Distribution of C_3 and C_4 Photosynthetic Pathways in Plants

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INTRODUCTION

Photosynthesis is the biochemical process by which every plant fixes carbon dioxide to form carbohydrates, and although the fundamental steps remain the same across all plants, slight tweaks have occurred throughout the history of the lineage to produce two main pathways, known as C_3 and C_4 photosynthesis. The main difference between the two lies in how carbon dioxide (CO_2) is incorporated into the photosynthetic pathway.

C_3 photosynthesis is textbook photosynthesis, where, in the leaf, ribulose 1,5-bisphosphate carboxylase-oxygenase (Rubisco) fixes carbon dioxide by combining it with Ribulose 1,5-bisphosphate (RuBP) to form two molecules of 3-phosphoglycerate (Jensen and Bahr 1977) (Figure 1). Rubisco also has the ability to act as an oxygenase, where, instead of using CO_2, it combines RuBP with O_2 to form one molecule of 3-phosphoglycerate and one of phosphoglycolate in a process known as photorespiration (Jensen and Bahr 1977) (Fig. 1). Phosphoglycolate can be toxic when given the chance to build up in the leaf, and conversion to metabolically useful molecules is costly (Ogren, 1984; Sage, 2004).

C_4 photosynthesis is theorized to have evolved because it reduces the amount of photorespiration that occurs (Sage 2004). Before being fixed by Rubisco, CO_2 is concentrated in a group of cells in the leaf called the bundle sheath. It is here that all CO_2 fixation by Rubisco takes place. This way, the plant is able to artificially keep CO_2 highly concentrated and greatly favor photosynthesis over photorespiration (Sage 2004). The process of CO_2 concentration does expend energy, so C_4 photosynthesis is favored over C_3 only when environmental conditions are such that the loss experienced during photorespiration outweighs the cost of concentrating CO_2 in the bundle sheath cells.

A number of environmental factors play into this relationship. The most obvious is

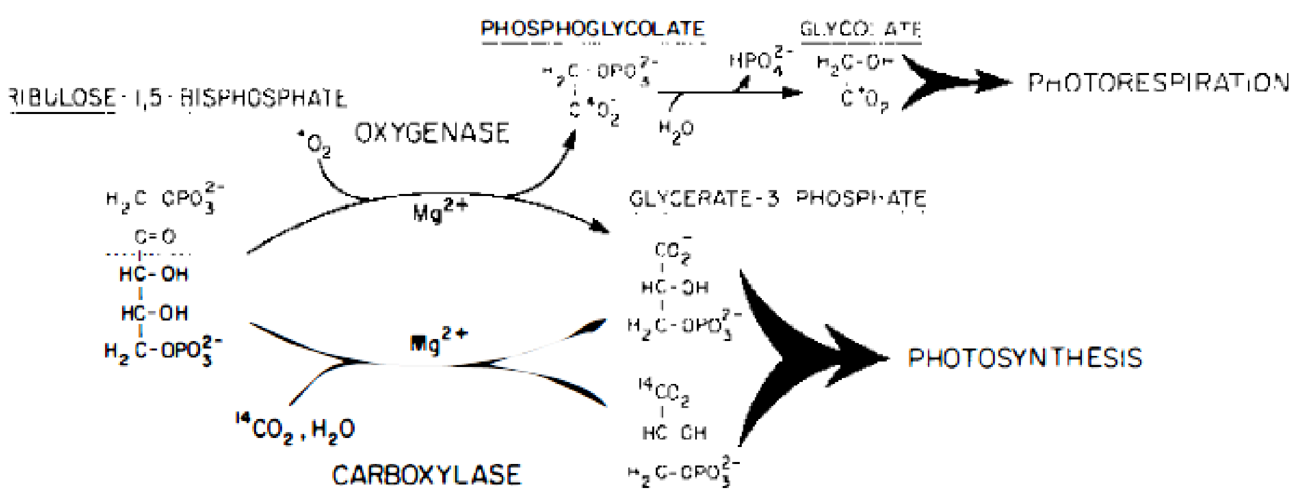

Figure 1: Reactions catalyzed by Rubisco (from Jensen and Bahr, 1977)

atmospheric concentration of CO_2. At lower CO_2 concentrations, the rate of photorespiration in C_3 plants increases significantly, but C_4 plants are unaffected. Temperature also plays a role, with higher temperatures favoring the growth of C_4 plants (Ehleringer et al., 1997). This is the main reason that C_4 plants are mostly called "warm-season grasses." The final variable that has a direct impact on C_3/C_4 abundances is light intensity with higher light intensities favoring C_4 growth (Tipple and Pagani, 2007). These climatic influences directly impact the relative abundance of C_3 and C_4 plants with all other factors held constant, but many other variables can play into how the distribution of these plants manifests itself.

Patterns of precipitation can also play a large role in determining whether an area is dominated by C_3 or C_4 plants. Since temperature plays a large role in determining which pathway is more efficient, seasonality can cause different parts of the year to favor the growth of different types of plants. This is then further modified by patterns of precipitation. For example, if more precipitation falls during the warmer months, more growth will be possible during the time that C_4 photosynthesis is favored.

Also, as previously mentioned, the C_4 plants with significant representation are predominantly grasses. So although climatic conditions play a role in what form of photosynthesis is more efficient, climate may be putting just as much pressure on what plant physiology is favored. For example, although one area may have temperatures that favor C_4 growth, the precipitation, soil type, etc. may be favoring the growth of trees (all C_3) over grasses, causing the formation of a C_3 forest rather than C_4 grassland (Collatz et al, 1997).

This relationship between climate and photosynthetic pathway are important when attempting to make paleoenvironmental reconstructions. The actual proportion of C_3 to C_4 plants is easily obtained from sediments through the measurement of carbon isotopes, and if this relationship is understood, we can potentially infer climatic information from this and vice versa. However, this is all highly contingent on our understanding of the relationship between the two. This is what I aim to investigate by testing two models of C_3/C_4 vegetation against actual data.

METHODS

Modern C_4 Distribution Data

To avoid as many confounding variables as possible, such as elevation and drastic changes in bedrock composition, I focused on obtaining modern C_4 abundance data from the

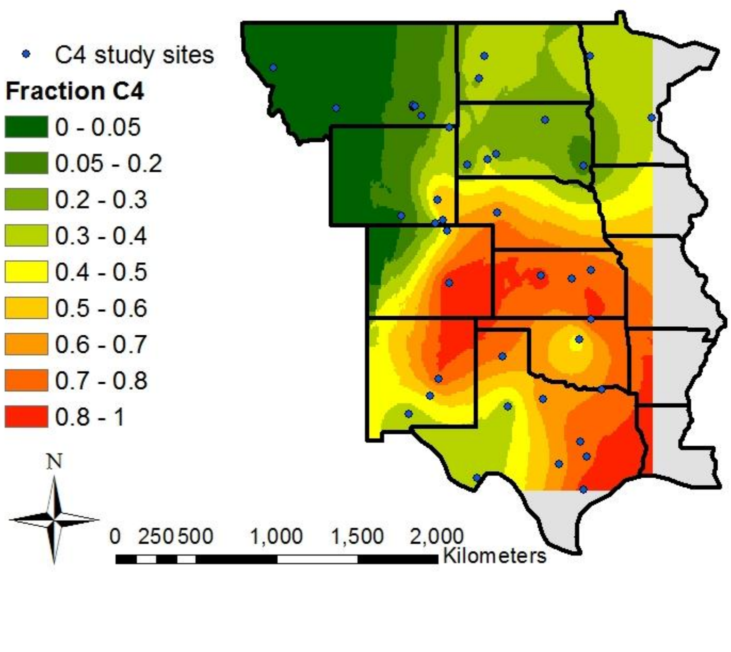

Figure 2: This map shows the fraction of vegetation that is C_4 across the western Great Plains of the United States. A Kriging interpolation using the C_4 study sites was used to construct it.

Great Plains region of the United States. Sites were drawn from Paruelo and Lauenroth (1996), who, in turn, drew their data from a slew of studies conducted from 1969 to 1992 (Table 1). For visualization purposes, a Kriging interpolation was carried out for %C_4 grasses between each study site (Fig. 2).

Table 1: Modern C4 abundance sites taken from Paruelo and Lauenroth (1996).

Site Name	Lat	Long	% C_4	Site Name	Lat	Long	% C_4
Jornada, NM	32.62	-106.75	0.31	S.H. Ordway Memorial Prairie, SD	45.33	-99.1	0.25
Osage, OK	36.95	-96.55	0.87	Konza Prairie, KS	39.1	-96.6	0.78
Pantex, TX	35.3	-101.53	0.72	Arapaho, NE	41.55	-101.8	0.7
Fort Stanton Experimental Ranch, NM	33.48	-105.55	0.5	U.S. Sheep Experimental Station, ID	44.25	-112.15	0
Texas Experimental Range, TX	33.33	-99.23	0.7	Wind Cave National Park, SD	43.53	-103.45	0.13
Black Gap Wildlife Area, TX	29.58	-102.92	0.31	Badlands National Park, SD	43.75	-102.33	0.48
Snyder, TX	32.97	-101.18	0.3	Alzada, MT	45.03	-104.47	0.4
OSU Agricultural Research, OK	36.05	-97.23	0.37	SSHA, WY	41.42	-107.17	0
Lincoln County, NM	34.28	-105.08	0.84	El Paso, CO	38.55	-104.5	0.95
Fayette, TX	30.58	-96.83	0.76	Hay Coulee, MT	45.82	-106.48	0.15
UCP, TX	29	-97	0.86	Kluver West, MT	45.87	-106.48	0.03
Blackland Prairie, TX	33.75	-96	0.71	Kluver North, MT	45.88	-106.47	0.12
San Antonio Prairie, TX	31.33	-97.17	0.8	Kluver East, MT	45.85	-106.37	0.05
Edwards Plateau, TX	30.25	-98.33	0.63	Fort Howes, MT	45.48	-106	0.02
Bison, MT	47.32	-114.27	0	Eastern South Dakota, SD	43.5	-97	0.11
Bridger, MT	45.78	-110.78	0.01	Pole Mountain, WY	41.12	-105.28	0.17
Cottonwood, SD	43.95	-101.87	0.18	Cheyenne, WY	41.25	-104.82	0.66
Dickinson, ND	46.9	-102.82	0.28	Wheatland, WY	42.07	-105.12	0.68
Hays, KS	38.87	-99.38	0.83	Red River Valley, MN	47.75	-96.62	0.4
CPER, CO	40.82	-104.6	0.44	Salina, KS	38.75	-97.62	0.8
Fort Berthold Indian Reservation, ND	47.75	-102.5	0.41	Cedar Creek, MN	45.4	-93.2	0.39

The Koch et al. (2004) Model

This model is the simpler of the two models being tested. It was constructed as a regression of multiple climatic variables against a set of modern C_4 abundance data. After selecting the variables that fit the data best, they came up with the following equation:

$$\%C_4 = -0.9837 + 0.000594(MAP) + 1.3528\left(\frac{JJA}{MAP}\right) + 0.2710(lnMAT)$$

MAP is mean annual precipitation, JJA is the mean precipitation in the summer months (June, July, August), and MAT is mean annual temperature.

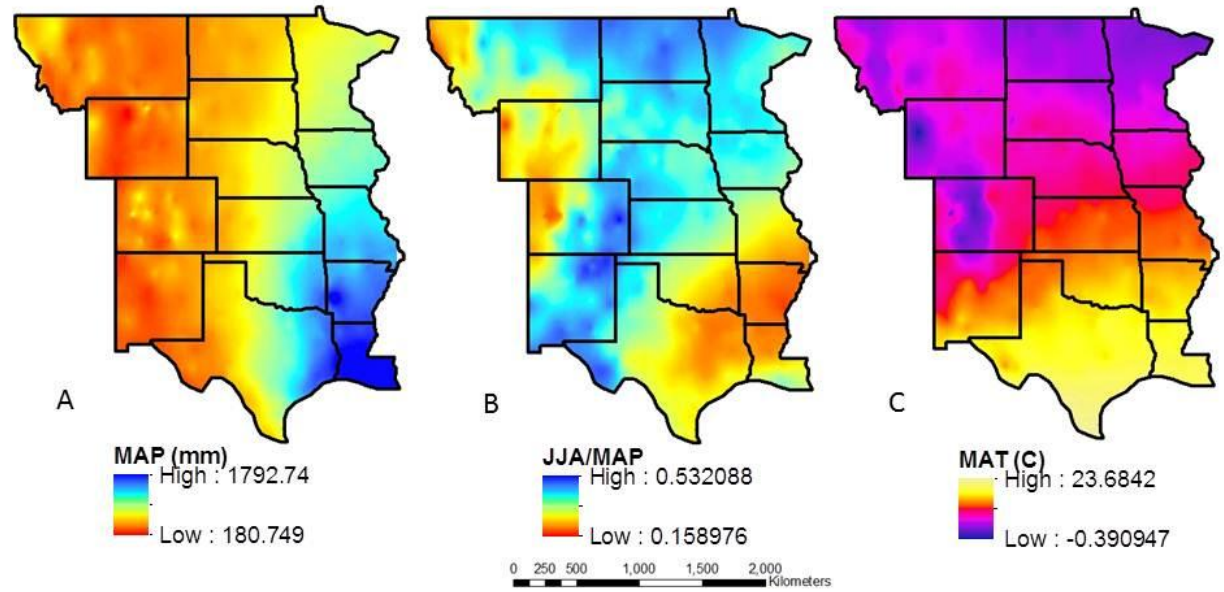

Figure 3: Map of the Great Plains with Kriging interpolations of MAP (A), JJA/MAP (B), and MAT (C).

Climate data was gathered from NOAA via www.climate.gov, and maps were constructed for the area of concern using the Kriging interpolation method between weather stations (Fig. 3). The raster calculator was then used to execute the equation shown above, yielding a map of C_4 abundance. However, because I did not want to minimize the error incorporated due to the interpolation method, I did not compare the Koch results to the interpolated actual C_4 distributions, but instead compared them on a site-by-site basis.

The Still and Powell (2010) Model

Although it seems that climate is the main driver for C_4 distributions, plant physiology also plays a role. Unlike the Koch et al. (2004) model, the Still and Powell (2010) model takes this into account by additionally incorporating vegetation data from the MODIS and Global Land Cover Map 2000 (GLC) datasets.

The process of reconstructing C_4 abundance begins by specifically obtaining the percent herbaceous layer and applying a climatic mask. The mask consists of areas that have at least one month with mean precipitation over 25mm and mean temperature over 22°C (Fig. 4). All areas outside of this mask are set to 0, whereas the areas inside are considered hospitable to C_4 grasses. Once this mask is applied, the % herbaceous data are modified according to the type of vegetation cover present, as indicated by the GLC data. If the GLC indicates that the area is shrubland, for example, the entire % herbaceous value is attributed to C_3 vegetation. The

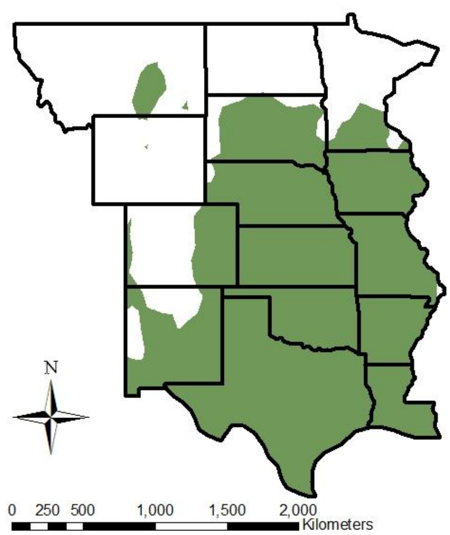

Figure 4: A map of the viable areas for C_4 plant growth under the Still and Powell (2010) model. The green marks all areas with at least one month of over 25mm mean precipitation and 22°C mean temperature.

opposite is true for grasslands, and ambiguous classifications, such as evergreen forest (open canopy), split the % herbaceous value in half for C_3 and C_4 vegetation.

RESULTS

Koch et al. (2004)

The model yielded a reconstruction of C_4 vegetation that ranged from 3% to 82% (Fig. 5A). A distinct trend with decreasing amounts of C_4 was observed, which matches the latitudinal trend observed in MAT for the area. When compared to the actual C4 abundances, discrepancies varied from -37% to +48% with a mean absolute difference of 17% (Fig. 6).

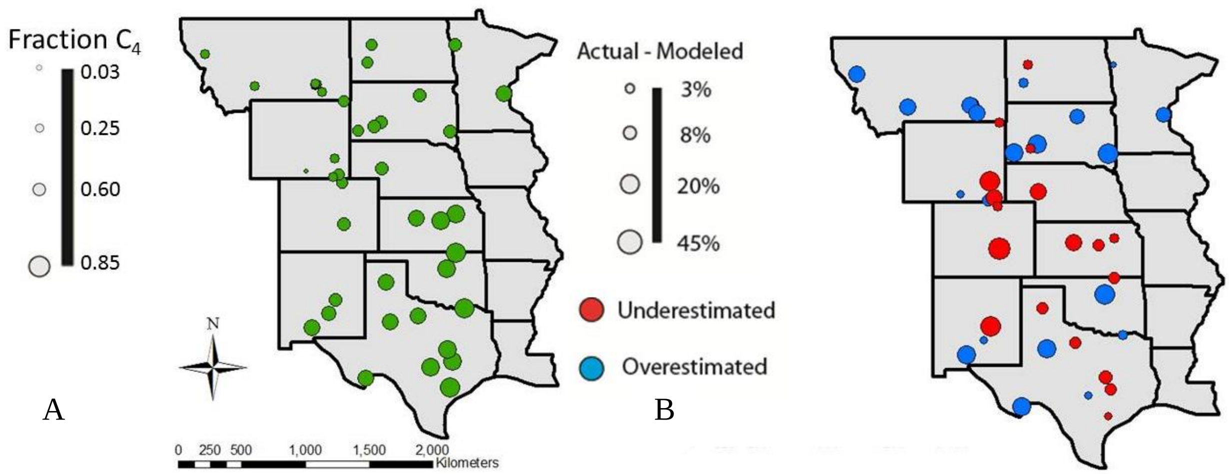

Figure 5: Maps showing the C_4 abundance modeled by the Koch et al. (2004) model (A) and the difference between the actual and reconstructed C_4 abundances (B).

Still and Powell (2010)

The model yielded a wide variety of C_4 abundances ranging from 0% outside the climate mask and inside shrubland to 84% (Fig. 7A). Aside from the sites modeled to have 0% C_4 vegetation, the smallest amount of C_4 vegetation is 30%. The large discrepancies in modeled values when compared to the true data are largely caused by this gap and the amounts of sites set to zero by the climate mask or GLC data are largely responsible for. The difference between the actual and modeled values ranges from -41% to +84% (Fig. 7B). Of note is the fact that the model accurately predicts a couple of sites that have no C_4 vegetation and sit well outside of the hypothesized climatic boundary beyond which no C_4 plants can grow. Average absolute difference between the actual and modeled values is 28%.

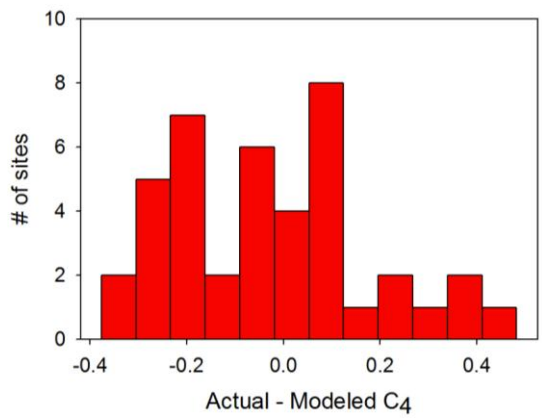

Figure 6: Histogram showing the distribution of differences between the actual and modeled C_4 abundances.

One noticeable result is that some sites have very incorrectly modeled C_4 abundances. The largest of these had modeled C_4 values of 0% despite large % herbaceous values. This was due to the adjustment dictated by the GLC data. For example, one site had 84% herbaceous

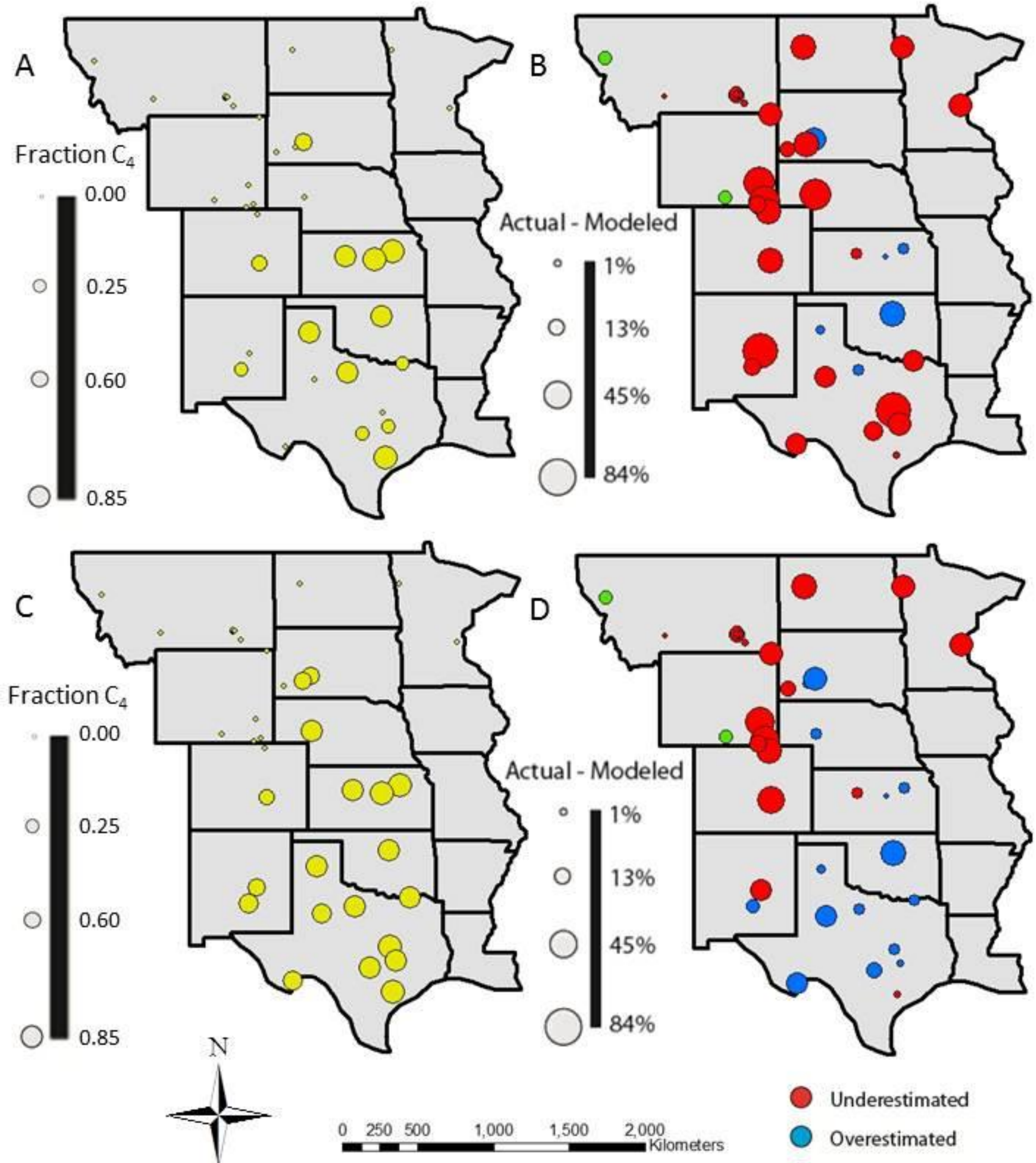

Figure 7: The results of the Still and Powell (2010) model. (A) Modeled C_4 abundance. (B) Difference between the actual and modeled C_4 abundance. (C) C_4 abundance under the Still and Powell (2010) model without adjustments according to GLC data. (D) Difference between the actual and non-GLC modeled C_4 abundance.

vegetation, but the GLC data said it was shrubland, meaning that, according to the model, the C_4 abundance would be set to zero. Because of the clear problems caused by this step in model construction, I created another set of modeled values that excludes adjustments made according to GLC data. The range in C_4 abundances is indistinguishable from that for results influenced by GLC data (Fig. 7C). Differences between modeled values and actual values, however, were much smaller, with the range of differences extending from -41 to +68 (Fig. 7D). Additionally, the mean absolute difference between the actual and modeled values is lowered to 20%. The histogram of actual-modeled difference shows the wide range in inaccuracies, but the majority of errors fall in the ±20% range (Fig. 8).

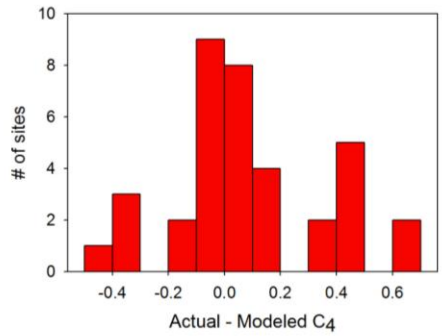

Figure 8: Histogram of the difference between the actual C_4 abundances and non-GLC modeled values.

DISCUSSION

Both models appear to have their respective problems that cause varying levels of inaccuracy. The Koch et al. (2004) model may have been a good regression on the original dataset, but it likely does not incorporate enough non-climatic influences, such as plant physiology to present a more accurate picture. The Still and Powell (2010) model seems to deal with the exact opposite problem. Although it deals with a variety of influences, it does not incorporate enough of the gradation that a regression offers and instead modifies the data in terms of absolutes that has a hard boundary for when C_4 grasses disappears. This is evidenced in the large gap of %C_4 values between 0% and 30%. Additionally, it is surprising to see that the model reconstructs 0% C_4 abundance at multiple sites that are surrounded by other sites with very high %C_4 values, which is entirely because of the other source of complete C_4 elimination, the GLC data.

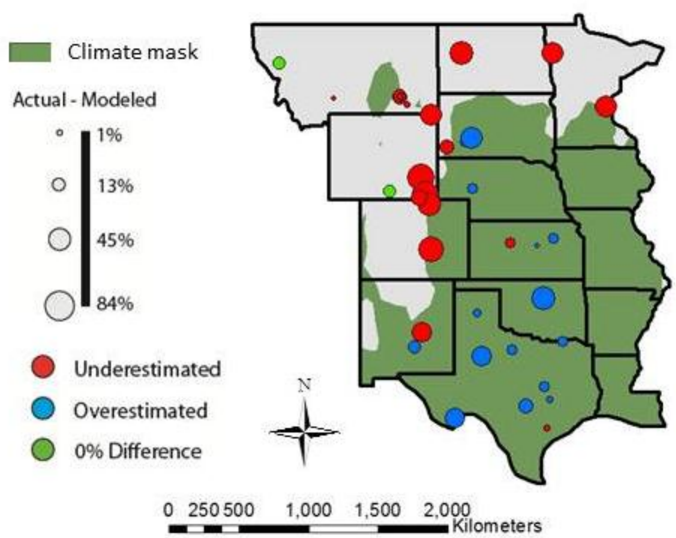

Figure 9: Map showing the relationship of the climate mask to the inaccuracies of the non-GLC Still and Powell (2010) model.

Eliminating this last step in the Still and Powell (2010) model does a good job of getting rid of some of the drastically inaccurate values, but there are still a good amount of dramatically underestimated sites. When the climate mask is placed on top of the actual-modeled map, it is evident that most remaining large underestimations are due to the hard barrier the climate mask presents (Fig. 9). This model might do better if it adopts the regression-based approach that Koch et al. (2004) take and gradually phase out C_4 vegetation rather than dispose of them all at once.

It is likely that such a model will not be perfect either, and the incorporation of other variables may have to be considered. The occurrence and intensity of wildfires, for example, exert strong influences on the amount of trees present on a grassland savanna, with increasing amounts of fire suppressing the establishment of trees (Bond 2008). Incorporation of this information would undoubtedly provide a better model for the factors that play into C_4 plant distributions. The presence of herbivores is another factor likely to play a role, but little has been researched on the subject (Bond 2008).

Additionally, all of these studies are typically conducted with the assumption that these modern systems are in equilibrium, an assumption that one cannot make as often as our climate continues to change. Trees especially take a long time to get established and can be phased out just as slowly, so the distribution of vegetation we see today might be more reflective of a past climate.

Finally, we do not know what the natural variability in this system is. Perhaps we may never get better differences than ±20%. Models such as the ones tested in this study still have a long way to go, but are definitely well on the path towards understanding all of the complexities of this system.

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