

The influence of seasonal water availability on global C₃ versus C₄ grassland biomass and its implications for climate change research[☆]

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Abstract

Climate-change induced alterations in the global distribution of cool season (C₃) and warm season (C₄) grasses would impact the global carbon cycle and have differing, local effects on range and agricultural production. We hypothesize that a major influence on C₃/C₄ distribution may be the seasonal timing of water availability with respect to the different C₃ and C₄ growing seasons. An algorithm expressing this hypothesis (the SAW hypothesis for Seasonal Availability of Water), estimates C₃ versus C₄ grass biomass from climate data. Sensitivity analysis indicated that temperatures used to delineate the start and end of the C₃ and C₄ grass growing seasons were more important than photosynthetic responses to temperature. To evaluate the SAW hypothesis, this algorithm was applied globally on a 1° × 1° latitude–longitude grid. When compared with vegetation survey data at 141 locations in North America, Argentina, Australia, and South Africa, SAW algorithm predictions yielded an R² of 0.71. Error resulted primarily from comparing large grid cells to plot data, interannual variability of climate, and from gridding measured climate to data-sparse locations with a single lapse rate of air temperature with elevation. Application of the SAW algorithm to a climate change scenario suggested that changes in temperature and precipitation patterns could offset C₃ photosynthetic advantages offered by elevated atmospheric CO₂ concentrations. These results underscored the importance of accurately representing the timing and spatial distribution as well as the magnitude of temperature and precipitation in scenarios of future climate.

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1. Introduction

The global distribution of cool season (C₃) versus warm season (C₄) grasses is expected to shift with changes in climate and elevated atmospheric CO₂ (Long, 1991; Morgan et al., 1994; Chen et al., 1996; Drake et al., 1996; Ehleringer et al., 1997; Epstein et al., 1997; Collatz et al., 1998; Sage et al., 1999). C₃ and C₄ grasses often differ in forage quality and, on a

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single range, grow during different parts of the year. Reductions or increases in either grass could require adjustments to grazing plans or stocking rates and, in extreme cases, alter total production. In some areas, C₃ grasses and crops have C₄ weeds or vice versa and changes in their relative distribution could favor or hamper production depending upon the species involved. Therefore, a climate-sensitive model estimating how the relative C₃/C₄ grass biomass might change would be useful to policy makers for assessing the potential impacts of climate change on agricultural systems.

Climate induced changes in grasslands are also of more general interest. Grasslands are a major component of terrestrial vegetation, and, recently, the Intergovernmental Panel on Climate Change (IPCC) has examined the potential impacts of climatic change and vegetation's role in the earth's carbon cycle (Schimel et al., 2000; IPCC, 2001). In this regard, grasses with the C₃ photosynthetic pathway differ significantly from C₄ grasses. Therefore, to estimate the carbon cycling through grass at each location, the relative amounts of C₃ versus C₄ grass biomass must be known (Ehleringer, 1978; Farquhar et al., 1989; Ehleringer and Monson, 1993; Lloyd and Farquhar, 1994; Tieszen et al., 1997; Knapp and Medina, 1999; Long, 1999). A static map of this distribution will not suffice because the relative amounts of C₃ versus C₄ grass is, itself, hypothesized to change with climate and the resulting feedbacks must be represented. Therefore, a climate-sensitive model estimating relative C₃/C₄ biomass is a necessary addition to global carbon models used to advise government policy makers on the possible impacts of climate change.

The processes that control the global distribution of C₃ and C₄ grasses have not been clearly described. Most studies of the geographical distribution of C₃ and C₄ grasses focused upon species because species lists (floras) offered global coverage (Teeri and Stowe, 1976; Teeri, 1979; Prentice et al., 1992; Sage et al., 1999). On a site-by-site basis, the distribution of C₃ versus C₄ grasses was found to be a complicated function of microclimate, site history, herbivory, soil conditions, burning, topography, seed dispersal and competition (Teeri, 1979; Pearcy and Ehleringer, 1984; Ripley, 1992; Ehleringer et al., 1997; Hill et al., 1997; Sage et al., 1999; Matsinos and Troumbis, 2002; Peters, 2002). Ehleringer and Björkman (1977)

examined the temperature controls on photosynthetic carbon gain or quantum yield. They noted that C₃ plants were favored at low temperatures and C₄ plants were favored at high temperatures. The crossover temperature was estimated to be 25–30 °C. After further examination, it was lowered to 18–23 °C (Pearcy and Ehleringer, 1984) and then to 21 °C (Ehleringer et al., 1997). Applying this hypothesis to climatology for the North American Great Plains, Ehleringer et al. (1997) estimated a crossover latitude where C₃ grass yields to C₄ dominance to be about 45°N. Field surveys have essentially confirmed this hypothesis and placed the crossover latitude at 43–45°N (Epstein et al., 1997; Tieszen et al., 1997). When viewed at global or regional scales, the C₃ grasses prefer cooler environments compared to the C₄ grasses. This preference is expressed spatially, with the C₃ species dominating in the higher latitudes and altitudes, and temporally with the earlier start of the C₃ growing season at temperate latitudes (Teeri and Stowe, 1976; Dickinson and Dodd, 1976; Chazdon, 1978; Tieszen et al., 1979; Boutton et al., 1980; Rundel, 1980; Ode et al., 1980; Collins and Jones, 1985; Cavagnaro, 1988; Cabido et al., 1997).

In 1994, Lloyd and Farquhar produced a worldwide estimate of the C₃ versus C₄ grass distribution from climate. They globally applied a regression equation derived for Argentina (Cavagnaro, 1988) to estimate C₃ and C₄ grass species abundance as a function of temperature (really altitude). Then, climatic constraints suggested by Collatz and Berry (in Berry, 1994) were used to constrain C₄ dominated grasslands to produce a map of the proportion of photosynthesis undertaken by C₄ plants. No validation statistics were presented, but the predicted global C₄ grass distribution appeared qualitatively correct and represented the observed distribution with “reasonable accuracy” (Lloyd and Farquhar, 1994, p. 208).

Recently, studies have addressed the distribution of C₃ versus C₄ biomass, as opposed to species. The distinction can be important. For example, at the Central Plains Experimental Range (CPER) in Colorado, USA, 59% of the species are C₃ but these species account for only 10% of the biomass (Paruelo and Lauenroth, 1996). Paruelo and Lauenroth (1996) analyzed the fractional biomass of C₃ grasses to total grass (C₃G) for the North American Great Plains. They found a correlation ($R^2 \sim 0.5$) between C₃G

and mean annual temperature in combination with winter-to-summer precipitation. Surprisingly, precipitation was the dominant factor, not temperature. Paruelo et al. (1998) showed that this correlation also worked well in Argentina. From photosynthetic quantum yields, Collatz et al. (1998) deduced that C₃ photosynthesis is competitively advantageous below a mean monthly air temperature of 22 °C and C₄ photosynthesis is advantageous above 22 °C. Applying this deduction to 1930–1960 climate data, they produced a map of the world's grasslands divided into the three broad categories: all C₃, all C₄, and mixed C₃/C₄. Counting only months with at least 25 mm precipitation, areas with monthly means continually below 22 °C are predicted to be all C₃ grass. Areas continually above 22 °C are all C₄ grass. Grasslands with at least 1 month (but not all) with a mean temperature >22 °C are mixed C₃/C₄. Although illuminating, none of these approaches are fully satisfactory for incorporation into global climate change studies. Paruelo et al. (1998) correctly cautioned about applying their results globally; extrapolation of statistical relationships beyond the range of the data can cause large errors (Gold, 1977). Algorithms that predict a simple “mixed C₃/C₄” category from long-term climate data are not totally sufficient either. Small differences in C₃G in the mixed category, when applied over large areas, can become significant sources or sinks of carbon.

Therefore, a climate-sensitive model for estimating C₃G in the mixed areas is still needed and the question remains; what is the process controlling the global distribution of C₃ and C₄ grass biomass? Cavagnaro (1988), Lloyd and Farquhar (1994), and Paruelo and Lauenroth (1996) found precipitation and temperature important, but they did not describe a specific process incorporating these variables. Collatz et al. (1998) indirectly referred to a process by basing their map upon a temperature determined from quantum yields and incorporating a minimum precipitation limit. However, Long (1983, 1991, 1999) argues that the temperature responses of C₃ and C₄ quantum yields do not scale up to productivity differences, and temperature limitations on other physiological processes control the distribution of C₃ and C₄ vegetation. His argument is compelling since temperature not only affects the maximum rate and quantum yield of photosynthesis, but also affects practically every other

process of plant growth, development and survival (Larcher, 1995; Long and Woodward, 1988). If not quantum yields, how does temperature interact with precipitation to produce the observed C₃G?

Our experience suggests that it is the seasonal availability of moisture that controls the global distribution. This hypothesis is reflected in Paruelo and Lauenroth's correlations, and makes theoretical sense. In general, grasslands are water limited, existing where there is enough rainfall to sustain plant production, but not enough for trees which would out-compete the grasses for light (Woodward, 1987; Ripley, 1992). In temperate latitudes, C₃ grasses start growth early and have sole access to the water stored in the soil from melting snow and spring rains (Fig. 1). C₄ grasses start later as temperatures warm, and both grasses will have access to available water, primarily from rainfall. Finally, as temperatures warm further, C₃ grasses undergo senescence (the so-called summer-slump; Riesterer et al., 2000) so C₄ grasses will have sole access to available water from rainfall (Fig. 1). Temperature limits the potential growing season of each grass but, if there is no water available, the grass will not grow.

Therefore, we hypothesized that the process that controls relative C₃ and C₄ biomass is seasonal access to available water which is partitioned by differences in the growing seasons and utilized with a water use efficiency (WUE = photosynthetic carbon produced/water used) that changes seasonally. In this study, we examine this hypothesis (hereafter referred to as the SAW hypothesis for Seasonal Availability of Water) by applying it globally and comparing its C₃G predictions to existing vegetation studies. After evaluating the SAW hypothesis in relation to these studies, we examine its implications for climatic change by applying it to a probable climate change scenario.

2. Methods and materials

2.1. The SAW algorithm

To examine the SAW hypothesis and its implications for climate change studies, we developed a simple biogeographical model (called the SAW algorithm) that estimated the relative distribution of C₃ versus C₄ grassland biomass by relating the temperature

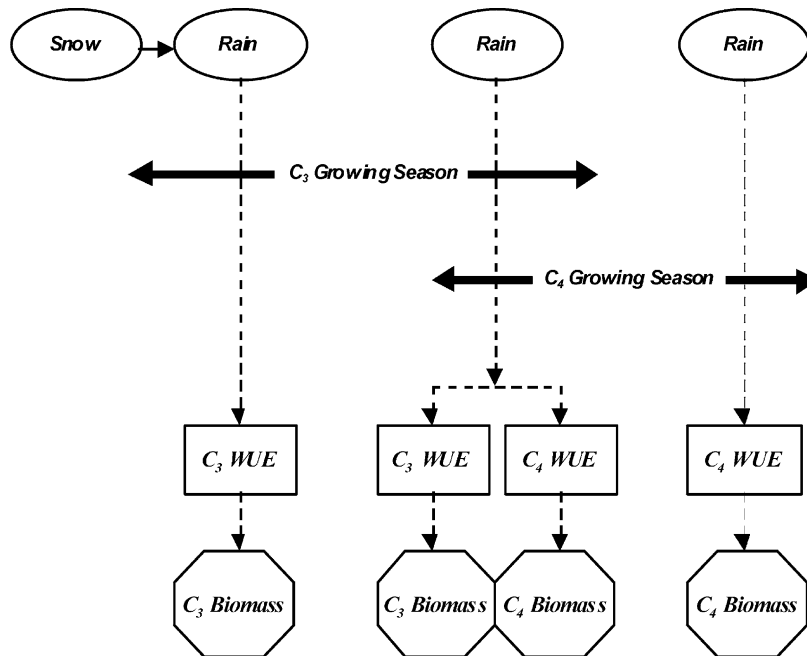


Fig. 1. The essential process underlying the SAW hypothesis. The SAW (Seasonal Availability of Water) hypothesis determines the relative C₃ vs. C₄ biomass for grasslands from the partitioning of available water by the preferred growing seasons. C₃ plants start growth first and use the water stored over the cold dormant season. Relative abundance is calculated from available water using a simplified algorithm that calculates water use efficiency (WUE) from daily air temperature. The C₃ and C₄ growing seasons are estimated from a 30-day running average of maximum daily air temperatures.

controlled growing seasons and their interaction with temperature controlled grass water use efficiency.

Since our objective was to examine the SAW hypothesis on a global scale and to evaluate its implications for climate change studies, we configured the SAW algorithm as a dynamic process model (Peng, 2000) that simulates one aspect of grass physiology (WUE) to estimate the grasses daily response to available water. The SAW algorithm is therefore similar to other recent, dynamic physiologically-based, process models like ALBIOC (Roelandt, 2001) and ECOTONE (Peters, 2002). However, it is much less ambitious in scope than these models and includes only the three sub-processes necessary to express the SAW hypothesis, requires only two input data fields available at global scales and considers only generic C₃ and C₄ grasses to keep initial parameterization to a minimum. In contrast, although only the minimum of processes are included, the SAW algorithm captures the daily interaction between these sub-processes with a true, daily time step.

2.2. The C₃ and C₄ growing seasons

The limits of the preferred growing seasons (hereafter called growth windows) are estimated from air temperatures (Monson and Williams, 1982; Dickinson and Dodd, 1976). Areas of mixed C₃/C₄ grasses are assumed to be in the mid-latitudes where there is a fair degree of seasonality in temperature. The grasses would then follow an annual cycle of growth and dormancy. The winter season is assumed to be a dormant period for both grasses.

Threshold values for a 30-day running average of maximum air temperature ($^J T_x$ for year-day J) are used to signal the day of opening and closing of C₃ and C₄ growth windows. These temperatures were labeled T_1 , T_2 , T_3 , and T_4 (Fig. 2). As the air temperature drops in the fall, there is potential for a short C₃ growing period. However, the C₃ grasses have already established themselves for the next year; hence, this second growth window was not included.

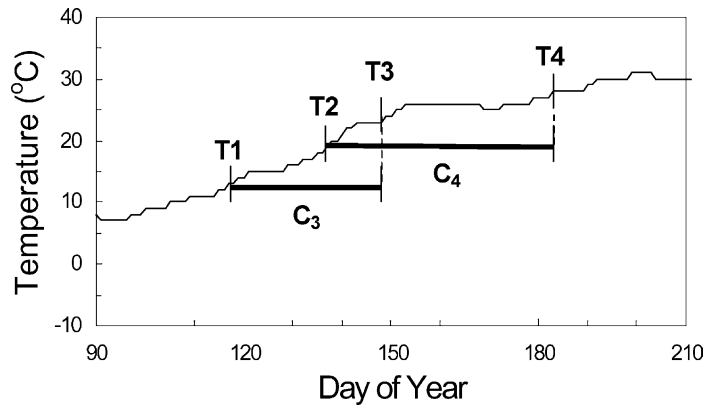


Fig. 2. Temperature limits of the C₃ and C₄ growth windows estimated from a 30-day running average of maximum air temperature. The thin line is the 30-day running mean of the daily maximum temperature ($^J T_x$) for day of the year, J , at the CPER, near Nunn, CO. The C₃ growth window starts on the day when $^J T_x$ reaches temperature T_1 and ends when $^J T_x$ reaches temperature T_3 . The C₄ grass growth window opens on the day when $^J T_x$ reaches temperature T_2 and closes on the day when $^J T_x$ reaches temperature T_4 . Initial temperature limits are from Monson and Williams (1982).

The temperature limits for the C₃ and C₄ growth windows (Fig. 2) were selected using data from Monson and Williams (1982) obtained at the CPER. Initial sensitivity tests on data from the International Biological Programme (IBP) sites (Table 2) indicated that T_1 (for C₃ grasses) and T_4 (for C₄ grasses) explained most of the variation in C₃G. The initial value of T_1 from the CPER was too low for northern sites (Bison and Bridger sites in Table 2). It is reasonable to assume that C₃ grasses adapted to cooler areas would begin growth earlier to take advantage of available

water from spring rains and snow melt. Therefore, T_1 is calculated for each location (Table 1), so that C₃ growth would begin with frost-free conditions ($^J T_n \geq -1^\circ\text{C}$, where $^J T_n$ is the 30-day running mean of minimum temperature on day J) and with sufficiently warm day-time temperatures ($^J T_x \geq -10^\circ\text{C}$). Similarly, the initial value for T_4 from CPER was too low for the more southern locations (Table 2). Therefore, T_4 is calculated for each location using a linear regression with mean annual temperature from the IBP sites (Table 1). With these adjustments to T_1

Table 1
SAW algorithm parameters for current climate and elevated CO₂ scenarios

Parameter	Current climate		Elevated CO ₂	
	C ₃	C ₄	C ₃	C ₄
Temperature coefficient function ($^J k_{C_p}$) ^a	T&J	T&J	R et al.	T&J
Temperature optimum (T_o , °C)	20	35	24	35
Temperature maximum (T_z , °C)	38	46	46	46
Maximum photosynthetic rate (A_p , $\mu\text{mol m}^{-2} \text{s}^{-1}$)	25	33	30	33
Maximum conductance (g_p , $\text{mmol m}^{-2} \text{s}^{-1}$)	270	75	243	68
C ₃ growth start (T_1 , °C) ^b	$^J T_x$ when $^J T_x \geq 10^\circ\text{C}$ and $^J T_n \geq -1^\circ\text{C}$			
C ₄ growth start (T_2 , °C)	21	21	21	21
C ₃ growth end (T_3 , °C)	24	24	26	26
C ₄ growth end (T_4 , °C) ^c	$\max\{1.745T_{\text{annual}} + 11.143, 27^\circ\text{C}\}$			

^a T&J: Thornley and Johnson (1990); R et al.: Rastetter et al. (1991). Temperatures were rounded to nearest °C.

^b $^J T_x$ and $^J T_n$ are the 30-day running means of daily maximum and minimum temperatures.

^c T_{annual} is the mean annual temperature, and $\max\{x, y\}$ is the maximum of two terms x and y .

Table 2
SAW algorithm performance after parameterization at the IBP sites^a

Site	Location		T1	T4	Observed C ₃ G	Predicted C ₃ G
	Latitude	Longitude				
Bridger, MT	46	–111	14	25	1.00	1.00
Dickinson, ND	47	–103	17	27	0.80	0.81
Bison, MT	47	–114	10	27	1.00	1.00
Cottonwood, SD	44	–102	19	27	0.80	0.86
CPER, CO	41	–105	12	28	0.10	0.04
Hays, KS	39	–99	15	33	0.00	0.00
ALE, WA	46	–120	10	33	1.00	0.83
Konza, KS	39	–97	10	35	0.10	0.23
Pantex, TX	35	–102	17	36	0.10	0.00
Jornada, NM	33	–107	19	37	0.00	0.00
Osage, OK	37	–97	14	38	0.00	0.00

^a IBP: International Biological Programme.

and T4 only, the predicted C₃G was reasonably close to observed C₃G at the 11 IBP sites (Table 2), using daily climate data from the single year, 1970.

2.3. Estimating the relative biomass

For a unit area of grassland, the fraction of C₃ biomass (C₃G) is defined as the biomass of C₃ photosynthetic grasses (M_{C_3}) divided by the total biomass of both C₃ and C₄ grasses (M_{C_4}) or $C_3G = M_{C_3}/(M_{C_3} + M_{C_4})$. M_{C_3} and M_{C_4} are indirectly related to the sum of net primary production (kg C m^{-2} per year), so they were estimated as $M_{C_n} = \text{WUE}_{C_n} \times E_{C_n}$, where the subscript n is 3 for C₃ photosynthesis and 4 for C₄ photosynthesis, E_{C_n} is the water transpired ($\text{mol H}_2\text{O m}^{-2}$ per year), and WUE_{C_n} is the annual average WUE. Substituting these expressions into the definition for C₃G yields

$$C_3G = \frac{\text{WUE}_{C_3} \times E_{C_3}}{(\text{WUE}_{C_3} \times E_{C_3}) + (\text{WUE}_{C_4} \times E_{C_4})} \quad (1)$$

which ignores any seasonal changes. Rearranging the right-hand side of Eq. (1) yields $C_3G = 1/[1 + (\text{WUE}_{C_4}/\text{WUE}_{C_3}) \times (E_{C_4}/E_{C_3})]$ which suggests that C₃G should be relatively insensitive to absolute estimation errors in WUE_{C_3} , E_{C_3} , WUE_{C_4} or E_{C_4} as long as the $\text{WUE}_{C_4}/\text{WUE}_{C_3}$ and E_{C_4}/E_{C_3} ratios are correct. This limits the impact of any oversimplification in the algorithms that are used to estimate photosynthesis or stomatal conductance (see

below and Appendix A). The daily amount of water transpired is assumed to be proportional to the daily water available, ^JWat ($\text{mm H}_2\text{O}$), because evaporation losses are small with canopy closure. Because WUE varies day to day depending on temperature and humidity, Eq. (1) is converted to the sum of daily values:

$$C_3G = \frac{\sum_{C_3} (^J\text{WUE}_{C_3} \times ^J\text{Wat})}{\sum_{C_3} (^J\text{WUE}_{C_3} \times ^J\text{Wat}) + \sum_{C_4} (^J\text{WUE}_{C_4} \times ^J\text{Wat})} \quad (2)$$

where J is the day of the year, \sum_{C_3} is the summation over the C₃ growth window (T1–T3, Fig. 2), and \sum_{C_4} is the summation over the C₄ growth window (T2–T4, Fig. 2).

There are many detailed and rigorous models of ecosystem processes to estimate C₃ and C₄ productivity and WUE (e.g. Hunt et al., 1996; Svirezhev, 1999; Roelandt, 2001). However, detailed models describe processes not included in our hypothesis and require parameters and initial conditions that are difficult or impossible to obtain at regional and global scales. Estimation of these input data inevitably leads to ambiguity in evaluating the results. In addition, since the SAW algorithm is designed to be more sensitive to changes in the ratio of C₃ to C₄ WUE rather than the absolute values, a simple algorithm that adequately estimates this ratio from temperature alone should suffice (Fig. 3). Consequently, to examine our hypothesis, we used simplified algorithms that adequately de-

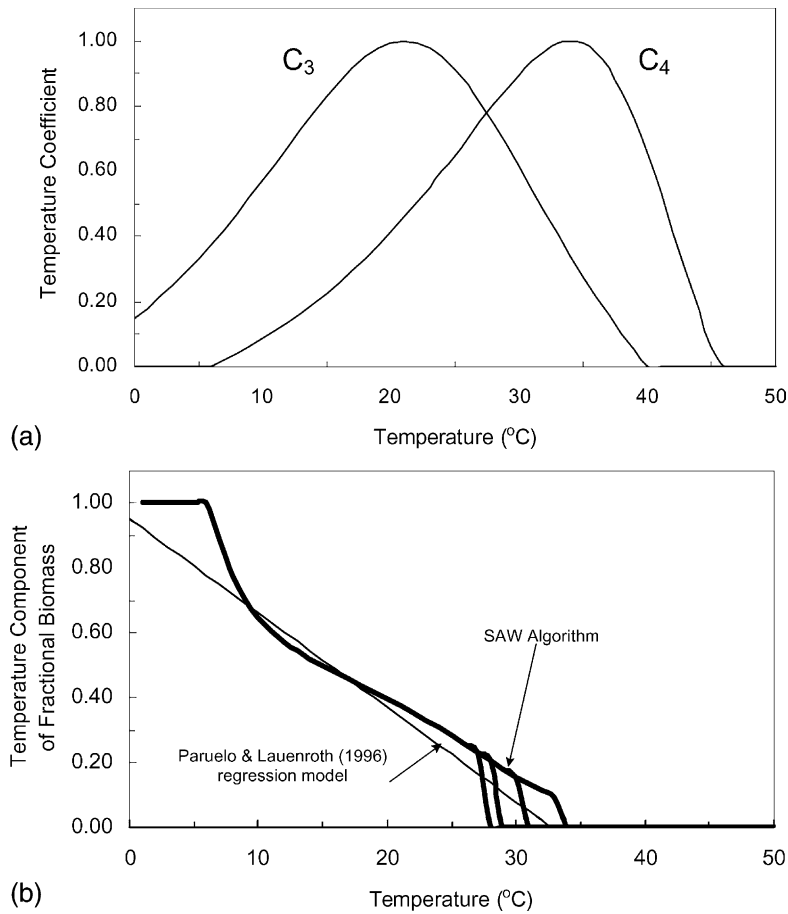


Fig. 3. (a) C₃ and C₄ photosynthesis temperature coefficient and (b) fractional biomass of C₃ grass (C₃G[T]) as estimated by the temperature only component of the SAW algorithm (thick lines) compared with the Paruelo and Lauenroth (1996) regression model (thin line). The temperature coefficient represents the portion of the maximum average rate of photosynthesis that each grass reaches at a given temperature (Thornley and Johnson, 1990). The temperature components of the SAW algorithm $C_3G[T] = WUE_3[T]/(WUE_3[T] + WUE_4[T])$, where WUE₃ is the C₃ WUE and WUE₄ is the C₄ WUE and the Paruelo and Lauenroth model $C_3G[T] = 1.1905 - 0.02909T - 0.2383Biome$, where Biome = 1.0 for grasslands) reflect typical grassland conditions where the total water transpired is independent of temperature (all water will be used in a water limited environment). Both algorithms produced similar responses to temperature under these conditions. The SAW algorithm stops photosynthesis at high vapor pressure deficits (determined from daily dew point temperature) yielding the four thick lines descending to zero from the main curve at about 30 °C. From left to right, the lines indicate dew point temperatures of 5, 10, 15, and 20 °C respectively.

fine the growing seasons (Fig. 3; T₁–T₃ for C₃ and T₂–T₄ for C₄) plus estimate water availability and capture the seasonal variability of the ratios of C₃ to C₄ WUEs (Appendix A) without requiring unavailable data. Although we fully recognize their importance and probable influence on C₃G, other processes, such as herbivory, burning and nitrogen utilization, are not included since they were not integral to the hypothesis.

2.4. Sensitivity analysis

As a preliminary test of the SAW algorithm, a sensitivity analysis was performed on data from the IBP sites using different values of the algorithm parameters. The most important parameters for prediction of C₃G were T₁, T₂, T₃, and T₄, emphasizing that, in the algorithm, the growing-season temperature limits for C₃ and C₄ grasses were generally more important than

photosynthetic responses to temperature. However, at the limits, setting $T1$ earlier or $T4$ later in the year had little effect on C_3G because $JWUE_{C_n}$ was limited by cold air temperatures. As expected, C_3G was insensitive to absolute changes of C_3 and C_4 photosynthetic rates and stomatal conductances, as long as the C_3/C_4 ratios of either remained the same.

2.5. Global assessment of the SAW hypothesis

To evaluate our primary hypothesis, the SAW algorithm was applied globally using a gridded climate data set for 1983–1996. C_3G was calculated for each year, then the average predicted C_3G was calculated from an average of the 14 annual values. Estimations of C_3G were then compared to existing vegetation surveys.

A proper quantitative evaluation of the SAW algorithm requires daily climate at the vegetation study site covering the time period immediately preceding the survey. Although necessary for a global study, gridded climate contains average values for the entire cell that may, or may not, reflect the microclimate at the survey location. In addition, the actual dates of collection are not mentioned in most of the vegetation surveys. Consequently, the reported C_3G at the study sites should not be assumed to be in equilibrium with the climate data used for evaluation (Kirilenko et al., 2000). Despite these difficulties, a quantitative evaluation was attempted and extra effort was devoted to clarifying the resulting uncertainties. The timing difference between the surveys and climate data was addressed by assuming that C_3G changes slowly. Then, if the SAW hypothesis is generally reasonable and correct, its average prediction should be close to the surveyed values. Therefore, the 14-year average C_3G prediction was used rather than the more volatile annual numbers. Annual predictions were examined, however, and their variation explored. Problems associated with comparison between large-grid-cell-based predictions and point survey data were addressed directly in the analysis (see Section 3.1).

2.6. Global, gridded, climate data set

The climate data set was compiled using the same methodology as Piper and Stewart (1996). It con-

sisted of daily minimum and maximum temperature ($^{\circ}C$), and daily precipitation (mm H_2O) for the years 1983–1996 on $1^{\circ} \times 1^{\circ}$ of latitude–longitude grid. Grid cell elevations were obtained from the ETOPO5 data set (spatial resolution of 5 arcmin) and weighted by area onto the $1^{\circ} \times 1^{\circ}$ grid (Hunt et al., 1996). Temperatures for data-sparse, mountainous areas were interpolated from temperatures at low-elevation stations and adjusted for elevation (Piper and Stewart, 1996).

2.7. Vegetation surveys

Vegetation surveys available for North America (Paruelo and Lauenroth, 1996), Argentina (Paruelo et al., 1998), Australia (Hattersley, 1983), South Africa (Vogel et al., 1978), Kenya (Tieszen et al., 1979), and Egypt (Batanouny et al., 1988) were assembled to obtain observed C_3G at 152 locations. Only the surveys related by Paruelo and Lauenroth (1996) and Paruelo et al. (1998) were of relative abundance of biomass. The other surveys were of relative abundance of species, and were included because the importance of having global coverage outweighed errors caused by equating abundance of species with biomass. Some data points were eliminated, because the grass cover was less than 5%, yielding a total of 141 points used in model assessment.

2.8. Comparison statistics

To compare surveyed data with the SAW algorithm predictions, goodness-of-fit (R^2) was calculated from $R^2 = 1 - \sum (y - y_{pre})^2 / \sum (y - y_{mean})^2$, where y is the observed value, y_{pre} is the predicted value of C_3G at a particular location (Mayer and Butler, 1993), and y_{mean} is the mean C_3G for all data used. The mean absolute error (MAE) was calculated from $MAE = \sum \text{abs}(y - y_{pre}) / n$, where n is the number of points and abs is the absolute value (Mayer and Butler, 1993). Other analyses were categorical, C_3G from 0.00 to 0.10 were assumed to be equivalent to all C_4 vegetation and C_3G from 0.91 to 1.00 were assumed to be equivalent to all C_3 vegetation. The mixed C_3/C_4 categories are 0.11–0.30 (20%), 0.31–0.50 (40%), 0.51–0.70 (60%), and 0.71–0.90 (80%).

2.9. Assessment of the SAW hypothesis by comparison with the Collatz model

When examined as biogeographical limits, the growth windows set by T_1 , T_2 , T_3 , and T_4 produced a three region pattern of all C_3 , all C_4 , and mixed C_3/C_4 , that is, at first glance, similar to Collatz et al. (1998). The similarity warranted a closer look at the SAW algorithm relative to the Collatz model and their predictions were compared, grid cell by grid cell. Since the Collatz et al. logic was designed for monthly climate, monthly averages were generated from the daily values in the 1983–1996 gridded climate data set (Table 5). Only the 6034 grid cells classified specifically as grassland (including tundra and agriculture; Hunt et al., 1996) were used.

2.10. Assessing implications of the SAW hypothesis to climate change research

General Climate Models (GCMs) predict that expected doubling of atmospheric CO_2 will cause increases in the global average temperature along with changes in both the temporal and spatial variation of temperature and precipitation (Keeling et al., 1989; Gates, 1993). By design, the SAW algorithm is sensitive to changes in the temporal and spatial variation of temperature and precipitation allowing examination of their interaction with the changes in plant physiology. C_4 grasses may benefit from increased temperatures compared to C_3 grasses (Long, 1991; Chen et al., 1996; Drake et al., 1996). However, C_3 grasses should benefit more from elevated atmospheric CO_2 concentrations than C_4 grasses (Long, 1991, 1999; Eamus, 1991; Drake et al., 1996; Ehleringer et al., 1997; Wand et al., 1999). These physiological responses are incorporated into the SAW algorithm with simple parameter changes (Appendix A).

2.11. Climate change simulations

To assess the implications of the SAW hypothesis to climate change studies, three simulations were performed on data from the conterminous USA. To establish a basis for comparison, the SAW algorithm was applied, without parameter modifications, to the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP) mean historical daily climate data (Kittel

et al., 1995). Then, to examine responses to temperature and precipitation changes alone, the SAW algorithm was applied, again without change, to the Canadian Climate Centre—Global Climate Model (CCC-GCM; Kittel et al., 1995). This scenario, consisting of predicted monthly deviations from the historical data, was recommended to us (T.G.F. Kittel, personal communication) as the most current on the VEMAP Phase I CD-ROM (Kittel et al., 1996).

The WUE portions of the SAW algorithm were then parameterized to include the effects of doubled atmospheric CO_2 (Appendix A) as suggested by Long (1991). Thus modified, the SAW algorithm was applied to the CCC-GCM scenario to examine the interactions between climate and the CO_2 altered water use efficiency. Applying these parameters placed the C_3 photosynthetic optimum temperature slightly outside of the C_3 growth window. Although not mentioned by Long (1991), it is likely that C_3 grasses would adapt their growing season to account for their altered photosynthetic character under increased atmospheric CO_2 concentrations. Therefore, for these simulations, the C_3 growth window temperature limit, T_3 , was increased beyond the new C_3 photosynthetic optimum temperature (Table 1).

3. Results

3.1. Results of global assessment

The 14-year average global distribution of C_3G estimated by the SAW algorithm was qualitatively similar to the pattern produced by surveys from around the world (Fig. 4). All C_3 grass was predicted to occur at high latitudes and altitudes, and all C_4 grass was predicted to occur in the tropics, even though the SAW algorithm was developed for temperate regions. Going from warm to cooler regions, there is gradual transition from C_4 to C_3 grasses (Fig. 4). The C_4/C_3 grass crossover latitude in the North American Great Plains was approximately 42–43°N (yellow to green in Fig. 4) which is in good agreement with the observed 43–45°N observed (Epstein et al., 1997; Tieszen et al., 1997) and the 45°N predicted by Ehleringer et al. (1997) from quantum yields.

Classification of predicted and observed C_3G into three categories, all C_3 , all C_4 and mixed C_3/C_4

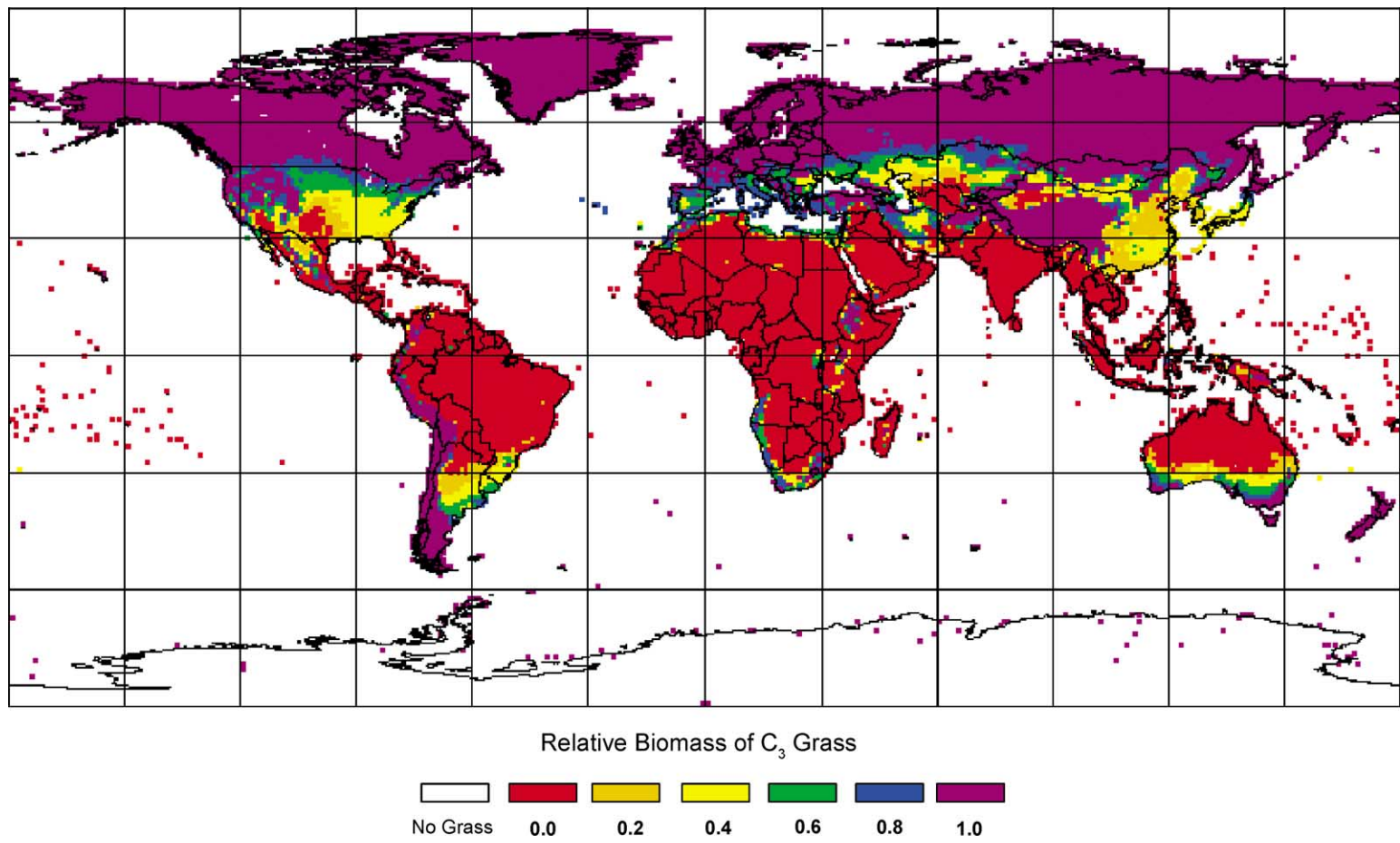


Fig. 4. The fractional biomass of C₃ grasses (C₃G) for the world predicted by the SAW algorithm. The values are the average C₃G from 14 years of daily climate data (1983–1996).

Table 3
Error matrix from classification of SAW algorithm predicted C₃G^a

Observed	Prediction (from the 1983–1996 average C ₃ G)		
	All C ₃	Mixed C ₃ /C ₄	All C ₄
All C ₃	26	7	0
Mixed C ₃ /C ₄	6	61	7
All C ₄	0	11	12

^a Includes the 1° latitude × 1° longitude grid cells with at least one point of observed data. Grid cells with multiple observed points were used once.

resulted in overall accuracy of 76% (Table 3). Observed all C₃ and mixed regions were predicted with greater than the overall accuracy (79 and 82%, respectively; Table 3). Observed all C₄ areas were predicted to be mixed about half the time. However, the majority of the incorrectly classified points were in New Mexico and Arizona, USA. Both of these areas have temperature and precipitation patterns that should allow for some growth of C₃ grasses in the spring and suggested another parameter may be necessary to limit C₃ grasses in hot, arid regions.

The SAW algorithm predicted the surveyed values within 0.2 at most locations (Fig. 5). Quantitative comparison of the SAW algorithm predicted C₃G versus surveyed data resulted in an overall $R^2 = 0.71$. Although an indicator of general performance, this number is misleading because of the large number of

observed and predicted values in the all C₃ and all C₄ regions. Comparison in the mixed C₃/C₄ regions alone resulted in an $R^2 = 0.5$ which is similar to results from the Paruelo and Lauenroth (1996) regression model. At low observed C₃G, only five points of the 74 introduced most of the error. When they were removed from the analysis, the SAW algorithm produced an R^2 of 0.54, with an MAE of 0.19 for the mixed regions.

There was no bias revealed for the different areas of the world, including Australia, Egypt, Kenya, and South Africa (Fig. 5). Consequently, there was little difference in errors between predicted C₃G and data based on measured biomass or data based on species abundances. However, lack of bias does not indicate that species abundances are good estimators of relative C₃ and C₄ biomass.

The spatial resolution of the climate data (about 110 km at the Equator) is coarse when compared to each survey point. Consequently, there were three 1° × 1° grid cells that contained several survey points (Table 4). The mean absolute difference between the points and their mean is about 0.08 (Table 4), which is a large fraction of the MAE (0.19). Therefore, some of the disagreement between the predictions and the survey data are not the result of errors in the SAW algorithm, but rather result from the multitude of habitats averaged together in a single grid cell.

Climate varied considerably over the 1983–1996 period with some years reflecting influences from El

Table 4
Variation in surveyed point data within three mixed C₃/C₄ grid cells^a

Cell	Location				Elevation (m)		C ₃ G		
	Site		Grid		Site	Grid	Observed	Mean	Predicted
	Latitude	Longitude	Latitude	Longitude					
1	45.82	−106.48	45.5	−106.5	896	1098	0.81	0.87	0.64
	45.87	−106.48			939	0.97			
	45.88	−106.47			945	0.80			
	45.85	−106.37			945	0.92			
2	−36.00	−63.80	−36.5	−63.5	120	120	0.93	0.79	0.42
	−36.00	−63.80			0.84				
	−36.00	−63.80			0.91				
	−36.50	−63.00			0.49				
3	−38.00	−65.50	−38.5	−65.5	220	183	0.90	0.95	0.50
	−38.50	−65.00			0.94				
	−38.50	−65.00			1.00				

^a Grid cells are 1° latitude × 1° longitude.

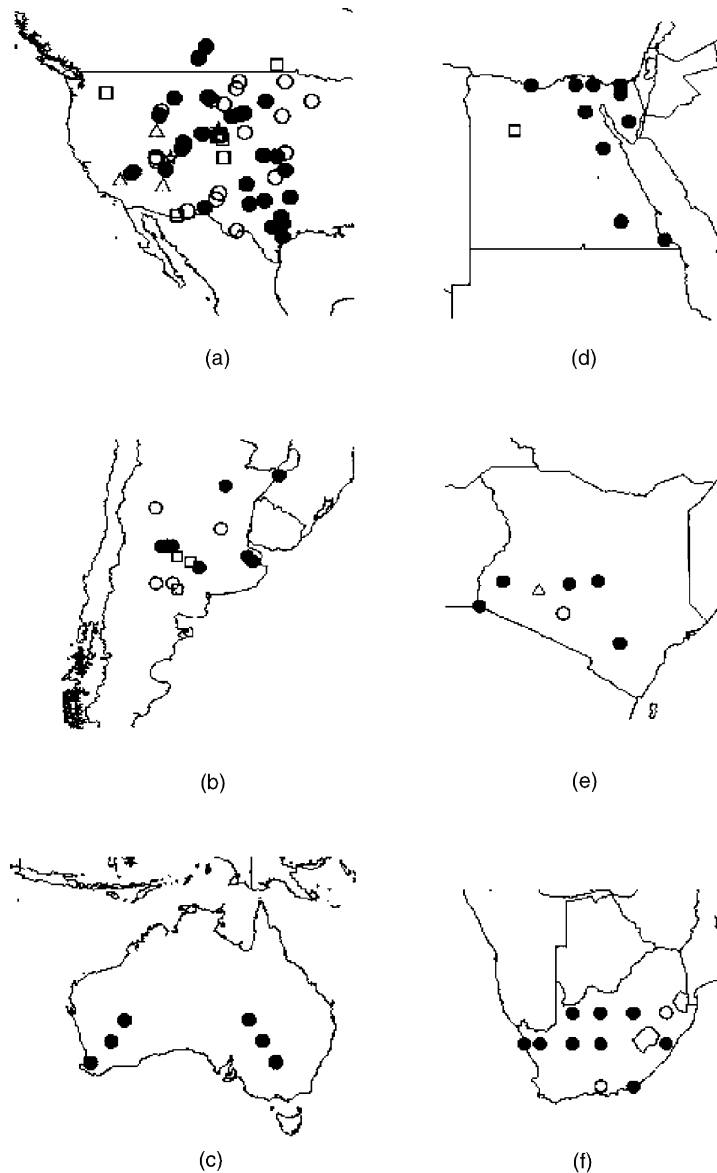


Fig. 5. SAW algorithm predictions vs. surveyed values of the fractional biomass of C₃ grasses (C₃G) in (a) North America, (b) Argentina, (c) Australia, (d) Egypt, (e) Kenya, and (f) South Africa. Symbols indicate the absolute value of the difference between observed and predicted C₃G at the point: (●) 0.0–0.20; (○) 0.21–0.40; (□) 0.41–0.60; (△) 0.61–0.80; (☆) 0.81–1.00.

Niño, La Niña, volcanic eruptions (Mount Pinatubo), or record-breaking temperatures. On average, climate variation affected predicted C₃G as shown by the year-to-year differences in MAE (Fig. 6). Climatic variability also affected the classification into all C₃, all C₄, and mixed C₃/C₄ categories. The years with the high-

est MAE (1985, 1992, 1995, and 1996) (Fig. 6), had the lowest overall accuracy of classification and the years with the lowest MAE (1988 and 1989; Fig. 6), had the highest overall accuracy (data not shown).

Interannual variation in C₃G was greater for individual grid cells (Fig. 7). For example, in Montana, USA,

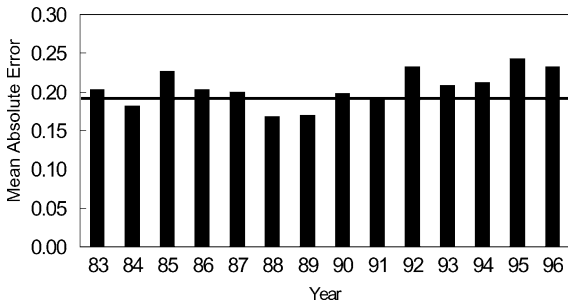


Fig. 6. Annual variation of the mean absolute error (MAE) between predicted and observed C₃G for the grid cells containing the 141 survey points. The solid horizontal line indicates the average MAE for the period from 1983 to 1996.

the predicted C₃G varied from <5% for an extremely dry year to 100% for two cool years (Fig. 7). However, in Texas and Kansas, USA, the weather for many years would suggest these areas could be all C₄ vegetation, yet in 1995 for Texas, C₃G was 99% (Fig. 7). Thus, the global reasonableness of SAW hypothesis predictions was the direct result of having multiple years worth of gridded climate data from which to obtain an average.

A plot of the errors in predicted C₃G error versus elevation revealed a systematic bias. C₃G was overestimated at high elevations and underestimated at low elevations (Fig. 8). This was, in part, an artifact of gridding low-elevation weather station data to high-elevation grid cells by applying a single lapse rate

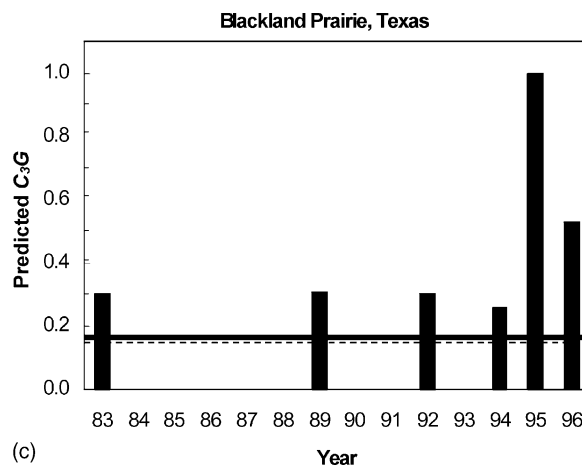
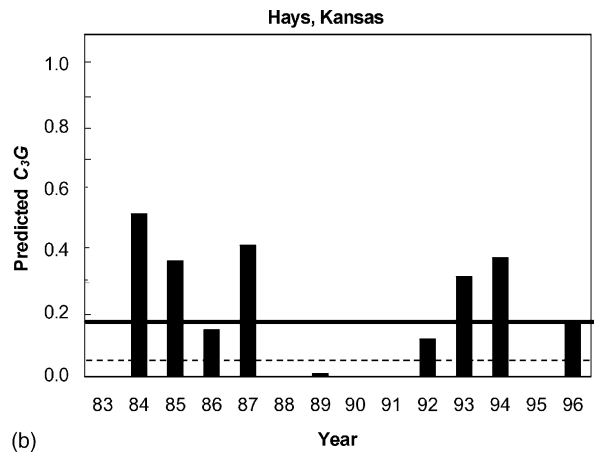
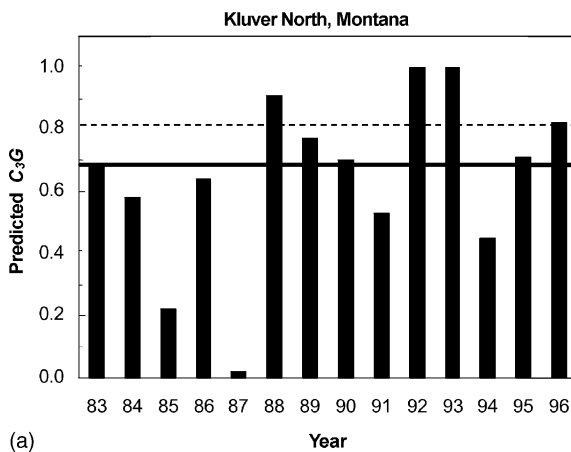


Fig. 7. SAW algorithm predicted fractional biomass of C₃ grasses (C₃G) vs. year showing the variation over 14 years at: (a) Kluver North, Montana; (b) Hays, Kansas; and (c) Blackland Prairie, Texas. Solid lines show the average predicted C₃G and the dashed lines show the observed C₃G for each site.

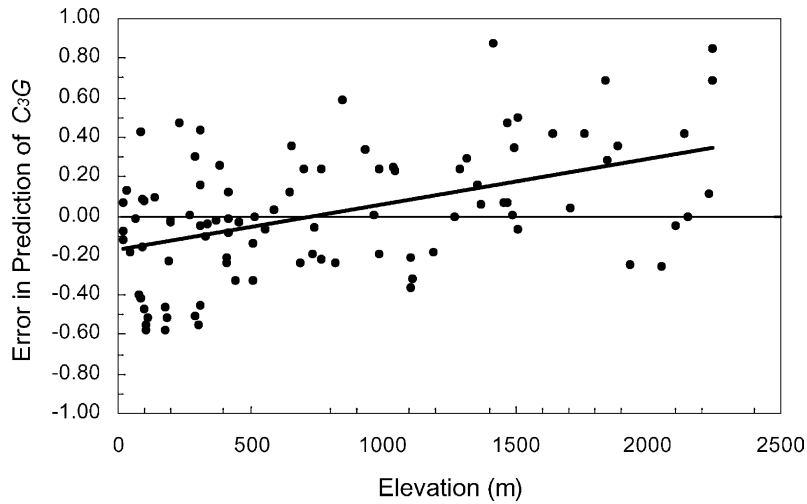


Fig. 8. Error of SAW algorithm predicted fractional biomass of C_3 grasses (C_3G) vs. elevation. The under-estimation of C_3G at low elevations may be caused by errors in the station meteorological data. Over-estimation at higher elevations may come from applying a single lapse rate of temperature with elevation to extrapolate low-elevation weather observations to data-sparse, high altitude regions or from overestimation of soil water capacity in mountainous areas.

of temperature with elevation. Since the majority of the low-elevation points with the greatest error in Fig. 8 are from an area in Argentina identified with station data that was about 3°C too high (Piper and Stewart, 1996), error could also result from these warmer temperatures forcing an under-prediction of C_3G by the SAW algorithm. Soil moisture is strongly related to the variation of observed C_3G with elevation (Tieszen et al., 1979) suggesting another possible cause of the bias. The SAW algorithm assumes soil water storage is 150 mm at all locations (see Appendix A). However, it is likely that less water would be stored at higher elevations, since there is usually less soil. Since

high-elevation temperatures favor C_3 grass, use of the 150 mm value would result in an over-prediction of C_3G .

3.2. Results from comparison between the SAW hypothesis and the Collatz model

When C_3G values between 0.11 and 0.9 were combined into one mixed class, the overall similarity between the SAW hypothesis and the Collatz et al. (1998) model was 82% (Table 5). Most of the similarity came from the SAW algorithm $T_2 = 21^\circ\text{C}$ being close to the 22°C Collatz et al. (1998) crossover temperature

Table 5
Comparison of Collatz et al. (1998) and the SAW algorithm predictions^a

Collatz et al. category	SAW algorithm C_3G ^b					All C_3 (0.91–1.00)
	All C_4 (0.00–0.10)	Mixed C_3/C_4				
		0.10–0.30	0.31–0.50	0.51–0.70	0.71–0.90	
All C_4	1168	10	19	17	6	2
Mixed C_3/C_4	561	249	332	291	189	38
All C_3	34	8	23	98	254	2735

^a Fourteen years of $1^\circ \times 1^\circ$ climate data (Piper and Stewart, 1996) were used for both models.

^b Numbers in boldface indicate agreement between the SAW algorithm and the Collatz model. A total of 6034 grid cells were examined; with 4964 showing agreement and 1070 showing disagreement. Since, at the equator, each grid cell is approximately $12,000\text{ km}^2$, the total area of disagreement is 12–13 million km^2 .

for quantum yields of photosynthesis. In the SAW algorithm, when JTx is always less than 21 °C, the C₄ growth window would never open resulting in an all C₃ grass prediction (Fig. 2). In addition, C₃ grasses should not be present when JTx is always greater than the 21 °C required for the opening of the C₄ growth window (T_2 , Fig. 2). Without a cooler period before the opening of the C₄ window, C₃ grasses would be

forced into continuous competition with C₄ grasses, favored by the warmer temperatures, resulting in low values of predicted C₃G. It is not known why the start of the C₄ growing season should coincide with the quantum yield crossover temperature.

The apparent similarity could obscure important differences between the SAW hypothesis and the Collatz model. First, the SAW algorithm resolved the mixed

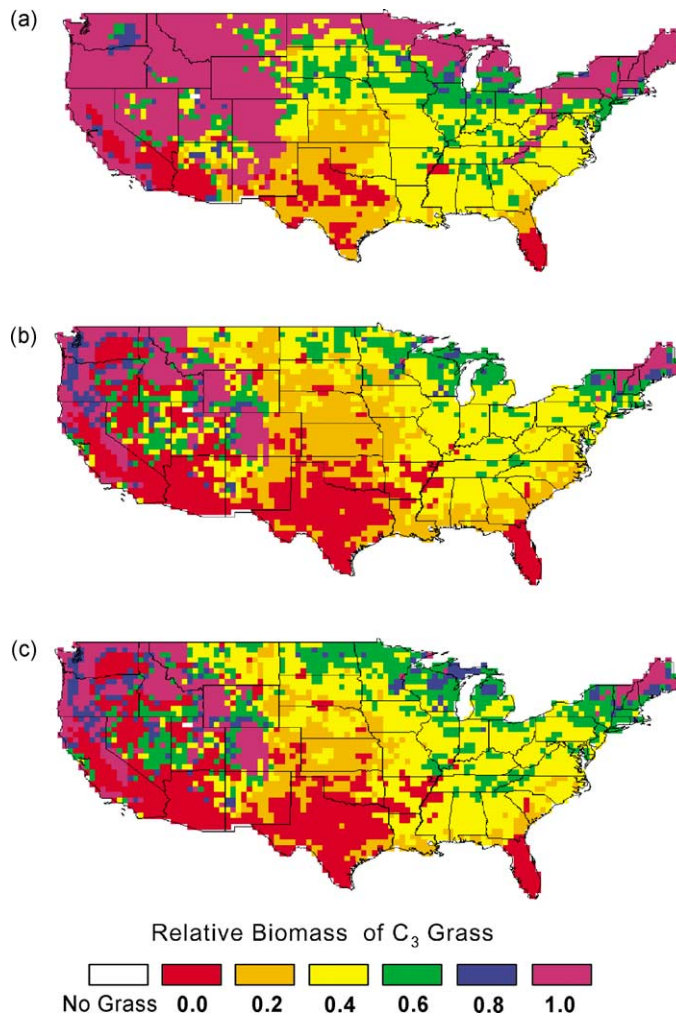


Fig. 9. Effects of climate change on the C₃/C₄ grass biomass distribution in the United States predicted by the SAW hypothesis. The top panel (a) shows predictions of the fractional biomass of C₃ grasses (C₃G) from the VEMAP historical climate data (Kittel et al., 1995). The middle panel (b) shows SAW algorithm C₃G estimates produced for the climatic change scenario from the Canadian Climate Centre—General Climate Model. This simulation reflects changed climate as differences in precipitation and temperature patterns alone and no adjustment was made to the water use efficiencies in the SAW algorithm in response to elevated CO₂. The bottom panel (c) shows estimates of C₃G for the changed climate scenario after the water use efficiencies in the SAW algorithm were increased to account for doubled CO₂ (Table 1).

areas into a continuous value of C_3G for use in global carbon models; the Collatz et al. model could not. Second, the two algorithms differed at 1070 grid cells covering an area of approximately 12–13 million km² (Table 5). Since the temperature limits were similar, most of the differences would come from variation in water availability.

3.3. Results of climate change simulations

In the first climate change simulation with the SAW algorithm applied to the VEMAP historical climate data, observed values (Parelo and Lauenroth, 1996) showed an agreement with predicted C_3G (Fig. 9a) that was similar to that achieved with the global 1983–1996 climatic data (Fig. 4). MAE and R^2 (results not shown) were approximately the same.

Under the CCC-GCM climatic change scenario, the SAW algorithm parameterized for no CO₂ increase, predicted C_3G to strongly decrease in three major areas (Fig. 9b). In the eastern USA and the central Great Plains, increases in air temperatures caused decreased C_3G . In the western USA, decreases in wintertime moisture storage reduced the water availability to C_3 grasses (Fig. 9b).

The third simulation, with the SAW algorithm parameterized for doubled CO₂, showed that increases in the C_3 WUE partially mitigated the predicted reduction in C_3 grasses in the eastern USA and central Great Plains (Fig. 9c). However, there was still an overall decrease in predicted C_3G compared to Fig. 9a. There was no mitigation by elevated CO₂ in the western USA (Fig. 9c) where reduced water availability stymied any possible gains from increased WUE.

Global Climate Model predictions of climatic change under doubled atmospheric CO₂ vary, and only one possible scenario was used. In addition, the SAW algorithm is intentionally simplified to test specific hypotheses. Consequently, these simulations should not be considered rigorous predictions of future C_3/C_4 distributions, but rather point to how changes in temperature and precipitation patterns can impact the global distribution of C_3G .

4. Conclusions

This study examined the SAW hypothesis which stated that the relative C_3/C_4 grassland biomass in

an area results from the partitioning of available water by the preferred growing seasons of C_3 versus C_4 grasses. We did not directly test this hypothesis, but examined the reasonableness of its predictions compared to the vegetation surveys. Despite uncertainties introduced by using gridded climate data and existing vegetation point surveys, comparison of the vegetation studies with the 14-year average C_3G predicted by the SAW algorithm shows significant agreement and gives a reasonable, global representation of average algorithm performance.

The substantial interannual variation in predicted C_3G raises several interesting questions. How fast does C_3G change and how many years of climate should be considered when applying the SAW algorithm to cause a turnover in photosynthetic type? Does the distribution of annual grasses follow an annual pattern estimated by the SAW algorithm, while the distribution of perennials changes more slowly over multiple years? To answer these questions and improve the accuracy of future analysis, further survey data, gathered with climate change in mind, is needed. In this case, data on the year-to-year variation of biomass contributed by each photosynthetic pathway along with detailed weather information collected at the same location will be more useful than simply the addition of more sites.

The simplified SAW algorithms were useful in examining the specifics of the SAW hypothesis. Their simplicity reduced unplanned interactions among the algorithm logic, initial conditions, and driving climatic data. The SAW algorithm components, designed to react to differences in the ratio of C_3 and C_4 WUE rather than the absolute values, permitted focus to be placed on the broader functioning of the SAW hypothesis rather than details of the WUE calculation. The sensitivity analysis combined with global simulations suggested that temperatures delineating the beginning and end of the C_3 and C_4 growing seasons (T_1 , T_2 , T_3 and T_4) were the most important input parameters for the prediction of C_3G . More work on T_1 and T_4 is necessary to understand their variation with climate and/or latitude and to identify reasons for apparent over-prediction of C_3 grasses in the warmer areas.

Improved predictions of C_3G might be made with a complex ecosystem process model that attempts complete, rigorous representations of inter-plant competition for light and other resources, photosynthesis, stomatal conductance, and a detailed hydrologic

budget. However, greater improvement might come by incorporating other, known influences to the distribution of C_3G . Ultimately, this is a data availability issue (Medlyn, 1999; Alexandrov et al., 2002). Influences like herbivory, burning timing and frequency, and possibly, soil type and moisture capacity (Bachelet et al., 1998, 2000; Collins et al., 1998; Riedo et al., 2000) could be incorporated into the SAW hypothesis, but their impact could not be evaluated until gridded global data sets of these variables are available. In addition, a more complete examination of the impacts of the climate change scenarios should include probable climate change-induced changes in T_1 , T_2 , T_3 , and T_4 which will only become possible when a more detailed record of C_3 and C_4 grassland phenology is available.

Comparison of the SAW algorithm with the Collatz et al. (1998) model revealed similarities in classification into the three broad categories (all C_3 , mixed, all C_4), but there were also significant differences in the relative areas covered. The similarities also mask fundamental differences in the hypothesized mechanisms underlying the two algorithms, quantum yield versus the relative efficiency in using seasonally available water. In addition, the SAW algorithm resolved the mixed class into a continuous value of C_3G for use in climate change/carbon cycling models and the Collatz model did not. A modification to the original Collatz approach using a ratio of months favoring C_3 to months favoring C_4 has been tried in order to produce a continuous value of C_3G in the mixed areas (P.E. Thornton, personal communication). Although this approach provides a continuous C_3G , and, on average, may produce an acceptable C_3G estimate, it assumes that only one grass grows at a time, and it does not account for the impact of precipitation amounts or the relative water use efficiencies during periods when the grasses grow simultaneously, and they do grow simultaneously (Dickinson and Dodd, 1976).

The relative advantages of the C_3 and C_4 photosynthetic pathways in response to elevated atmospheric CO_2 and climatic change are important questions for conservation of native plant communities and enhancement of agricultural production. Our exercise with one climate change scenario and a simple algorithm suggests the benefits of elevated CO_2 to C_3 photosynthesis may not be enough to offset the impacts of rising temperatures and changes in precipitation

patterns. For these simulations, we attempted to give the greatest reasonable advantage to C_3 grasses with elevated CO_2 to ameliorate the effects of increasing temperature. However, the effects of temperature in some areas and the effects of precipitation in other areas clearly dominated under the VEMAP scenario used.

Two other studies have examined this issue, at least in part, on smaller grassland areas. At a northern mixed-grass prairie site in Saskatchewan, Canada, Mitchell and Csillag (2000) used the CENTURY model (Parton et al., 1996) to investigate the impacts of different climate change scenarios. They found that simply increasing atmospheric CO_2 concentrations had little effect on C_3 grass productivity unless precipitation was increased as well. They also investigated the impacts of gradual warming over 200 years and found that its effects depended “partially on the seasonal timing of that warming, but mostly on the concurrent changes in moisture availability” (Mitchell and Csillag, 2000, p. 101). Another CENTURY-based model, ECOTONE (Peters, 2002), examined the interaction between three potentially-dominant species on a shortgrass steppe in New Mexico, USA by simulating recruitment, growth, and mortality processes of individual plants. Peters found that the temporal partitioning of soil water was important to the dominance of C_4 grasses.

Despite significant differences in design, both of these models produced results that agree with ours. In contrast to the SAW algorithm, which is designed to simulate C_3G specifically from the ratio of simplified WUE-based estimates of C_3 and C_4 grass productivity, CENTURY is a general grass productivity model that simulates the cycling of water and nutrients (carbon, nitrogen, phosphorous, etc.) through various levels, or pools, in the soil–plant–atmosphere continuum. Like the SAW algorithm, but on a monthly time step, CENTURY determines potential photosynthetic production as an empirical function of temperature. This production is then limited by moisture, nutrient availability, and shading. Somewhat more sophisticated, ECOTONE uses CENTURY for its grass productivity module but also includes a daily soil water availability module along with functions simulating seedling recruitment and mortality processes.

Since it explicitly includes nutrient availability and shading to limit production, CENTURY is more

generalized than the SAW algorithm. However, operating on a monthly time step with monthly average climate data, it cannot capture all of the variation in a precipitation-driven productivity pattern. Despite this, it pointed to the same result regarding C_3 versus C_4 productivity as the SAW algorithm did; that, when evaluated with realistic rainfall patterns, moisture availability controls the final grass production, even if nutrient availability and CO_2 fertilization of C_3 photosynthesis are included. It is not a surprising result when you consider that, under most conditions in a grassland, water is scarce and the number of real, good, growing days are limited. Therefore, although our large-area, generic grass simulations or these two small-area simulations certainly do not settle the issue of whether CO_2 fertilization will compensate for global warming, they do suggest some intriguing possibilities and underscore the importance of accurately representing the timing and spatial distribution as well as the magnitude of temperature and precipitation in scenarios of future climate.

Considering the uncertainty introduced by the variability of climate and observed data, the good performance of the SAW hypothesis indicates that a substantial portion, but not all, of the mechanisms responsible for the spatial distribution of C_3G were included. Therefore, this study is a positive step toward explaining how climate and grass physiology may interact to determine the spatial distribution of C_3 versus C_4 biomass in grasslands.

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Appendix A

A.1. Water use efficiency component of the SAW algorithm

On day J , the ${}^JWUE_{C_n}$ is estimated by dividing the average photosynthetic rate by the average rate of transpiration so that

$${}^JWUE_{C_n} = \frac{\xi A_{C_n} {}^Jk_{C_n}}{g_{C_n} {}^Jvpd P^{-1}} \quad (A.1)$$

where the temperature-dependent photosynthetic rate ($\xi A_{C_n} {}^Jk_{C_n}$) is estimated from ξ , a constant equal to 66.7×10^{-9} ($kg\ C\ \mu mol\ CO_2^{-1})(mol\ H_2O\ mm\ H_2O^{-1}$) for unit conversion, A_{C_n} , the average photosynthetic assimilation rate ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$), and ${}^Jk_{C_n}$, a dimensionless coefficient set by the day-time mean air temperature (Thornley and Johnson, 1990). This coefficient ranges from 0.0 to 1.0 and represents idealized photosynthesis as a function of temperature (see below). The transpiration ($g_{C_n} {}^Jvpd P^{-1}$) is estimated from g_{C_n} , the average leaf conductance ($mol\ H_2O\ m^{-2}\ s^{-1}$), Jvpd , the vapor pressure deficit (kPa) at the mean day-time air temperature, and P , the standard atmospheric pressure (kPa) based on elevation (Campbell and Norman, 1998). At large vapor pressure deficits (≥ 3.5 kPa for C_3 ; ≥ 5.0 kPa for C_4), ${}^Jk_{C_n}$ is set to 0 reflecting stomatal closure. Day-time mean air temperature (${}^JT_{day}$) is calculated as $T_{day} = 0.29 {}^JT_{min} + 0.71 {}^JT_{max}$, where ${}^JT_{max}$ and ${}^JT_{min}$ are the maximum and minimum air temperatures on day J (Larcher, 1995). ${}^JT_{min}$ approximates the dew-point temperature to calculate Jvpd (Winslow et al., 2001).

Initial parameters were selected from the literature. The resulting C_3G (Eq. (2)) was tested with climate data from 11 United States International Biological Programme (IBP) grassland sites (Table 2). Published values for A_{C_n} (Monson et al., 1986), g_{C_4} (Hunt et al., 1996), and T_z and T_0 (Larcher, 1995) required no modification (Table 1). On the other hand, the average value for C_3 leaf conductance, $g_{C_3} = 220\ mmol\ m^{-2}\ s^{-1}$ (Hunt et al., 1996), resulted in the C_3 grasses having an unrealistically high water use efficiency, so g_{C_3} was increased to $270\ mmol\ m^{-2}\ s^{-1}$ (Table 1).

For simulations under current concentrations of atmospheric CO_2 , ${}^Jk_{C_n}$ for both C_3 and C_4

photosynthesis was calculated as (after Thornley and Johnson, 1990):

$${}^J k_{C_n} = \frac{\alpha \exp(-a/{}^J T_{\text{day}})}{1 + \exp(b - c/{}^J T_{\text{day}}) + \exp(d - q/{}^J T_{\text{day}})} - \left(\frac{\beta}{m}\right) \exp\left(\frac{-h}{{}^J T_{\text{day}}}\right) - \delta \quad (\text{A.2})$$

Coefficients in Eq. (A.2) were modified to represent both photosynthetic pathways (Fig. 3). For C₃ photosynthesis, the coefficients α , a , b , c , d , q , β , m , h , and δ are 2.6×10^{11} , 7374.223, 9.834366, 2965.76, 62.36542, 18357.36, 4.1×10^{11} , 20, 8041.181, and 0.2, respectively. For C₄ photosynthesis they are 3.2×10^9 , 6516.996, 17.18914, 5610.352, 91.40048, 28467.45, 1.2×10^9 , 20, 6148.493, and 0.2, respectively.

For simulations under doubled atmospheric CO₂, stomatal conductances for both C₃ and C₄ grasses were reduced by 10% (Table 1). The average photosynthetic rate was increased 20% for C₃ grasses. The temperature response of C₃ photosynthesis was changed to match, as closely as possible, the curve produced by Long (1991), which shows an increase in C₃ photosynthetic rate at all temperatures, along with an increase to the photosynthetic temperature optimum. In this case, Eq. (A.2) did not give sufficiently high photosynthetic rates at lower temperatures. Instead, an equation from Rastetter et al. (1991) was used:

$${}^J k_{C_p} = \exp[a({}^J T_{\text{day}} - T_0)] \exp\left[a(T_z - T_0) \ln\left(\frac{T_z - {}^J T_{\text{day}}}{T_z - T_0}\right)\right] \quad (\text{A.3})$$

where T_z is the maximum temperature at which photosynthesis can occur (Table 1), T_0 is the optimum temperature at which photosynthetic rate is maximum (Table 1), and a is a constant equal to 0.22. To allow C₃ species to make maximum use of these changes, the C₃ growth window temperature limit, T_3 , was increased so that the new C₃ photosynthetic optimum temperature lies within the C₃ growing season (Table 1).

A.2. Available water component of the SAW algorithm

A simple soil water budget estimates the daily water available (${}^J \text{Wat}$, mm H₂O). Daily precipitation is classified as rain or snow by the mean air temperature

given by ${}^J T_{\text{mean}} = 0.5({}^J T_{\text{max}} + {}^J T_{\text{min}})$. One millimeter of daily rainfall is assumed to be intercepted and evaporated. Snow accumulates while ${}^J T_{\text{mean}} \leq 0^\circ\text{C}$ and melts when ${}^J T_{\text{mean}} > 0^\circ\text{C}$. Before the start of the C₃ growth window, rain and snowmelt are added to the water stored in the soil. Evaporation and sublimation remove water from the soil and snowpack, respectively (Winslow, 1999). The maximum soil storage is assumed to be 150.0 mm H₂O. Liquid water in excess of the maximum soil storage is removed as runoff. The soil water budget is initialized by first setting soil storage and snowpack to 0 and calculating the water budget over the wintertime to the start of the C₃ growth window. At the start of the C₃ growth window, ${}^J \text{Wat}$ is set to equal the stored soil water, which is used by the C₃ grasses. In most cases this amount is small, because in temperate grasslands, most of the precipitation falls during the growing season (Ripley, 1992). For each day thereafter, ${}^J \text{Wat}$ is only the net daily rainfall, if any.

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