Response of North American ecosystem models to multi-annual periodicities in temperature and precipitation

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Abstract

Ecosystem models typically use input temperature and precipitation data generated stochastically from weather station means and variances. Although the weather station data are based on measurements taken over a few decades, model simulations are usually on the order of centuries. Consequently, observed periodicitics in temperature and precipitation at the coutinental scale that have been correlated with large-scale forcings, such as ocean-atmosphere dynamics and lunar and sunspot cycles, are ignored. We investigated how these natural climatic fluctuations affect aboveground biomass in ecosystem models by incorporating some of the more pronounced continental-scale cycles in temperature (4, 11, 80, 180 year periods) and precipitation (11 and 19 year periods) into models of three North American forests (using LJNKAGES) and one North American grassland (using STEPPE). Even without inclusion of periodicities in climate, long-term dynamics 'of these models were characterized by internal frequencies resulting from vegetation birth, growth and death processes. Our results indicate that long-term temperature cycles result in significantly lower predictions of forest biomass than observed in the control case for a forest on a biome transition (northern hardwoods/boreal forest). Lower-frequency, higher-amplitude temperature oscillation caused amplification of forest. biomass response in forests containing hardwood species. Shortgrass prairie and boreal ecosystems, dominated by species with broad stress tolerance ranges, were relatively insensitive to climatic oscillations. Our results suggest periodicities in climate should be incorporated within long-term simulations of ecosystems with strong internal frequencies, particularly for systems on biome transitions.

Introduction

Models of terrestrial ecosystems have been used primarily to understand long-term responses of large systems to both static and changing environmental conditions (Shugart and West 1977; Davis and Botkin 1985; Pastor and Post 1986, 1988; Running and Coughlan 1988; Overpeck et al. 1990; Ågren et al. 1991; Kienast 1991; Rastetter et al. 1991). Output response depends both on the functions within the models and on the functional format of the input (e.g., temperature and precipitation) data. While the level of complexity of internal mechanisms is continually being refined (e.g., Smith and Urban 1988; Friend et al. 1993; Lauenroth et al. 1993), representation of input data is

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typically relegated to simple stochastic equations based on means and variances in climate data. There are at least two problems with this approach: (1) ecosystem models are typically run on timescales that exceed the length of the original input climate data series by at least an order of magnitude, and (2) it ignores climate studies (Michaels and Hayden 1987; Stocker and Mysak 1992) that have demonstrated that significant deterministic fluctuation exists in climate variables at frequencies relevant to internal cycles resulting from birth, growth and death processes of vegetation dynamics (Shugart 1984; Neilson 1986).

Background

Periodic behavior in precipitation and temperature series has been observed at a variety of spatial and temporal scales. Naturally-occuning frequencies have been attributed to the El Niño-Southern Oscillation (ENSO) (2-10 years), sunspot and double sunspot cycles (1 I and 22 years), and the lunar cycle (18.6 years), as well as other longer cycles (> 40 years) which have explanations ranging from extended sunspot cycles to ocean-atmosphere interactions (Stocker and Mysak 1992, Burroughs 1992). For example, a lunar cycle with a period of about 19 years has been reported from rain-gauge records of the western U.S. (Kerr 1984; Cunie and O'Brien 1990). Sunspot and double-sunspot cycles have been correlated with drought cycles based on tree-ring data and rain-gauge records (Vines 1982; Currie and O'Brien 1990). Data from ice cores in northern Canada contained three main frequencies in precipitation, two of which were attributed to sunspot and double-sunspot cycles, and a third with a period of 3.8 yrs that may correspond with an El Niño cycle (Holdsworth *et al.* 1992). Estimated amplitude for these cycles is in the range of 5- 10% of annual mean precipitation (Vines 1982; Currie and O'Brien 1988).

Cycles in. annual temperature have also been reported, although these are more variable. Periodicities from 10 to 100 years in mean annual temperature were reported by Wigley and Raper (1990). Broecker (1975) found 80 and 180 year periods of global temperature based on 1000 years of ice-core data. A ten year periodicity in temperature with an amplitude of about 0.6°C approximating the periodicity of a sunspot cycle was reported by Jones et *al.* (1986). Recent studies have linked solar cycle variability with terrestrial temperature response (Kelly and Wigley 1992; Schlesinger and Ramankutty 1992; Rind and Overpeck 1993; Lean and Rind 1994). Investigating temperature response to ENS0 events from 1880 to 1984, Ropelewski and Halpert (1986) found ENSO events occurring every 2 to 10 years. Quinn and Neal (1992) reported a mean 3.9 year period for ENSO from the historical record since 1526. Oscillation ranges of the longer cycles (> 50 year) were as much as 4°C (Broecker 1975), while oscillation ranges of shorter cycles tended to be less than 1°C (Jones et *al.* 1986; Wigley and Raper 1990). In a recent review, Stocker and Mysak (1992) proposed ocean-atmosphere interactions as a possible cause for cycles with periods ranging from 50 to 400 years. While the occurrence of periodicities is thus well documented, causal links remain unclear except in the case of the ENSO (Mitchell 1976, Enfield 1989, Burroughs 1992).

Climatic inputs in ecosystem models primarily govern rates and limit the extent of processes. Temperature affects process rates in vegetation models, particularly the rates of photosynthesis, carbon allocation, respiration and decomposition (Ågren et *al.* 1991; Lauenroth et *al.* 1993): Water availability can limit photosynthesis through its effect on stomatal conductance (Ågren et *al.* 1991), or can affect regeneration and mortality probabilities (Pastor and Post 1985; Coffin and Lauenroth 1990). Although these external variables constrain the possible response of internal model variables such as biomass, the nonlinear nature of biological functions can lead to unexpected responses to variations and trends in climate constraints, particularly near critical endogenous thresholds (Shugart et *al.* 1980; O'Neill *et al.* 1989). Even small changes in an external variable such as temperature have been shown to result in significant shifts in biomass and available soil nitrogen in simulations of a forest ecosystem (Cohen and Pastor 1991).

Attributes of terrestrial ecosystems such as biomass can contain internal frequencies which correspond to synchronous demographic processes, e.g., birth-death cycles, growth spurts due to com-

petitive release, and **dieback** resulting from pressures such as climate or herbivory (Shugart 1984; 1987; **Neilson** 1986; Urban et **al.** 1987). Such ecosystems are thus inherently nonlinear; so analysis of general ecosystem **responses** to a suite of input structures is not straightforward **(DeAngelis** and Waterhouse 1987). Yet, some techniques from linear systems analysis, such as frequency analysis, can be applied to evaluate responses of nonlinear systems **(Emanual** et **al.** 1978; Shugart 1984). Models are **filters** that, depending on their internal structure (e.g., connectivity, component process rates), pass, attenuate and/or amplify signals depending on input frequency (Brown 1983; **O'Neill** et **al.** 1986; **DeAngelis** et **al.** 1986). Modification of output can occur when an input signal occurs either synchronously with a dominant internal model frequency resulting in signal amplification (i.e., resonance) or **desynchronously** with internal frequencies resulting in attenuation of a model output signal. **Gosz** and **Sharpe** (1989) have discussed such, signal modifications in the **context** of **biome** transitions, hypothesizing that vegetation in such areas would be very responsive to changing environmental constraints due to the mixture of lifeforms (e.g., grasses, shrubs, trees) with different structural characteristics. In comparing the dynamics of a grassland and a forest, Coffin and Urban (1993) found that response to cyclic variation in available moisture was associated with differences in **life** history traits. The forest responded strongly to a **single** frequency corresponding to the' lifespan of the dominant species, while the grassland composed of perennial plants with **clonal** growth exhibited a weaker response at all frequencies of the external constraint.

Michaels and Hayden' (1987) have called for more realistic representation of climate **in** ecosystem models, emphasizing the non-random nature of climatic processes. The standard stochastic approach does not account for acute disturbance events (e.g. hurricanes) or long-term climate anomalies (e.g. protracted drought), both of which may result in species-specific response thresholds being reached or exceeded. Currently regional- and continental-scale ecosystem and biome models are being developed to assess the response of the **bio-**

sphere to climatic variability and change (**Burke** et **01.199** 1; **Neilson** et **al. 1992; Lauenroth** et al. 1993). The adequacy of ecosystem models, particularly gap models, to represent climate **change** effects has been under recent scrutiny **(Bonan** and Sirois 1992; Weinstein 1992).

Approach

Our primary objective was to determine the effect of known periodicities of climate in inputs to **terrestrial** ecosystem models, as opposed to modeling climate simply as stochastic variation about a **long-**term **mean.** We modeled four ecosystem types in North America, ranging from **shortgrass** prairie to boreal forest to eastern deciduous hardwoods. We selected well-documented temperature and precipitation cycles that are relevant on a continental scale for North America and expected to be temporally relevant for these models. The cycles were chosen **to** be representative rather than exhaustive, spanning timescales from **sub-decadal** to **multi-century** (Table 1).

Methods and analyses

Study sites and models

We selected one grassland and three forest ecosystems in which to study sensitivity to cyclical climate inputs. Forest ecosystems included a boreal forest in **Ontario (49°N, 82°W),** a forest comprising a transition from boreal to northern hardwoods in Minnesota **(47°N, 92°W),** and an eastern deciduous hardwood forest in Tennessee **(35°N, 86°W).** The grassland system was a shortgrass prairie in **northcentral** Colorado **(41°N, 108°W)** dominated by blue **grama** *(Boutelouu gracilis)*

All three forest ecosystems were modeled using **LINKAGES,** a forest growth model developed for eastern North America (Pastor and Post 1985, 1986) from the **JABOWA/FORET** family of gap based forest dynamics models (Botkin **et al.** 1972; Shugart and West 1977). Gap models simulate recruitment, growth and mortality of individual

Table **1. Temperature and precipitation periodicities used in the simulations.**

Temperature

Period	Amplitude	References
4 yrs	0.6°C	Ropelewski and Halpert 1986, Holdsworth *et al*. 1992, Quinn and Neal 1992
11 yrs	0.6°C	Jones *et al*. 1986, Wigley and Raper 1990
80 yrs	1.2°C	Broecker 1975, Stocker and Mysak 1992
180 yrs	1.2°C	Broecker 1975, Stocker and Mysak 1992

Precipitation

Period	Amplitude	References
11 yrs	.075*Mean	Vines 1982, Currie and O'Brien 1988, 1990
19 yrs	.075*Mean	Kerr 1984, Currie and O'Br 1988, 1990

plants on a single plot through time, with plot size corresponding to the size of a mature dominant 'individual plant in the ecosystem. **Trees** growing on model plots compete for available light, water and nutrients under varying temperature constraints. Recruitment and mortality are simulated as stochastic processes while growth is deterministic. Species-specific input data such as plant growth characteristics and litter decomposition parameters were as reported in Pastor and Post (1985). Soil type for all forests was standardized to a loam having a field capacity of **28.0%** and a wilting point of 13.3% (Pastor and Post 1985).

The shortgrass prairie was simulated using the gap-based model STEPPE (Coffin and Lauenroth 1990; Lauenroth *et* al. 1993; **Coffin** and Urban 1993). In contrast to the forests, the most intense competition in semi-arid grasslands is assumed to **occur** below ground. Growth is a function of temperature, precipitation, and interactions with other plants in the plot. Regeneration and mortality are driven by annual precipitation. Two important differences exist between STEPPE and LINK-AGES. The timestep of LINKAGES is monthly whereas that for STEPPE is annual. Soil moisture and nitrogen dynamics are explicitly included in LINKAGES; by contrast, these resources are lumped into a 'resource abundance curve' controlled by annual precipitation in the version of STEPPE used here (Coffin and Lauenroth 1990).

Climatic Input

Temperature and precipitation are computed stochastically in LINKAGES and **STEPPE** by adding a normally distributed random deviate to a long-term mean at each timestep. Variance used in computing the random component is based on meteorological **datasets** that are typically 30 years in length. To simulate cyclic patterns in temperature and precipitation, we modifled this computation with a sine wave component:

$$T_i(t) = T_i + A \cdot \sin(2\pi(Y-H)/L) + N_{ti}(t)$$
$$P_i(t) = P_i + A \cdot \sin(2\pi(Y-H)/L) + N_{pi}(t)$$

where T_i and P_i are mean temperature and precipitation, respectively, for time i, A is amplitude, Y is current year in the model run, H is horizontal shift, L is period of the climate cycle simulated, and $N_{ti}(t)$ and $N_{pi}(t)$ are normal deviates computed from the variance in temperature and precipitation data, respectively, for time i.

For the simulations, we used initialization periods from 500 to 750 years for **forest** systems and 200 years for grassland systems. Such periods were necessary to overcome transient model responses due to model runs starting on bare ground. These initialization periods were determined from preliminary model runs (Emanuel *et al.* 1978; Shugart and West 1981; Coffin and Lauenroth 1990). Amplitudes and frequencies for temperature and precipitation cycles were selected to represent some of the more predominant climate signals and to span

as many orders of magnitude as we thought likely to be relevant to the internal frequencies of the ecosystem simulated (Table 1). We selected the horizontal shift, H, such that it would equal zero at the end of the initialization period to standardize timing of cyclic behavior among runs. From that point, we collected model biomass estimates for at least 1500 years for each model run. The longest important period previously reported for gap models is 200–250 years (Emanuel *et al.* 1978). Thus we collected data for more than four times the length of the longest period, as suggested by Jassby and Powell (1990). Each resulting time series then was detrended by performing a linear regression and using the residuals as the resulting data series.

Analysis

Difference in biomass between the mean of 30 plots for the control run and 30 plots for a given treatment run (Table 1) for each simulated ecosystem was determined using a two sample t-test ($p = 0.01$; Zar 1984, p. 126) for each year for 1500 years following the initialization period (for a given year, plots in all model runs are independent). The proportion of years either significantly low or high compared to the control case was tabulated to display the long-term effect of a given treatment scenario on biomass. Frequency analysis was used to determine dominant cycles in model biomass under various input scenarios (Platt and Denman 1975; Emanuel *et al.* 1978). This analysis provided an objective basis for comparing biomass response between control and cyclic input at each site, as well as among different sites for each input scenario. Power spectral density functions (SAS/ETS 1982) were generated for the biomass residual time series for each of the climate scenarios at each site. White-noise tests (Fisher's Kappa, Kolmogorov-Smirnov) were conducted to determine if the biomass time series in each case could be distinguished from a series randomly distributed in time. For 1500 observations, critical values showing significant periodicity at $p < 0.01$ were: Fisher's Kappa > 12.0 and Kolmogorov-Smirnov statistic > 0.042 (Fuller 1976).

Results

White-noise tests showed that significant non-random periodicities in aboveground biomass existed in all ecosystems simulated, even for all control scenarios (*i.e.*, random climate). This indicates that all systems contained internal frequencies, regardless of climatic input. For control scenarios, Fisher's Kappa values were 44.7 for shortgrass prairie and at least an order of magnitude higher than the critical value for all forest ecosystems. Similarly, Kolmogorov-Smirnov statistics for control cases were 0.5 for the shortgrass prairie and from 0.84–0.91 for the forest systems. Generally, strength of non-random periodicities as indicated by white noise tests increased in the order: Shortgrass prairie < Boreal forest ≈ *Eastern* hardwoods < Northern hardwoods/boreal transition forest.

Precipitation treatments produced no pronounced differences in biomass for any of the ecosystems (Fig. 1). Grassland biomass was relatively unaffected by differences in temperature input (Figs. 2a, 3a). Biomass in the boreal forest was similarly unaffected (Figs. 2b, 3b). Generally, hardwood forest biomass was most affected by differences in temperature cycles, with lower-frequency and higher-amplitude temperature oscillations (80 or 180 year period with 1.2°C amplitude) causing marked responses (Figs. 3c, d). The simulated transitional forest (boreal/northern hardwoods) showed a large drop in biomass for lower-frequency, higher-amplitude scenarios (Fig. 3c).

Mean biomass remained constant for all scenarios except for low-frequency temperature cycles in the Minnesota transition forest (Table 2). Biomass showed greater variation for lower-frequency, higher-amplitude cycles both in the eastern hardwoods and in the boreal/northern hardwood transition forest. The proportion of years in which mean treatment biomass differed from mean control case biomass significantly at the $p = 0.01$ level showed the same pattern, with the greatest significantly different proportions occurring for the mixed transition forest and for the eastern hardwood forest. Low-frequency, high-amplitude oscillation resulted in decreased mean biomass in the transition forest relative to the control case, while in the
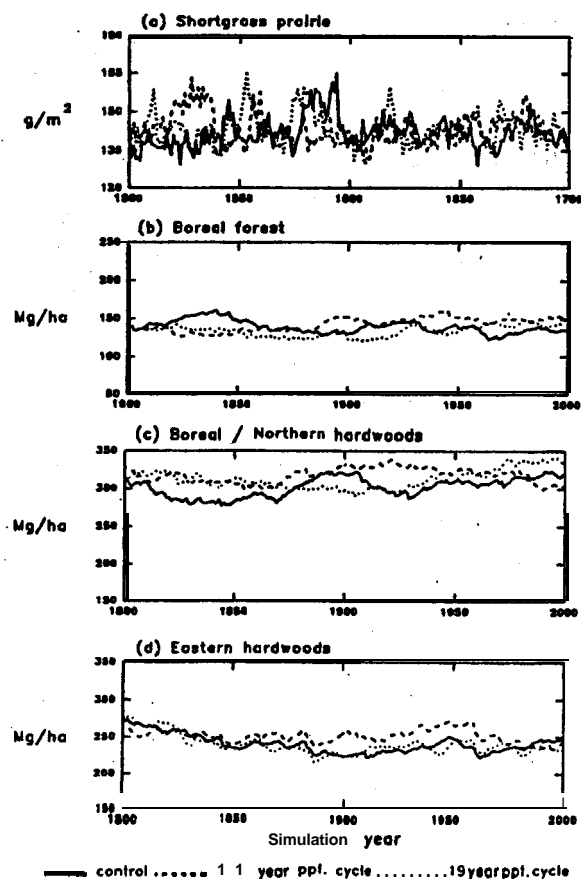
Fig. 1. Simulated biomass of four ecosystems in response to climatic functions for precipitation for a 200-year time interval following model initialization. Complete model runs were for at least 1500 years following initialization. Simulations arc control plus treatments of 11 year and 19 year precipitation cycles; each simulation included random variability in precipitation. Simufated ecosystems, from top to bottom, are (a) shortgrass prairie, (b) boreal forest, (c) boreal/northern hardwoods transition forest, and (d) eastern hardwoods.
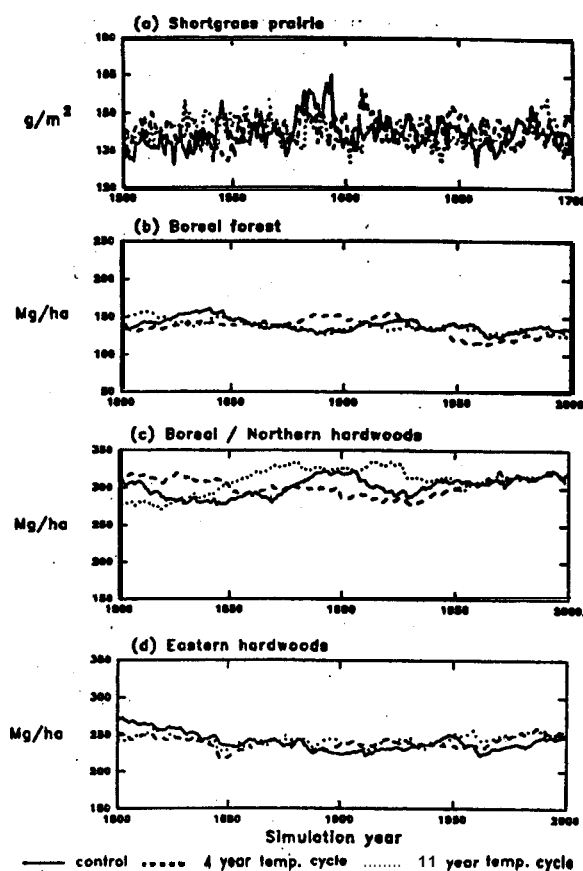
Fig. 2. Simulated biomass of four ecosystems in response to shorter-term climatic functions for temperature for a 200-year time interval following model initialization. Complete model runs were for at least 1500 years following initialization. Simulations are control plus treatments of 4 year and 11 year temperature cycles; each simulation included random variability in temperature. Simulated ecosystems, from top to bottom, an (a) shortgrass prairie, (b) boreal forest, (c) boreal/northern hardwoods transition forest, and (d) eastern hardwoods.

boreal and eastern hardwood forest mean biomass was r&different among treatments and control case (Fig. 3, Table 2).

Grassland spectral density estimates varied somewhat (Fig. 4a, e) under both different precipitation and temperature input structures. Forest systems (Figs. 4b–d, 4f–h) showed striking differences, however, both among sites and among input structure scenarios, particularly with respect to temperature. Generally, high-frequency temperature and precipitation input structures attenuated biomass response as indicated by reductions in the spectral

density estimates. In contrast, low-frequency temperature cycles tended to amplify biomass responses. Amplification of biomass response from low-frequency climate drivers increased moving southward from boreal forest through mixed hard-'woods to oak-hickory hardwood forest (Figs. 4f–h).

Discussion

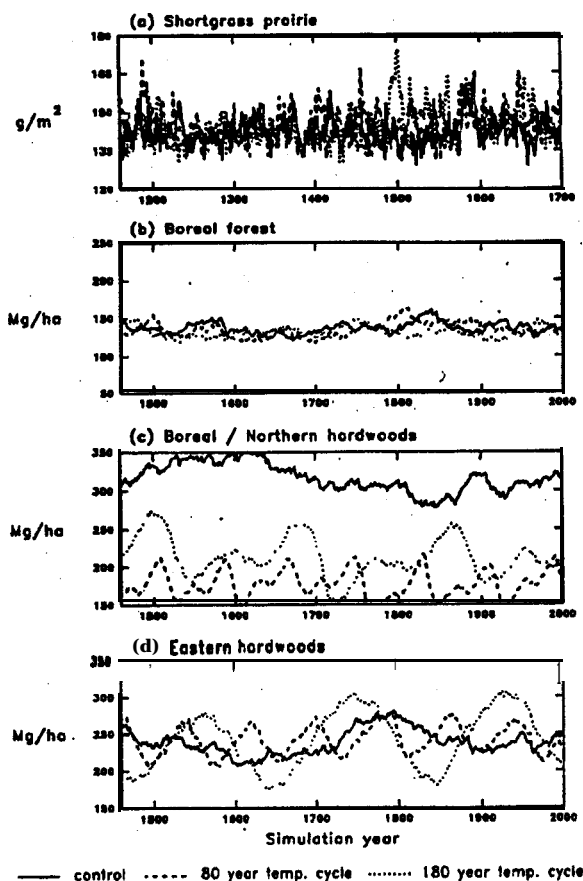Our approach allowed us to make a broad comparison using a common variable, annual aboveground

(a) Shortgrass prairie

(b) Boreal forest

(c) Boreal / Northern hardwoods

(d) Eastern hardwoods

Simulation year

——— control ····· 80 year temp. cycle ········ 180 year temp. cycle

Fig. 3. Simulated biomass of four ecosystems in. response to longer-term climatic functions for temperature for a 200-year time interval following model initialization. Complete model runs were for at least 1500 years following initialization. Simulations arc control plus treatments of 80 year and 180 year temperature cycles; each simulation included random variability in temperature. Simulated ecosystems, from top to bottom, are (a) shortgrass prairie, (b) boreal forest, (c) boreal/northern hardwoods transition forest, and (d) eastern hardwoods.

biomass, across several contrasting systems. The individual-based models used here are hierarchically structured (Shugart 1984; Urban et *al.* 1987; Shugart and Urban 1989) and so provide a multi-level depiction of response to various input scenarios. Multi-level analysis allows determination of underlying mechanistic causes which produce upper-level responses (Allen *et al. 1984).* Interpretation of an upper-level pattern can lead to misinterpretation unless lower-level mechanisms -are evaluated (dale et al. 1989; Yeakley and Cale 1991). In a hierarchical sense, annual biomass is an

upper level ecosystem attriiute. The main focus of our discussion is species-level mechanisms which produced system-level biomass responses to various types of climatic forcing.

We found that simulated forest systems were more strongly affected by periodic climate signals than the simulated grassland system. In the grassland, only precipitation cycling exerted any amplification on the biomass signal, at approximately a 1 10– 120 year lag (Fig. 4a). The relative insensitivity of the shortgrass prairie to the induced climatic periodicities is related to the climatic tolerance of the dominant species, blue grama (*Bouteloua gracilis),* and the high level of climatic variability inherent in the system even when climatic periodicities are ignored. The mortality function for blue grama is not dependent on a maximum age (Coffin and Lauenroth 1990), as it is for trees modeled in LINKAGES (Pastor and Post 1985). Thus, there is less cycling of biomass inherent within the grassland model in comparison with the forest models. Blue grama has a shallow root distribution and is able to respond rapidly to small precipitation events (Sala and Lauenroth 1982, Coffin and Lauenroth 1991). These small events make up a significant proportion and a less variable amount of annual precipiation (Sala et *al.* 1992). As a result, blue grama is modeled as being relatively insensitive to changes in annual precipitation (Coffin and Lauenroth 1990). Also, the amplitudes of the continental-scale periodicities we implemented are relatively small compared to the variance in precipitation (i.e., amplitude of the periodicity was 7.5% of the mean vs. coefficient of variation for annual precipitation was 25.6%). Temperature is assumed to influence the rate of growth of blue grama but not regeneration probability, (Coffin and Lauenroth 1990). In concert these factors suggest biomass dynamics in the shortgrass prairie should be relatively insensitive to the continental scale periodicities in climate reported in the literature.

In contrast, forest systems showed substantial biomass responses, both in terms of amplification and attenuation, to precipitation and temperature oscillations. The boreal ecosystem was the least responsive forest, showing a minimal reponse to precipitation cycling (Figs. Ic, 4b) and an amplified

Table 2. Long-term differences in biomass. Data used were from the last 1500 years of each simulation. Treatment mean was compared to control mean at a p = 0.01 significance level for each year. Shown is proportion of all years for which a significant difference was found. Treatments are indicated by P for precipitation and T for temperature cycles, followed by period of cycle (yrs).

Shortgrass prairie

	Mean [g/m²]	Std Dev [g/m²]	sii Low [%]	Non-sig [%]	Sig High [%]
Control	143.5	5.7		-	
P - 11	144.1	6.3	23	49	28
P - 19	143.9	6.0	22	52	25
T - 4	143.0	6.0	27	51	22
T - 11	142.9	5.5	27	51	23
T - 80	144.1	6.1	24	50	26
T - 180	144.1	6.6	24 '	48	28

Boreal forest

	Mean [Mg/ha]	Std Dev [Mg/ha]	Sig Low [%]	Non-sig [%]	Sig High [%]
control	136.1	7.7		-	
P - 11	136.6	8.2	28	U	28
P - 19	135.0	6.9	34	38	28
T - 4	135.9	9.2	32	42	27
T - 11	137.4	6.8	22	48	31
T - 80	134s	8.2	34	41	25
T - 180	133.2	9.5	40	35	25

Boreal/Northern hardwoods

	Mean [Mg/ha]	Std Dev [Mg/ha]	sii Low [%]	Non-sig [%]	Sig H i [%]
Control	310.0	18.0			
P - 11	316.2	13.3	24	32	u
P - 19	314.4	13.1	27	28	45
T - 4	300.7	11.1	44	37	19
T - 11	303.6	17.8	43	31	27
T - 80	184.2	32.3	99	1	0
T - 180	222.0	44.4	93	4	3

Eastern hardwoods

	Mean [Mg/ha]	Std Dev [Mg/ha]	Sig Low [%]	Non-sig [%]	Sig High [%]
Control	242.9	14.7			
P - 11	240.5	13.8	34	42	25
P - 19	243.1	14.7	25	47	28
T - 4	243.4	13.2	25	46	30
T - 11	242.5	9.5	30	41	29
T - 80	238.8	20.6	39	33	28
T - 180	242.5	40.6	43	11	45

response to only the lowest frequency (180 year period) temperature fluctuation (Pig. 4f). The lack of sensitivity of boreal forest biomass to climatic periodicity is probably 'due to the relatively broad temperature tolerance of spruce (*Picea spp.*), which comprises over 94% of forest biomass. Spruce is relatively insensitive to growing season temperature variation (250–1990 degree days) and to winter temperature minima (Pastor and Post 1985), which reduced the effects of sequential cold winters or hot summers in the treatment simulations. Aspen (*Populus tremuloides*) biomass did decrease during
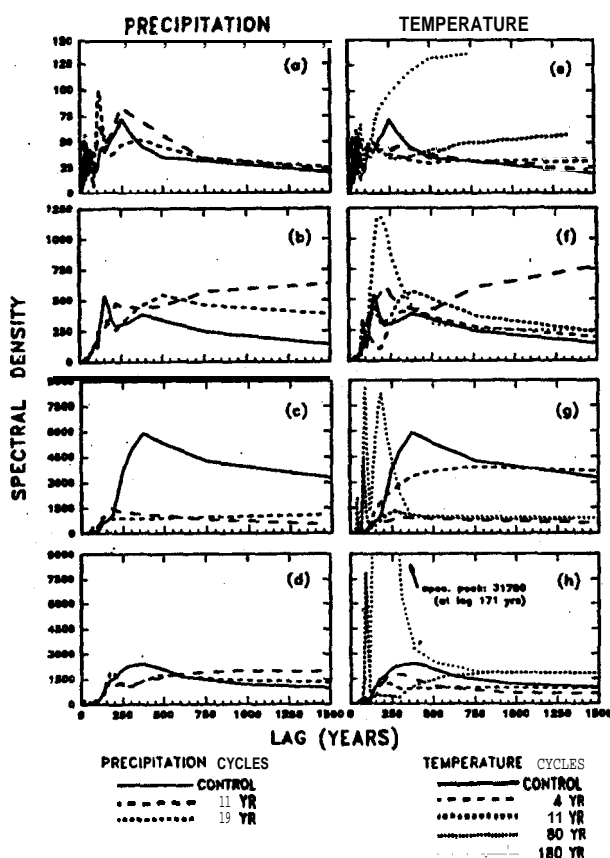
Fig. 4. Spectral density of simulated biomass for four eco-systems in response to various climatic functions. Precipitation simulations (left side) were control, 11 year cycle and 19 year cycle; temperature simulations (right side) were control, 4 year, 11 year, 80 year and 180 year cycles. Simulated ecosystems. from top to bottom, are (a, e) shortgrass prairie, (b, f) boreal forest, (c, g) boreal/northern hardwoods transition forest, and (d, h) eastern hardwoods. Note that spectral density scale differs among ecosystems.

some sequential cold periods, but it was a minor componeniof total biomass. Drought events for the boreal forest rarely occurred under any scenario and were not a factor.

Response of the hardwood/boreal transition forest (NE Minn) to low-frequency, high-amplitude temperature fluctuations (80 and 180 year periods) occurred in two predominant phases (Fig. 3c). At high temperatures occurring in the early part of the cycle, sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*), both representative of forests south of the transition. zone, increased. in

biomass. Later in the cycle, as temperature decreased, white spruce (*Picea glauca*) biomass increased while sugar maple and yellow birch biomass decreased. The net result was a bimodal spectral density plot with a major peak corresponding to the dynamics of warm-weather species and a minor peak corresponding to dominance by the cold-adapted white spruce (Fig. 4g). Under the high-frequency temperature cycles and the precipitation periodicities, the spectral density peaks in the transition forest were attenuated relative to the control run. The most probable reason for this attenuation is that the shorter cycles of smaller magnitude de-synchronized mortality of the dominant tree among the 30 replications. In the control run, the dominant species was sugar maple, with about 50% of the aboveground standing biomass. The maximum age of sugar maple in LINKAGES is 300 years, and the peak in spectral density occurred at about 350 years (Fig. 4c, g). Thus, after a tree-fall event in the control run, a large amount of biomass would be lost, and a replacement maple tree would not reach canopy height and die again for another 300 years. Introduction of the high-frequency temperature cycles and the precipitation experiments improved growing conditions, allowing growth spurts which were spread out in time relative to the control run; as a result, biomass did not show as strong a cyclic response. Another contributing factor is the method LINKAGES uses to calculate mortality in trees, When there were two consecutive years of low growth, probability of mortality increased to 0.34 for a tree. In the high-frequency cycles for both precipitation and temperature, the number of years with consecutive poor growth was not enough to increase species-specific mortality sufficiently to induce biomass cycles as occurred in the low-frequency cycles, yet it was sufficient to decouple the 30 replications in time so that there was not a consistent cycle in biomass for the dominant tree species (sugar maple).

Eastern hardwood forest response to temperature periodicity was striking for the low-frequency, high-amplitude scenarios (Fig. 4h). Eastern hardwood dominants, i.e. tulip poplar (*Liriodendron tulipifera*), hickory (*Carya spp.*) and oak (*Quercus spp.*) species showed drought stress responses to

temperature **shifts,** with higher temperature phases of the low-frequency cycle more than tripling the average number of growing season. drought days in comparison to lower temperature phases of the long-term cycle. Overall biomass decreased markedly during such periods of increased drought stress. As with the transition forest, attenuation was also **seen** for the eastern **hardwood forest** under the higher temperature cycle scenarios. In contrast with the transition forest, however, spectral **peaks** were never bimodal, indicating that all dominant **species** in this forest system responded similarly to stresses introduced by an oscillating climate.

The two ecosystems that were relatively insensitive to climatic periodicities, the **shortgrass** prairie and the boreal forest,' were' each dominated by a species with broad climatic tolerances. Grasslands, moreover, have much less internally-structured cycling. The higher spectral power estimates and white noise test statistics for forest systems under random climatic variation indicates that the forests modeled here possess much stronger internal frequencies than the shortgrass prairie. This results from the way regeneration and mortality are treated. Trees in the forest systems are modeled with increasing probability of death as they approach a species-specific expected longevity, with the probability of mortality in mature trees increasing greatly during stressful periods where water or light becomes limiting, particularly when stress conditions . occur in two consecutive years. Average lifespans for dominant tree species in the system (roughly **150–400** years) are therefore likely to be coupled to predicted **periodicities** in biomass. By contrast, *Bouteloua gracilis* is not assigned a maximum age. The **major** factor expected to influence periodicity in **STEPPE** is the probability of seed production, which is a function of annual precipitation.

Internal frequencies of an ecosystem associated with plant demographics can be modified by external periodicities in climate, particularly when the external signal becomes synchronized with the internal signal. Responses occurred in hardwood forests as larger-amplitude, lower-frequency temperature oscillations crossed biological thresholds for dominant species. Serial correlations in temperature caused significant differences in biomass

response in the boreal hardwood transition **zone** using LINKAGES (Cohen and Pastor 1991). The nature of model response is a function of the **characteristics** of the dominant species (Coffm and Urban 1993). We have extended the results of those studies **across** a broad geographic **and'** climatic range in North America. The climate **periodicities** we used were derived from long-term climate data series at timescales sufficient to capture low frequency dynamics in **these** models (Emanuel *et al.* 1978; Jassby and Powell 1990). These periodicities sometimes resulted in fundamentally different model responses when compared with simulations using the traditional approach of stochastic variation about a long-term mean. Further, at a biome transition, we found that both amplification and attenuation effects resulted from climatic oscillations, in **accordance** with Gosz and **Sharpe** (1989).

Our results showing significant differences between **the** standard input methodology and the cyclic input structures for hardwood forest biomass imply that the way ecosystem, modelers simulate climate input should be carefully considered. We recommend that preliminary sensitivity analyses be conducted in the frequency domain as a standard screening step (e.g., Dwyer and Kremer 1983). If climate is known to have significant multi-annual **periodicity(s)** and if the system being simulated has strong internal frequencies that can be amplified or attenuated by the input signal, predictions of **long-**term biomass response and system behavior will differ significantly from predictions using random climate input. This disparity could be particularly large when modeling vegetation at biome transitions.

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