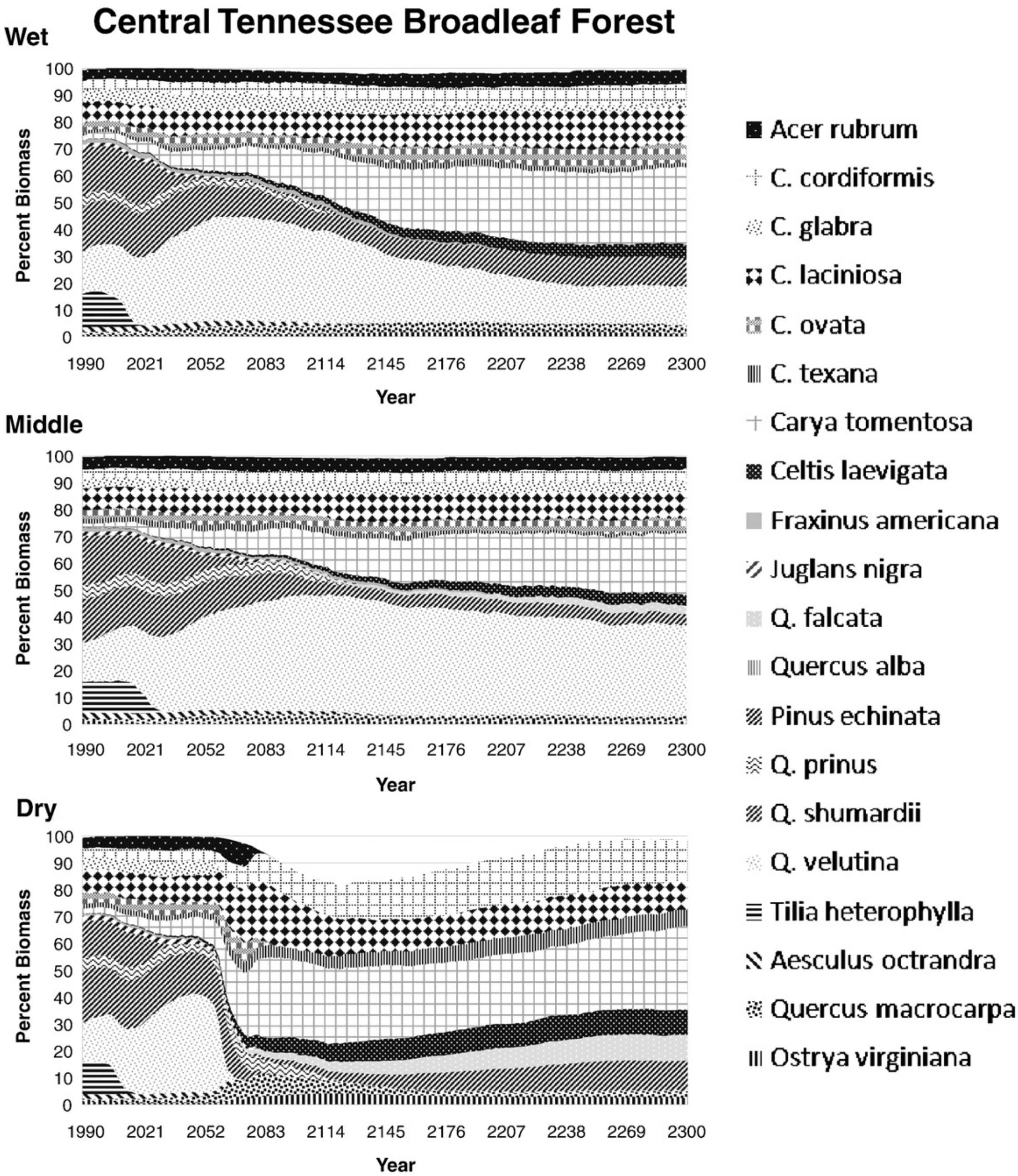

Fig. 7. Projected changes over time in biomass of major species for the Central TN Broadleaf Forest.

consistent with water stress gradients. Survival of sugar maple (*Acer saccharum*) has been demonstrated to be strongly affected by drought (Olano and Palmer, 2003) as is simulated in the Appalachian Forest projection (Fig. 6).

It is not surprising that the decline of oaks and other dominant species in the forest should foster an increase in biomass of hickories and other species. Widespread oak decline and mortality since 1999 throughout the Ozark Mountains of northern Arkansas and southern Missouri due to the red oak borer (*Enaphalodes rufulus*) has been accompanied by an increased the proportion of white oak and hickories in the overstory (Heitzman, 2003). In fact, many species have a positive response to increased temperature (Saxe et al., 2001).

White oak is of particular interest because it is now less common than before European settlement of North America (Abrams, 2003) and attains greater biomass over time in the climate change projections for the Appalachian Forest, Central TN Broadleaf Forest, and East TN Broadleaf Forest. Its decline in the 19th and 20th centuries are thought to be due to extensive land clearing, catastrophic fires, and then fire suppression and intensive deer browsing (Abrams, 2003). White oaks projected increase is likely due to drought conditions favoring that species (Tardif et al., 2006).

Chestnut oak (*Q. prinus*) is another species that has undergone change in recent centuries and that is more greatly affected by the projected climate changes. The demise of chestnut (*Castanea dentata*) as a result of the chestnut blight (*Endothia parasitica*) in the early 20th century gave rise to an increase in chestnut oak (Abrams et al., 1997). Climate changes project an increase and then decline in biomass in chestnut oak for the Appalachian Forest as basswood attains greater biomass. There is a simulated decline in chestnut oak biomass for the East TN Broadleaf Forest and Southern Mixed Forest. Field studies have demonstrated that chestnut oak has a complex response to drought and topographical aspect (Fekedulegn et al., 2003).

The results reported in this paper concur with the nontransient, equilibrium analyses by Iverson and Prasad (1998, 2001, 2002) that

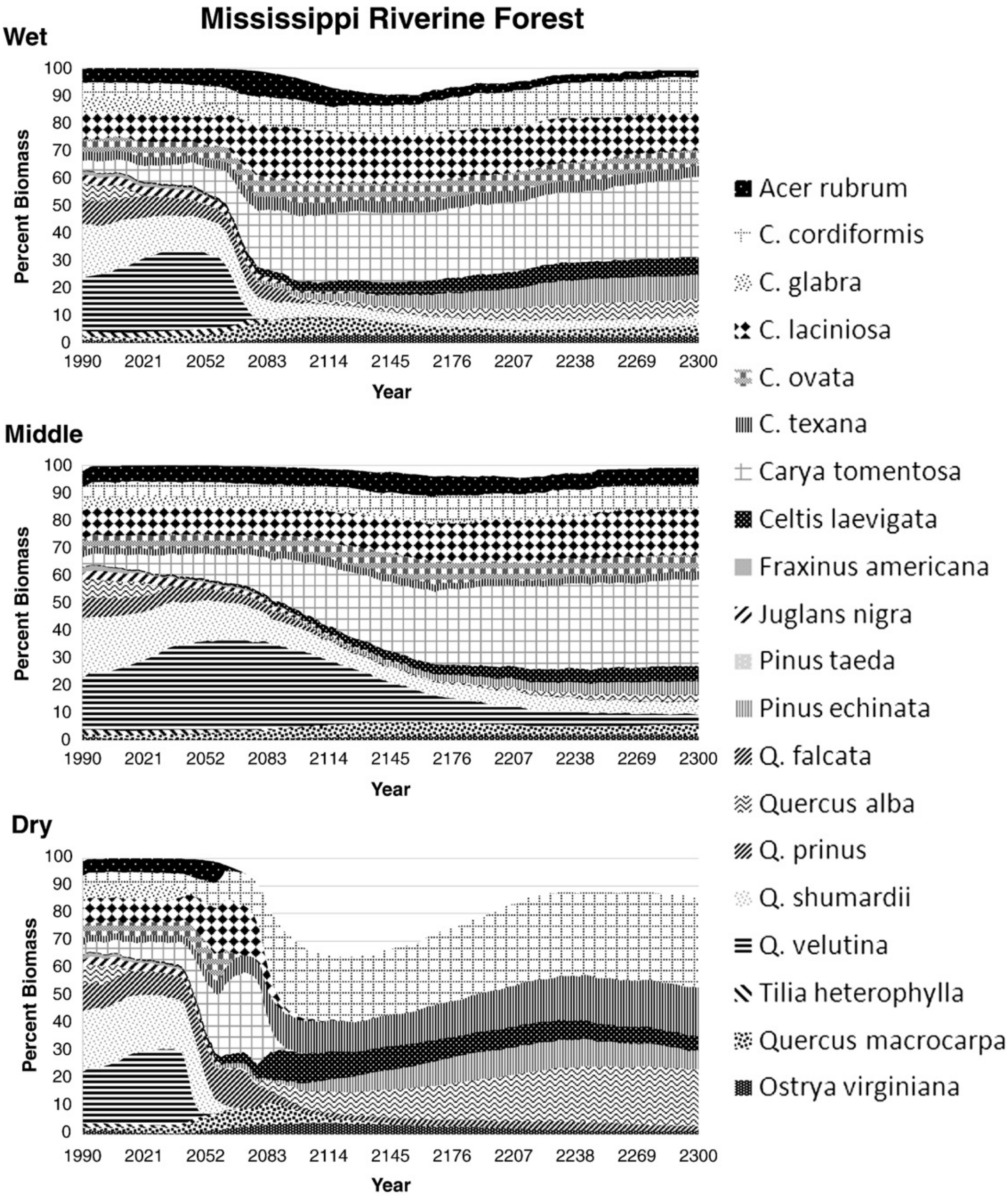

Fig. 8. Projected changes over time in biomass of major species for the MS Riverine Forest in Tennessee.

show great changes in abundance of many eastern US tree species following climate change. The implications of these changes in forest biomass and composition are likely to fall into several arenas. For example, changes in forest biomass and composition can affect water runoff in forested systems. Already, water yield from southeastern US varies greatly in both space and time (Sun et al., 2005). Currently, less than half of the annual precipitation that falls on forest lands is available for stream flow because of the hot climate and high evapotranspiration, and this amount may increase under scenarios projected for climate change in the region. Changes in land-use practices will likely exacerbate the variability of water yield in the region, particularly on the Cumberland Plateau where water is already a concern for residential development. Furthermore, ecosystem carbon storage can be influenced by changes in individual tree growth rate, reduced transpiration, or increases in fine root production (Post et al., 1992).

LINKAGES does not include potential effects of changes in atmospheric CO_2 concentrations. In another model study, Hanson et al. (2005) found that single-factor simulations of elevated CO_2 and temperature increases by 4 °C caused significant increases and decreases, respectively, in mean annual net ecosystem carbon exchange (NEE), whereas single-factor increases in winter precipitation and changes in ozone (O_3) produced minimal changes. In that study, direct effects of CO_2 were assumed to alter diameter increment annually so as to (1) achieve a +17% difference in stand level net primary productivity (NPP) in 100 years and (2) reduce canopy conductance by 12% annually. Their model showed that the combined effects of all of these factors caused a 29% reduction in mean annual NEE. Those results suggest that future CO_2-induced enhancements of gross photosynthesis are offset by temperature-induced respiration increases, water deficits, and O_3-induced reductions in photosynthesis (Hanson et al., 2005). Yet comparing the results from Hanson et al. (2005) to this study is difficult since our study does not include elevated CO_2 and the two climate change projections are quite different. A long-term forest field study of effects of increased CO_2 concentration in an East Tennessee sweetgum (*Liquidambar styraciflua)* forest shows that the most significant effects of increased CO_2 concentration occur in the forest understory and fine roots (Norby et al., 2005). In that study, increases in woody above ground biomass were negligible by year four of experimentally pumping of CO_2 into a forest system. Of course, four years is not a very long response time for a mature forest. Yet even obtaining this four year data in a valid experimental study is very costly — which speaks to the need to perform modeling experiments with long-lived species and to test the models with whatever limited data are available.

In contrast, similar experimental exposure of a loblolly pine (*P. taeda*) stand to Free Air CO_2 Enrichment (FACE) caused an increase in woody biomass (DeLucia et al., 2005). The LINKAGES model does not incorporate effects of elevated CO_2, which would require that the fixed allometry between stem volume and leaf area be made flexible (Norby et al., 2001) and, to date, no studies have demonstrated that species-specific allometric changes take place under enhanced CO_2 conditions. However, the model does simulate effects of a longer growing season on tree growth and acclimation of growth processes to changing temperature, which Norby et al. (2001) urge to be a part of climate change projections. Furthermore, LINKAGES does not incorporate physiological changes induced by air pollutants that may amplify climatic stresses, which are suggested to be important by McLaughlin and Percy (1999). In addition, this version of LINKAGES does not include multi-layered soil hydrology (Wullschleger et al., 2003). We also recognize that these projections of climate change effects on forests do not include other effects of climate change, such as alterations in disturbance regimes (Dale et al., 2001), trophic interactions (Schmitz et al., 2003), and current or future land use restrictions on forest that may affect forest migration patterns (Schwartz et al., 2001).

Price et al. (2001) suggest that the model assumption that seeds of all species are uniformly available may cause an overestimation of future species diversity and forest migration rates. However, in a model study of the potential for migration of four forest species in Ohio, Schwartz et al. (2001) developed a rule-based model that simulates the probability of an unoccupied cell being colonized by a species given a migration rate of 50 km/century. They found that the species studied are capable of colonizing virtually any forest area within Ohio over the next 100 years if climatic controls over the current distribution that currently inhibit northward movement are removed and that the availability of sites for tree establishment greatly affects simulated migration. In contrast, LINKAGES is not a place-based model and, therefore, does not include site limitations. Nevertheless, we think that the potential for any of the trees native to TN to establish is consistent with the Schwartz et al. (2001) result of broad colonization ability under climate change.

Assessing changes in tree species composition and biomass is only the beginning of assessing effects of climate change on forest systems. The remaining huge question is what are the effects of these changes. Effects of the warm temperatures alone on water retention for forest systems are expected to be large, and the secondary effects of reduced water availability will influence both natural and built systems. Furthermore, it is not clear how changes on forest systems may affect habitats of the vectors and hosts of infectious diseases that are already on the rise in Tennessee, such as Rocky Mountain spotted fever (Dumler and Walker, 2005). Effects on human health and behavior as influenced by vector-borne diseases for mosquito or tick vectors that occupy forest habitats have not yet been considered.

The relative contribution of dominant tree species to biomass changes under all scenarios. These compositional changes are likely to affect both land use and insect outbreaks. There will possibly be changes in recreational use of forests as the climate and the forest changes. Economic impacts on Tennessee forests resulting from climate change will have to be balanced by the ability of the forest industry to adapt. Key social impacts on Tennessee forests resulting from climate change may include the locations of forest most likely to be targeted for development or preserved for recreational use. Finally, and maybe most critically, what if climate change continues past 2080 instead of stabilizing as is projected in this analysis? The answers to most of these questions are unknown, but past modeling efforts have made it clear that models provide a means to evaluate understanding of the intricacies of ecological systems (Dale and van Winkle, 1998). The modeling results presented in this paper do not provide an explicit prediction of a specific future, but rather they indicate that anticipated rates of future climate change have a very real potential to affect both forest productivity and composition.

5. Conclusions

Climate change will have a strong effect on Tennessee forests. The climate change projections for Tennessee are for increased warming during all months for all regions of the state. Projected changes in precipitation for Tennessee are less consistent and within the long-term variability. “Dry” and “middle” GCMs project summers with more drought and a “wet” GCM projects all months to be wetter as compared to mean monthly precipitation from 1980 to 1997.

Modeling how these climate changes affect forests in Tennessee suggests major change in forest stand function, structure, and composition. The “dry” scenario has the greatest overall effect and the most enduring effect on forest biomass for the Southern Mixed Forest. The “dry” scenario also results in strong projected declines in biomass in the Mississippi Riverine Forest and the East TN Broadleaf Forest. In most other scenarios, the climate changes in 2030 and 2080 cause an initial decline in forest biomass, but, as one species is replaced by another, the total forest biomass typically regains its initial level. The high diversity of tree species in southeastern forests may be a key reason for the rapid recovery of forest biomass. Indeed, it is the forest system with the lowest diversity (the Southern Mixed Forest under the dry scenario) that has the lowest projected biomass over the long term. As climate changes occur in the southeastern forest system over the next decades, it will be useful to examine how changes in tree species diversity affects changes in forest ecosystem properties. These results suggest that biomass recovery following climate change is linked to diversity of the dominant trees, an observation that warrants further study, for it can influence ways that forest management may be used to mitigate effects of climate change on forest ecosystems.

Projections of tree species composition and biomass by ecological province provide the information needed to assess how climate change may affect a variety of ecological services. Next steps in this analysis include examining those implications on such factors as economic conditions [as Winnett (1998) urges] and putting climate change effects in the context of other stressors, such as land-use change [discussed by Dale (1997)] and invasive species.

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