VEGETATION REDISTRIBUTION: A POSSIBLE BIOSPHERE SOURCE OF CO, DURING CLIMATIC CHANGE

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Abstract. A new biogeographic model, MAPSS, predicts changes in vegetation leaf area index (LAI), site water balance and runoff, as well as changes in Biome boundaries. Potential scenarios of equilibrium vegetation redistribution under $2 \times CO₂$ climate from five different General Circulation Models (GCMs) are presented. In general, large spatial shifts in temperate and boreal vegetation are predicted under the different scenarios; while, tropical vegetation boundaries are predicted (with one exception) to experience minor distribution contractions. Maps of predicted changes in forest LAI imply drought-induced losses of biomass over most forested regions, even in the tropics. Regional patterns of forest decline and dieback are surprisingly consistent among the five GCM scenarios, given the general lack of consistency in predicted changes in regional precipitation patterns. Two factors contribute to the consistency among the GCMs of the regional ecological impacts of climatic change: 1) regional, temperature-induced increases in potential evapotranspiration (PET) tend to more than offset regional increases in precipitation; and, 2) the unchanging background interplay between the general circulation and the continental margins and mountain ranges produces a fairly stable pattern of regionally specific sensitivity to climatic change. Two areas exhibiting among the greatest sensitivity to drought-induced forest decline are eastern North America and eastern Europe to western Russia. Drought-induced vegetation decline (losses of *LAI),* predicted under all GCM scenarios, will release $CO₂$ to the atmosphere; while, expansion of forests at high latitudes will sequester $CO₂$. The imbalance in these two rate processes could produce a large, transient pulse of $CO₂$ to the atmosphere.

1. Introduction

Anthropogenic emissions of $CO₂$ and other greenhouse gases are expected to produce a global warming of as much as 1.5 to 4.5° C under the equivalent forcing of double pre-industrial CO₂ levels (Houghton et al., 1990). A global warming of such a magnitude could produce large shifts in the distribution of global vegetation (Emanuel et al., 1985; Neilson et al., 1989; Prentice and Fung, 1990; Smith et al., 1992). Extratropical biomes are expected to shift toward the poles, while equatorial biomes (forests) could expand or contract *in situ.*

Regions no longer suitable for forests could produce emissions of $CO₂$, while regions favoring additional vegetation growth could sequester $CO₂$ (Neilson et al., 1989; King and Neilson, 1992). Previous equilibrium estimates of terrestrial C storage under a $2 \times CO₂$ climate are equivocal as to whether the terrestrial biosphere would eventually be a source or a sink (Emanuel et al., 1985; Prentice and Fung, 1990; King and Neilson, 1992; Smith and Shugart, 1993; Smith et al., 1993). However, before equilibrium is ever attained, imbalances in the rates of CO_2 release from forest dieback and sequestering of CO_2 from forest growth during vegetation redistribution could produce a large, transient pulse of $CO₂$ into the atmosphere (King and Neilson, 1992; Smith and Shugart, 1993). Previous estimates of the transient 'carbon pulse', based on projected $2 \times CO_2$ equilibrium vegetation changes, indicate that the net rate of $CO₂$ release from the terrestrial biosphere could be as high as 40% of current anthropogenic emissions over a period of several decades (King and Neilson, 1992;

Water, Air, and Soil Pollution 70: 659-673, 1993. 9 1993 *Kluwer Academic Publishers. Printed in the Netherlands.* Smith and Shugart, 1993). Large uncertainties exist in these estimates, among the most important being 1) the potential magnitude of vegetation redistribution in the extratropics, and 2) whether or not tropical forests will expand or contract (King and Neilson, 1992; Neilson and King, 1992). These uncertainties are the subjects of this paper and are addressed using a new global biogeography model (Neilson, unpublished).

2. Methods

2.1. CLIMATE SCENARIOS

Scenarios of double CO₂ climate change, used to drive the vegetation model, were derived from five general circulation model (GCM) $2 \times CO₂$ equilibrium simulations. Climate scenarios were supplied by the Data Support Section within the Scientific Computing Division of the National Center for Atmospheric Research (NCAR). Model outputs for current and 2 x CO₂ climates were obtained from the following models: GISS (Goddard Institute of Space Studies, Hansen et al., 1988); UKMO (United Kingdom Meteorological Office, Mitchell and Warrilow, 1987); GFDL (Geophysical Fluid Dynamics Laboratory, Wetherald and Manabe, 1988); and OSU (Oregon State University, Schlesinger and Zhao, 1989). Both the GFDL R15 (ca. 4° x 5° grid) and R15 Q-flux versions were used. The Q-flux version of the GFDL model (GFDL-Q) includes a prescribed ocean-atmosphere coupling (Manabe et al., 1991). The coarse grid from each model was interpolated using a 4 point, inverse distance squared algorithm to a 0.5° x 0.5° , lat.-long, grid. The scenarios were applied as per recommended and calculated by the NCAR Data Support Section. Scenarios were constructed by applying ratios $(2 \times CO₂/1 \times$ $CO₂$) of all climate variables (except temperature) back to a baseline dataset, the IIASA 0.5 $^{\circ}$ resolution gridded climate dataset (Leemans and Crarner, 1991). Ratios were used to avoid negative numbers, but were not allowed to exceed 5, to prevent unrealistic changes in areas with normally low rainfall. Temperature scenarios were calculated as a difference $(2 \times CO₂ 1 \times CO₂$ and applied to the baseline dataset.

In addition to the published, gridded IIASA climate dataset, Leemans and Cramer have assembled additional datasets for relative humidity, vapor pressure (1771 and 1776 stations, respectively) and windspeed (ca. 3995 stations), and kindly shared these with us (Anonymous 1984a,b; Anonymous 1987a,b; Müller 1982) humidity, vapor pressure and temperature datasets were quality controlled (by the author) by using the temperature data to calculate the saturation vapor pressure, which, in combination with the vapor pressure, was used to calculate the relative humidity (RH). The calculated RH was subtracted from the actual RH (as contained in the separate data file) and the residuals plotted against the temperature. Above zero Celsius, the residuals clustered very close to zero. Residuals exceeding a 10% threshold (there were very few) were either discarded or corrected, if an obvious data coding error was detected. The data were then interpolated as RH values (four point, inverse-distance-squared) over the 0.5° grid and converted back to vapor pressure using the adiabatically-corrected grid temperature. This procedure may slightly underestimate high mountain humidity, but protects against physically impossible values obtained by interpolating vapor pressure directly from low elevations to neighboring mountains.

Winds were interpolated directly to the 0.5° grid using the same four point, inverse distance squared procedure. Mountain winds will be poorly captured by this procedure, but it represents the best available data at present. Future climate scenarios for vapor pressure were constructed using the ratio approach, described above. However, only current winds were used in the present study, since the change in future winds is quite extreme (GCM predictions) and carries many uncertainties (Marks, unpublished).

2.2. MODELING VEGETATION DISTRIBUTION

Site water balance and thermal constraints are thought to be the primary controls on the distribution of most of the world's vegetation (Whittaker, 1975; Box, 1981; Neilson and WuUstein, 1983; Neilson, 1987; Stephenson, 1990). All large-scale biogeography models incorporate these controls in some form or another, ranging from strictly statistical (e.g., Holdridge, 1947) to more fundamental approaches (Box, 1981; Prentice et al., 1992; Neilson et al., 1992; Neilson, unpublished). Site water balance is usually related to the vegetation distribution through some form of index, such as the ratio of actual to potential evapotranspiration, AET/PET, (Prentice et al., 1992), or the difference between potential and actual transpiration, PET-AET (Stephenson, 1990; Lenihan and Neilson, unpublished) integrated over an average annual cycle.

The water balance approach taken here differs from previous approaches by directly coupling the rate of transpiration to canopy conductance, a function of the surface area of leaves (leaf area index, LAI) and their stomatal conductance (Woodward, 1987; Neilson,

Figure 1. (a) MAPSS control (preliminary calibration, see key in Table 2). (b) Average percent change in LAI from five $2 \times CO₂$ climate scenarios.

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unpublished). The maximum LAI *(i.e., maximum rate of transpiration*) that can be sustained at a site without depleting soil water is calculated through a process of iteration. The calculated LAI integrates all of the factors that influence transpiration and site water balance, including snow formation and melt, canopy rainfall interception and evaporation, transpiration, soil drainage and runoff. Thus, the influence of site water balance on the distribution of vegetation can be directly calculated from LAI, rather than inferred through a water balance index. For example, the transition from closed forest to open forest or savanna occurs when the forest LAI falls below a certain canopy closure level. The model, described in detail elsewhere (Neilson, unpublished), is termed a Mapped Atmosphere-Plant-Soil System (MAPSS).

Maximizing the LAI that can be supported at a site with respect to the site water balance presumes that water is the primary limiting factor of the site carrying capacity. Current theory and empirical analyses tend to support this premise for most of the world's upland ecosystems (Woodward, 1987; Neilson et al., 1989; Stephenson, 1990). However, some systems are limited by available energy (e.g., high latitude systems), soil chemistry (e.g., serpentine soils), or possibly nutrients. It is assumed that north of the closed boreal forestthe open taiga/tundra and tundra regions are primarily energy limited (Woodward, 1987; Stephenson, 1990; Lenihan and Neilson, unpublished) and MAPSS does not calculate the water balance for those biomes. The maximum LAI is calculated at all other sites under the assumption that the site is water limited. However, when the calculated LAI reaches the maximum allowed by the model (currently set to 15), it is likely that energy rather than water is the primary limiting factor under the current climate. Nutrient limitations are currently not considered, nor are chemical constraints (e.g., serpentine soils). Poorly drained sites are also not considered in MAPSS.

Three basic vegetation lifeforms (trees, shrubs and grasses) are incorporated in the model. A site can support either trees or shrubs (not both) in competition with grass for light and water (Neilson, unpublished). The woody lifeforms project roots into the top two layers of a three-layer soil, while the grasses reach ouly into the surface soil layer. The third soil layer is present to accurately simulate unsaturated base flow from the soils. Within the light constraint of the woody vegetation, grasses compete with the woody vegetation for water in the surface soil layer as a function of their relative proportions of LAI (modified by stomatal conductance).

Canopy conductance, used in calculating transpiration is an exponential function of LAI, the form of which is common to many crop and atmospheric models (Abramopolous et al., 1988, Neilson, unpublished). Canopy conductance is also constrained by stomatal conductance,

which is a function of vapor pressure deficit and soil water potential. The current simulations are based on a generic sandy-loam soil with the surface layer being 0.5 m thick and the second layer 1.0 m thick. The third layer, providing base flow, is ca. 2 m thick.

Thermal limits on vegetation distribution (Woodward, 1987) define six latitudinal zones within MAPSS, tundra, taiga/tundra (open, boreal woodland), boreal, temperate, subtropical and tropical (Table 1). The tundra-talga/tundra and taiga/tundra-boreal ecotones are defined by growing degree day limits (base 0° C) of 735 and 1330, respectively (Lenihan and Neilson, unpublished). The boreal-temperate ecotone is defined by winter temperatm'es that fall below the supercooled freezing point of water (-40° C) , determined as the limit for most temperate hardwoods (Burke et al., 1976; Woodward, 1987) and is indexed by mean monthly temperatures below -16° C (Neilson et al., 1989; Neilson et al., 1992). The temperatesubtropical ecotone is defined by the high probability of hard frost (mean dally maximum temperatures below freezing) occurring, on average, in every year, and is indexed by a mean monthly temperature of ca. 1.25° C (Neilson et al., 1989; Neilson et al., 1992). First and last frosts are indexed by mean monthly temperatures less than 13° C (Neilson, unpublished). The subtropical-tropical ecotone is defined by the coolest winter month exceeding the 13^o index of last frost.

2.3. VEGETATION CLASSIFICATION

Vegetation types in MAPSS are classified from a functional perspective (Neilson et al., 1992). I have not attempted to adhere to any particular nomenclature. The classification separates closed forests, tree savannas, dense shrub communities (chaparral), shrub savannas, grasslands and deserts based on woody and grass LAI (Table 2). Above a specified woody LAI threshold, the woody vegetation is of the tree form and below the threshold is of the shrub form. The tree/shrub LAI threshold is set lower in the tropics than in the extratropical zones. I hypothesize that differences in land-use and natural disturbance regimes (fire and large herbivores) preclude widespread open savannas from the extratropical zones compared to those observed in the tropics.

Vegetation types are further split on whether their phenology is evergreen or deciduous, as determined by physiologically-based rules relying on the seasonality of weather (Marshall and Waring, 1984; Neilson et al., 1992; Lenihan and Neilson, unpublished). The tropical zone is defined as evergreen with drought-deciduous forms being indexed by a lower LAI than the closed, evergreen forests. The classification also splits vegetation based on broadleaf or microphyllous leaf form, again based on the seasonality of weather.

Vegetation types are further partitioned by the thermal zone. The subtropical vegetation types are all classified as 'warm mixed' in phenology (evergreen/deciduous) due to the wide variation in frost and cold adaptations. Within the temperate zone, broadleaf deciduous types are subdivided into 'deciduous broadleaf and 'cool mixed' based on an LAI threshold above which water limitations are reduced (Neilson et al., 1989). The growth of broadleaf, deciduous forms is optimal, but the cool conditions and short growing season also favor coldadapted conifers, thereby producing a mixture. Within the 'mixed' classes, the leaf form nile is used to designate a potential climax dominant. So, for example, the forests in the northwest coastal mountains (U.S.) are classified as warm mixed (subtropical zone), but microphyllous (conifer) dominant; while, the southeast U.S. is classified as warm mixed, but broadleaf dominant (Fig. la). Tropical seasonal and savanna types have been only broadly defined, based on LAI and, in the future, will be better defined using physiologically-based droughtdeciduous rules.

Grassland rules have been defined for tall, mixed, and short grass types; however, the grasslands require a fire regime to constrain the woody LAI component (Neilson et al., 1992).

Aggregation	Classification	LAI	Phen, Leaf		Zone
Tundra	1. Tundra	N/A	N/A	N/A	Boreal
Taiga/Tundra	2. Taiga/Tundra	N/A	N/A	N/A	Boreal
Boreal and Temperate Forest	3. Forest Evergreen Needle (Taiga) 4. Forest Evergreen Needle (Temperate) 5. Forest Mixed Cool (Temperate) 6. Forest Deciduous Broadleaf 7. Forest Mixed Warm (EN) 8. Forest Mixed Warm (DEB)	>3.75 >3.75 >11 3.75-11 >3.75 >3.75	E Е D/E Е D/E DÆ	M М B/M в B /M B	Boreal Temp Temp Temp S.Trop S.Trop
Boreal and Temperate Savanna	9. Tree Savanna Cool Mixed (EN) 10. Tree Savanna (Evergreen Needle) 11. Tree Savanna (Deciduous Broadleaf) 12. Tree Savanna Warm Mixed (EN) 13. Tree Savanna Warm Mixed (DEB)	$2 - 3.75$ $2 - 3.75$ $2 - 3.75$ $2 - 3.75$ 2-3.75	D/E Е D D/E D/E	B/M M в B/M В	Boreal Temp Temp S.Trop S.Trop
Tropical Forests	14. Tropical Forest Evergreen Broadleaf 15. Tropical Seasonal Forest (Moist)	>3.75 2-3.75	Е D/E	В в	Trop Trop
Tropical Savanna	16. Tropical Dry Forest/Savanna	$.65 - 2$	D/E	B/M	Trop
Non-Forest	17. Chaparral 18. Open Shrubland 19. Shrub Savanna Cool Mixed (EN) 20. Shrub Savanna Evergreen Micro. 21. Shrub Savanna Deciduous Broadleaf 22. Shrub Savanna Warm Mixed (EN) 23. Shrub Savanna Warm Mixed (DEB) 24. Shrub Savanna Tropical 25. Tall Grass Prairie 26. Mixed Grass Prairie 27. Short Grass Prairie 28. Semi-Desert Grassland 29. Tropical Desert 30. Subtropical Desert 31. Temperate Desert 32. Boreal Desert 33. Extreme Desert	$2.1 - 3.5$ 2.1 2.1 2.1 2.1 2.1 2.1 < .65 $0.9 - 6$ $.5 - .9$ A.5 .1.4	D/E D/E Е Е D D/E D/E Е	B/M B/M B/M M В B/M В B	All All Boreal Temp Temp S.Trop S.Trop Trop All All All All Trop S.Trop Temp Boreal All

Table 2. Preliminary classification and calibration of vegetation types within MAPSS.¹

¹N/A=Not applicable; E=evergreen; D=deciduous; B=broadleaf; M=microphyllous. Parenthetical abbreviations in 'Mixed' vegetation types indicate likely climax physiognomy; EN=evergreen-needleleaf; DEB=deciduous/evergreen broadleaf.

Desert classes are only separated by thermal zone, after having been classified as desert based on both woody and grass LAI conditions. An extreme desert category is defined where

rainfall is so low that the site water balance calculations cannot be solved.

Most of the classification rules are post-hoc determinations and they do not affect the functional calculation of LAI. The LAI threshold defining closed forest (>3.75, Table 2) is the only critical LAI threshold and is used for defining forest/non-forest boundaries. The fundamental importance of LAI calculations (beyond classification) is as a direct indicator of the vegetation carrying capacity with respect to site water balance.

The 33 vegetation classes serve to demonstrate the qualitative accuracy of MAPSS (Fig. la), but are less important from the perspective of global terrestrial carbon balance estimation. The aggregated tundra, taiga/tundra, temperate and boreal forest, temperate and boreal savanna, tropical forest, tropical savanna and non-forest classes (Table 2) are adequate for a first approximation of carbon pool changes and for validation testing of MAPSS.

Above and belowground carbon densities are based on Olson et al. (1983) and Zinke et al. (1984) as presented in Cramer and Solomon (in press). The vegetation classes used in Cramer and Solomon (in press) were aggregated to the levels described above and the carbon density values for each of their classes were averaged for the aggregated classification (Table 2).

Table 3. Above and belowground carbon density $(kg/m²)$.

2.4. CALIBRATION AND SENSITIVITY ANALYSIS

2.4.1. Calibration over the conterminous United States: Predicted monthly and annual runoff were calibrated on four small clusters of weather stations, generally over Alabama, Illinois, Nebraska and Oregon for a total of about 10 stations within a network of 1211 dispersed weather stations in the U.S. and about 1100 stream gauges (Neilson, unpublished). MAPSS was subsequently validated, using the full meteorological and stream gauge networks, over the eastern U.S. and shown to accurately estimate the annual water balance (runoff/precipitation) to within $\pm 10\%$ over most of the area and also accurately simulates the monthly runoff at individuai sites (Neilson et al., 1989). The residuals (predictions exceeding \pm 10%) are largely underpredictions of runoff, and occur in areas where the potential forest vegetation has been replaced by agriculture or other land uses and in mountainous terrain where valley rain gauges underestimate the precipitation catch in mountain watersheds. The predicted vegetation distribution was visually calibrated against a coarse classification based on Küchler (1964) and Dice (1943) (Neilson et al., 1992). MAPSS was then implemented on a dense grid of ca. 78,000 points (10 km cells) over the same spatial extent and visually appears to accurately predict vegetation and runoff in complex terrain (maps on file with the author). The successful transition from 1,211 points to 78,000 represents partial validation of both the

model and the distributed climate datasets over the 78,000 points (Daly et al., unpublished; Marks, unpublished).

empirical and simulated. Digital, empirical vegetation maps used are those of Olson et al. (1983) and Matthews (1984) although only intercomparisons with Olson et al. (1983) are presented here. Visual comparison utilized global (Bailey, 1989) and continental vegetation maps (UNESCO, 1981; White, 1983). MAPSS was also compared to the simulated vegetation from BIOME, another global vegetation model (Prentice et al., 1992).

The Kappa statistic, developed for biogeographic intercomparisons, was used to compare MAPSS output to the Olson et al. (1983) map and to the BIOME output (Monserud and Leemans, 1992). The BIOME comparisons are critical because they were produced under the same gridded temperature and precipitation datasets. In addition, the BIOME model utilized a global radiation calculation, a global cloud cover dataset and a spatially variable soil texture dataset for the PET water balance calculations, none of which were used by MAPSS (Leemans and Cramer, 1991; Prentice et al., 1992). However, MAPSS does require winds and humidity for PET calculations, datasets not required by BIOME.

3. Results

3.1. VALIDATION

The Kappa statistics for control runs of MAPSS and BIOME comparisons with the Olson et al. (1983) dataset, and the MAPSS-BIOME intercomparison are presented in Table 4. MAPSS and BIOME both compare favorably to Olson with a 'Good' rating from the Kappa statistic. The individual biome comparisons are quite parallel between the two models in comparison to Olson et al. (1983). In fact, the two models produce almost the same calibration with an average intercomparison Kappa statistic of .78 (Very Good, boreal and temperate savannas lumped with forests). Most of the temperate forest area in Olson et al. (1983) is occupied by cultivated lands rendering the Kappa statistic comparison ineffective for that class. Therefore, I have lumped temperate and boreal forests for the comparisons to Olson et al. (1983). The boreal/temperate (combined classes) and tropical forest intercomparisons are quite high between the two models (.83), nearing an 'Excellent' rating. The near congruity of the two

Figure 2. Control runs of MAPSS (a) and BIOME (b), using the coarse vegetation classification (Table 2).

models is most apparent upon visual examination (Fig. 2).

The version of BIOME that we analyzed does not contain a taiga/tundra open woodland, which in MAPSS was lumped with boreal and temperate forests for these comparisons. The poorest showing of MAPSS was in the talga/tundra comparison with Olson, barely producing a 'Good' rating. This comparison was worst in the Eastern Hemisphere, where larch forests are important, a type that has yet to be defined in MAPSS.

BIOME does not contain temperate and boreal savannas. The definition of these extratropical savanna types in MAPSS is more like a woodland than a savanna with LAI ranging from 2.0 to 3.5 (Table 2). The extratropical savannas, as defined in MAPSS, appear to be contained within the closed forest types of BIOME and produce a slightly improved intercomparison when lumped with forests in MAPSS (Table 4).

Extratropical	OSU	GISS	GFDL	GFDL-O	UK	<u>Average</u>
Tundra->Taiga/Tundra	4.34	4.63	4.27	4.86	3.68	4.36
Taiga/Tundra->Forest	7.72	8.29	9.17	8.99	9.41	8.72
Forest->Forest	24.29	25.43	18.75	22.93	19.07	22.09
Forest->Savanna	5.37	4.56	8.64	6.52	9.42	6.9
Forest->Non-Forest	.96	.62	3.21	1.16	2.11	1.61
Savanna->Non-Forest	3.37	2.77	4.08	3.57	3.76	3.51
Tropical						
Forest->Forest	15.22	13.93	13.73	12.65	8.43	12.79
Forest->Savanna	.83	2.12	2.32	3.4	7.62	3.26
Savanna->Savanna	17.8	18.36	17.82	17.34	17.87	17.84
Savanna->Non-Forest	.79	.97	1.59	2.11	1.56	1.4

Table 5. Area estimates (x 10^6 km²) of vegetation conversions and areas of stability (MAPSS) under $2 \times CO₂$ climate scenarios.

3.2. VEGETATION REDISTRIBUTION

3.2.1. Biome area changes: Both models produce large decreases in the areas of tundra and taiga/tundra (Fig. 3). MAPSS produces decreases in tundra across the five GCM scenarios (range 51% - 72%, \bar{x} =62%) and for taiga/tundra (38% - 64%, \bar{x} =62%). The two biomes are lumped in BIOME and decrease from 50% to 69% (\overline{x} =59%). MAPSS produces large increases in temperate and boreal savannas under the GFDL and UKMO scenarios (36% - 82%). Temperate forest area changes little in MAPSS under $2 \times CO₂$ climate, but it increases in BIOME. MAPSS generally produces slight decreases in tropical forests (except OSU) and BIOME produces slight increases (Fig. 3).

MAPSS predicts that the temperate forests in the conterminous U.S. could decrease in area by 30% to 94%, while in BIOME they remain virtually unchanged with the GFDL and UKMO scenarios presenting the most extreme shifts (Fig. 4). The differences between

Figure 3. Changes in area predicted by MAPSS (a) and BIOME (b) (average of five $2 \times CO$, climate scenarios).

MAPSS and BIOME in the extratropical forests are much reduced if the temperate and boreal savannas of MAPSS are lumped with closed forest. However, there is a considerable difference in the carbon density between the savanna and forest vegetation types (Table 3).

3.2.2. Vegetation type conversion: Forests shifting toward the poles will colonize treeless areas and sequester carbon through growth. At the opposite boundary, where forests are converted to non-forests, dieback and decay will release carbon to the atmosphere. Intervening areas will remain forested, but could still undergo drought-induced decline. Table 5 presents the area estimates for different types of vegetation conversion under different GCM scenarios (only conversions $> 1 \times 10^6$ km² in area are listed).

MAPSS predicts that of the combined boreal and temperate forests of the world, about 72% of the forested area (22 x 10⁶ km²) will remain forested with about 23% (6.9 x 10⁶ km²) being converted to savanna and an additional 5% being converted to non-forest (average over five GCM scenarios). Closed forest expansion into the taiga/tundra could, under $2 \times CO₂$ equilibrium conditions, add about 8.1 x 10^6 km² of newly-forested area (average over five GCM scenarios); while about 8.51×10^6 km² of closed forest are converted to savanna and non-forest (Table 5). Spatial changes in tropical forests are less remarkable (Table 5). Of the 16 x 10⁶ km² of forest in the control run about 13 x 10⁶ km² should remain forested. The UKMO climate was the most severe leaving only 8.4×10^6 km² as stable, tropical forest (Table 5).

3.2.2. Vegetation Density and Drought Response: Current boreal and temperate forests are predicted by MAPSS to experience a drought-induced reduction in LAI of 33% to 40%, respectively (average over five GCM scenarios, Table 6). The GFDL and UK scenarios are the most extreme with LAI reductions of about 50% each for both boreal and temperate forests (Table 6). Tropical forests average about 10% reduction in LAI across the five scenarios, with the OSU scenario producing the only predicted increase in LAI. Thus, most forested regions in the world are predicted to experience severe drought-induced decline, regardless of whether or not they are expected to remain forested (Fig. lb). The only areas predicted to increase in LAI are the high latitude areas of forest expansion, a few mountainous regions, and a few small areas in the tropics (Fig. 1b).

The predicted regional changes in LAI and forest contraction are surprisingly consistent among the five scenarios, excepting the OSU tropical response. The most severe losses of forests are consistently predicted by MAPSS to occur in the eastern United States and Canada and in the western region of the former Soviet Union (Figs. lb, 4a). The sensitivity of these regions to climatic change appears to result from the nature of the background regional climate, its seasonality and the relative steepness of the regional gradients in the background

climate.

Although widespread decline and death of forests is predicted, even in areas that remain forested, forests are predicted to regrow to approximately the original density in new locations. There is, under current climate, a gradient of increasing LAI from warm-temperate to coolboreal forests. A poleward shift in this gradient will produce a drought-induced LAI decline over the entire gradient, except near the poles where forests will expand into non-forest. Drought-induced forest decline of the magnitude estimated by MAPSS couid result in nearly complete forest dieback of extra-tropical forests, if the rate of climatic change is relatively fast, as is being currently predicted (King and Neilson, 1992).

Figure 4. GFDL 2 x CO_2 runs of MAPSS (a) and BIOME (b), using the coarse vegetation classification (Table 2).

3.3. CARBON BALANCE

The potential equilibrium change in total above and below ground carbon, due to climateinduced vegetation change, was calcuiated as the product of carbon density (Table 3) and the

Figure 5. Changes in total terrestrial carbon storage predicted by MAPSS (a) and BIOME (b) under five $2 \times CO₂$ climate scenarios.

change in area of each biome (Fig. 3). Three of five GCM scenarios under MAPSS produce net losses of carbon from the terrestrial biosphere due to equilibrium $2 \times CO₂$ climatic change (Fig. 5), in contrast to previous results (Prentice and Fung, 1990; Smith et at., 1993). MAPSS predicts losses of forests in the tropics, where other models predict gains. MAPSS also predicts more severe losses due to drought in extra-tropical forests than do other approaches (Fig. 3). The predicted high-latitude gains in forests by MAPSS are about the same as in other approaches.

Whether the global biosphere is predicted to contain more or less carbon under equilibrium conditions is of less importance than is the temporal trend of carbon fluxes under a rapidly changing climate. Using the equilibrium, area-weighted vegetation conversions (Table 5), the potential transient flux of CO₂ between the biosphere and atmosphere can be estimated (King and Neilson, 1992). The imbalance between decomposition and growth rates, due to forest dieback and regrowth or expansion, could produce a large, net transient "pulse" of $CO₂$ to the atmosphere. Our previous CO₂ flux estimates and sensitivity analyses indicated that net emissions of $CO₂$ could be as high as 3.4 Petagrams/year, about a 40% increase over current annual anthropogenic emissions (King and Neilson, 1992; Neilson et al., in press). The projected vegetation changes presented here (Table 5) are in agreement with the earlier estimates of vegetation change (King and Neilson, 1992; Neilson and King, in press). So, for this paper, the transient carbon pulse was not recalculated.

4. **Conclusions**

A new global vegetation model, MAPSS, has been developed for predictive biogeography under climatic change. Under controlled climate, MAPSS is very similar to another general vegetation model, BIOME (Prentice et al., 1992). However, under $2 \times CO_2$ climate, the two models diverge considerably with MAPSS exhibiting much greater sensitivity to water stress and loss of extra-tropical forests. MAPSS predicts tropical forest loss, while BIOME predicts tropical forest gains. The reasons for these differences are not fitUy understood, but are thought to involve the method of calculation of transpiration and the method of relating that transpiration to vegetation properties.

MAPSS predicts almost universal drought stress from climatic change over the world's forests. Drought stress, under five $2 \times CO₂$ climatic scenarios, would apparently provide the primary mechanism inducing forest decline and dieback. Forest dieback and vegetation conversion to different types could produce a large, net transient pulse of $CO₂$ to the atmosphere potentially producing a significant positive feedback to the processes of global warming.

These results do not consider the potential mitigating influence of the direct effects of $CO₂$ on vegetation water-use-efficiency, nor of the aggravating influence of carbon releases from the biosphere due to land use.

5. Acknowledgements

I would like to thank the many people who assisted in background investigations for this research over the past several years. Special thanks go to G. King, J. Lenihan and D. Marks for their continuing input on the issues discussed in this paper, t am particularly indebted to J. Chaney for the skill he brought in rendering this model into computer code and for its implementation over a network of workstations in a distributed computing environment. Additional thanks are accorded G. Koerper for his initial coding of the model. This document has been prepared at the EPA Environmental Research Laboratory in Corvallis, Oregon, USA, through cooperative agreement CR816257 with Oregon State University. It has been subjected to the Agency's peer review and approved for publication. Mention of trade names or eommercial products does not constitute endorsement or recommendation for use.

6. **References**

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