

Wind-bounded grasslands of North America

Brice B. Hanberry

USDA Forest Service, Rocky Mountain Research Station, Rapid City, SD 57702, USA

ARTICLE INFO

Keywords:

Ecotone
Evapotranspiration
Climate
Fire
Great Plains
Prairie
Prairie Peninsula
Precipitation
Wind

ABSTRACT

Climate may separate grasslands from surrounding forests and shrublands, but an alternative option is that grasslands are suitable for trees except in the presence of frequent fires, which are spread great distances by strong winds. To develop a ruleset that demarcated the central North American grasslands, I modeled grasslands using precipitation and its coefficient of variation, ratio of potential evapotranspiration to precipitation, climatic moisture index, July vapor pressure, and wind speed (i.e., a fire indicator) during 5000 (4900–5100) years before present, 1600–1699, 1800–1849, and 1850–1899. Wind speeds of 4.5 m s^{-1} at 10 m above ground height clearly bounded grasslands. For all time intervals, the random forests and extreme gradient boosting classifiers had accuracies of 0.96 to 0.97 in classification of reserved samples; wind speed was ranked as the most influential model variable (i.e., value of 100 out of 100 scale, with the next most influential variables at ≤ 25). The simulated wind patterns matched recent wind models from atmospheric reanalysis and the Global Wind Atlas downscaled from an atmospheric reanalysis. Wind boundaries were stable over time, shifting slightly northward during 11,000 years before present to recent decades. Although wind is related to precipitation, I directly mapped and modeled precipitation and derivatives. Therefore, I propose that wind is an index of fire spread in grassland biomes, where conditions are appropriate for both fire and woody vegetation. More research on wind models is required to confirm these results and determine how winds affect grassland formation and maintenance globally.

1. Introduction

The Great Plains grasslands of central North America (Fig. 1) contain major ecosystems of shortgrass, mixed grass, and tallgrass prairie, directly increasing in plant height with precipitation along a west to east gradient due to orographic wind flow. The western border generally follows the edge of the Rocky Mountains. The grasslands are surrounded by forests, shrublands, and desert to the west and south, and forests to the north and east. On the eastern border, rather than being circumscribed by a smooth boundary, an eastward projection of grasslands known as the Prairie Peninsula extends into eastern forests. The primary driving factor for the formation and maintenance of grasslands has been contested for more than a century, with the recognition that vegetation, climate, soils, and disturbance interact to reinforce or break boundaries (Transeau 1935).

The general consensus is that borders between ecoregions are explained primarily by climate (e.g., Transeau, 1935; Borchert, 1950; Harrington and Harman, 1991; Booth et al., 2006; Williams et al., 2009). Indeed, biomes are defined in response to climate, and simple climate rules allow for global climate classifications that generally align with

ecosystems (Trewartha, 1968; Hanberry and Fraser, 2019). Grasslands often are considered too dry for trees but differentiation between grasslands and forests can be challenging to force into a climate classification because of overlapping values in climate metrics (Hanberry and Fraser 2019). Therefore, the defining set of climate variables that separate grasslands and forests is unknown. Transeau (1935:431) proposed a set of climatic factors to delineate the border of North American grasslands, encompassing precipitation-evaporation ratios, midsummer (i.e., July) relative humidity, variable precipitation within and among years, and successive dry and wet periods and their length and intensity.

Another option is that fire maintained at least some grasslands by removing trees. Transeau (1935:423) recognized the counterview that the North American grassland: “seemed to be not really prairie but rather deciduous forest with trees absent because of ecological conditions long since terminated...the Prairie Peninsula represents a pyro-pyrrhic victory of [native humans] attempting to enlarge the native pastures, or to capture their grazing meat supply. This view had the backing of many prairie-born settlers to whom the fire peril and the treelessness were the only striking features of the prairie.” Fire is a well-established frequent historical disturbance in the Great Plains

E-mail address: brice.hanberry@usda.gov.

<https://doi.org/10.1016/j.ecolind.2021.107925>

Received 2 February 2021; Received in revised form 5 April 2021; Accepted 22 June 2021

Available online 28 June 2021

1470-160X/Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

grasslands, with fire regimes influenced by use of fire as a management tool by indigenous peoples (e.g., [Christy, 1892](#); [Williams, 1981](#)). Fire is more damaging to slow-growing trees, which are vulnerable until bark thickens, than to herbaceous plants, which have more relative biomass belowground than trees and are adapted to removal of aboveground biomass. Because trees grow faster on higher quality sites, fire frequency must increase with site productivity to control tree densities; therefore, the importance and frequency of fire likely increased from the western to eastern grasslands as precipitation and potential productivity increased. Precipitation produces herbaceous fuels followed by (summer) drought that dries fine fuels, which are optimal conditions for fire. When the antecedent wet period does not occur due to drought, production of herbaceous fine fuels is limited, and thus, fire occurrence is less likely ([Shuman et al., 2009](#); [Rogers et al., 2014](#)). Conversely, a lengthy wet period with limited drying of vegetation also decreases the chance of fire. In consequence, even though it may be tempting to attribute control of fire by climate, fire-climate associations often are inconsistent ([Davis 1977](#)).

A spatially continuous map of fire over time is not available, but wind is one potential index for the spread of fire over flat terrain, as is present in central North America. In combination with moderate precipitation that promotes herbaceous growth for fuels followed by dry intervals, strong (westerly) winds drive fire over large flat extents without impedance by fire breaks ([Christy, 1892](#); [Sauer, 1950](#)). Flat terrain is a natural fire shed or spread whereas fire breaks encompass water and wetlands, rocky outcrops, and rough and steep topography of bluffs, escarpments, and ridges ([Christy, 1892](#); [Bruner, 1931](#); [Wells, 1965](#); [Davis, 1977](#)). Trees occurred in fire-protected locations throughout the Great Plains grasslands and because the prevailing westerly winds spread fire eastward, trees typically were present or more abundant on the leeward side of water and wetland firebreaks ([Christy, 1892](#); [Gleason, 1922](#)). Lastly, fire occurrence is amplified by deliberate ignitions from humans. [Shantz and Zon \(1924:16\)](#) wrote: “Aided by high winds, these fires swept with great rapidity across the grasslands of the prairies and plains, and early settlers and travelers could find safety only by starting backfires, since the broad band of burning grass...” was often 100 to 200 m across. [Christy \(1892\)](#) noted that a strong wind and level grass could cause fires hundreds of kilometers in length but where herbaceous vegetation is sparse, fire will not spread without a powerful wind.

The factors that differentiate central grasslands from eastern forests and other surrounding ecosystems have remained a century-long question that requires long-term patterns of moisture and wind (i.e., an index of fire) to determine the relative influence of moisture and fire on limiting tree densities. To develop the ruleset, I mapped and modeled wind speed, annual precipitation and its coefficient of variation, ratio of precipitation to potential evapotranspiration, climatic moisture index, and July vapor pressure over time for grasslands and surrounding non-grassland ecoregions. I displayed these variables for 1600 to 1950, which is an interval that includes the earliest travel accounts by Euro-American explorers of the Great Plains grasslands ([Hart and Hart 1997](#)). Pollen reconstructions indicate that grasslands occurred 11,000 years ago ([Williams et al., 2009](#)), but generally analogous climate and vegetation formed about 5000 to 7000 years ago, including expansion of grasslands globally ([Keeley and Rundel, 2005](#); [Anderson, 2006](#)). Thus, I modeled these variables at 5000 (4900–5100) years before present, 1600 to 1699, 1800 to 1849, and 1850 to 1899, spanning the timeline of when North American grasslands may have been fully formed to recent tree expansion into grasslands ([Christy, 1892](#); [Gleason, 1922](#)).

2. Methods

Only one debiased and downscaled historical climate dataset (0.5° resolution; [Lorenz et al., 2016a, 2016b](#)) is available that includes wind speed, to my knowledge, at 10 m above ground; however, wind speed patterns remain consistent above this height, albeit increasing in speed ([Fig. 2](#); [Badger and Jørgensen 2011](#); viewer at <https://globalwindatlas.info>). The paleoclimatic simulation was from the CCSM3 general circulation model with decadal means from TraCE-21 ka ([Liu et al., 2009](#); [He et al., 2013](#)). The CCSM3 model is complete and fully complex, forced by prescribed trends in orbital parameters, ice sheet extent and height, sea level, greenhouse gases, and meltwater pulses to the North Atlantic. Generally, general circulation models have demonstrated consistent overall relative performance, albeit with better performance depending on region and variable.

To examine the relationship between climate variables related to moisture and wind speed (i.e., the fire index) with grasslands and surrounding biomes over time, I quantified total annual precipitation (mm) and precipitation coefficient of variation, mean vapor pressure (kPa), wind speed (m s^{-1}), the ratio of mean total annual precipitation to mean

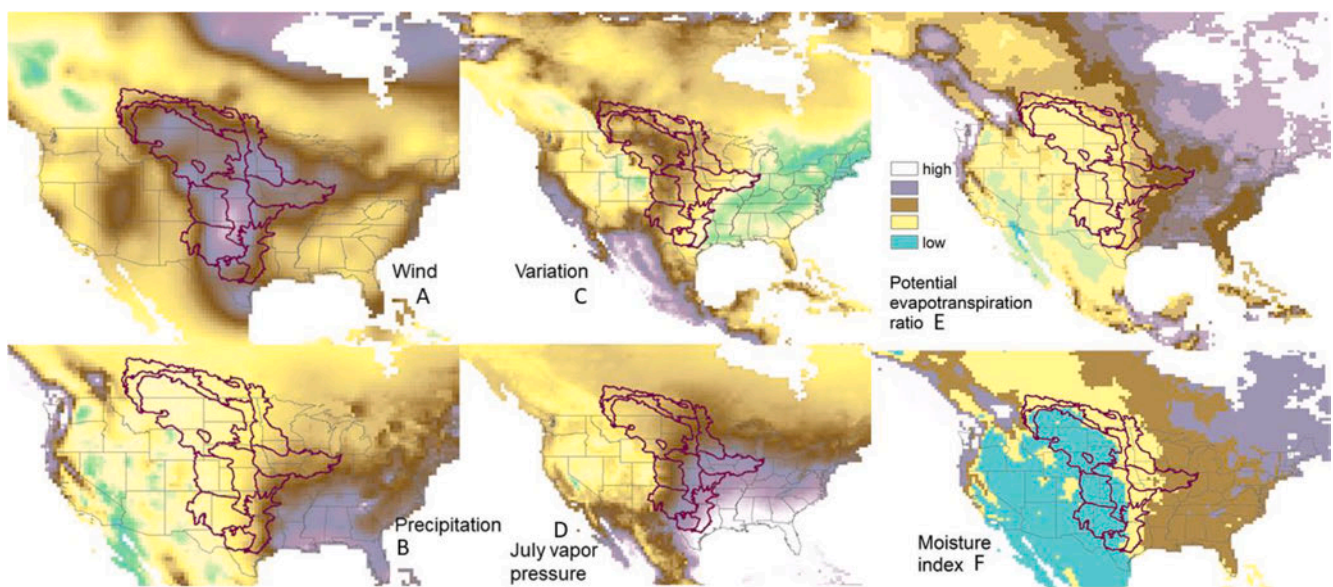


Fig. 1. The Great Plains grasslands of central North America (outlined) and wind speed (A; m s^{-1} at 10 m above ground), precipitation (B; mm), precipitation coefficient of variation (C), July vapor pressure (D; kPa), ratio of precipitation to potential evapotranspiration (E), and climatic moisture index (F) during years 1600–1950.

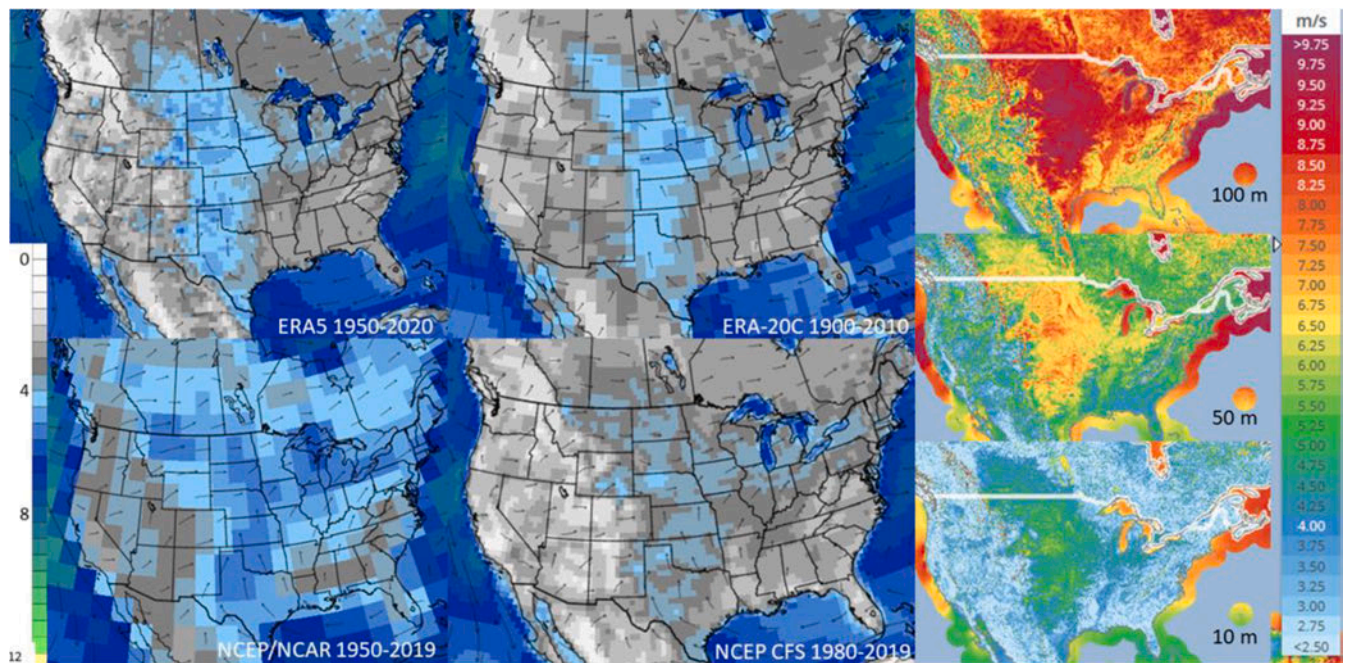


Fig. 2. Wind speeds (m s^{-1}) at 10 m above ground from reanalysis models (A; Climate Reanalyzer 2020) and wind speeds (m s^{-1}) at 100 m, 50 m, and 10 m above ground from the Global Wind Atlas, a downscaling of reanalysis model ERA5 (B; Badger and Jørgensen, 2011; Global Wind Atlas, 2021).

total potential evapotranspiration, and climatic moisture index. The climatic moisture index is similar to the precipitation to potential evapotranspiration ratio but on a -1 to 1 scale. For years 1600 to 1950, I mapped precipitation and coefficient of variation for monthly precipitation, the evaporation ratio, and climatic moisture index July vapor pressure, and wind speed.

I then formally modeled the relationship between these variables and two classes of grasslands and non-grassland ecosystems surrounding the North American grasslands (Olson et al. 2001) for time intervals of 4900–5100 years before present, 1600–1699, 1800–1849, and 1850–1899. Additionally, I used the variable of soil water content at 10 cm, although values were only for current years (Hengl and Gupta 2019). I applied random forests and extreme gradient boosting classifiers, which use different approaches to develop an ensemble model from multiple models. The random forests classifier averages models whereas boosting classifiers sequentially add models to the ensemble to correct errors made by prior models; application of two classifiers helps confirm similar results and identify divergences. I selected equal prevalence rates, or the same sample size for grasslands and random samples of non-grasslands, for a total of 2350 samples. I partitioned the datasets into training (75% of samples) and test sets (reserved samples), trained the model with 10-fold cross-validation, and then predicted for the test sets with the caret package (Kuhn, 2008; R Core Team, 2021).

Lastly, I extracted wind speeds at $\geq 4.5 \text{ m s}^{-1}$ for 1600 to 1950 and 4900 to 5100 years before present, encompassing the modeled intervals, and additionally 9900 to 10,100 years and 10,900 to 11,100 years before present, to demonstrate wind speed continuity throughout the interval of reconstructed central North American grasslands. I examined recent wind patterns in atmospheric reanalysis models (Fig. 2A; Climate Change Institute 2021, viewer at <https://ClimateReanalyzer.org>) and the Global Wind Atlas, downscaled from 30 km resolution of European Centre for Medium-Range Weather Forecasts ERA5 reanalysis (Fig. 2B; Badger and Jørgensen 2011, viewer at <https://globalwindatlas.info>, Global Wind Atlas, 2021; Hersbach et al. 2020). I also processed the Livneh et al. (2013) wind dataset for the conterminous United States to demonstrate another wind model.

3. Results

Wind speeds at $\geq 4.5 \text{ m s}^{-1}$ at 10 m above ground visibly constrained the Great Plains grasslands, including the extension into eastern forests, unlike other variables (Fig. 1A–F). For models of all intervals and both classifiers, accuracy was very high at 0.96 to 0.97 correct predictions for withheld samples of both grassland and non-grassland classes (Table 1). Wind speed was the most influential variable, at a value of 100 for a scale of a 100. The greatest value for other variables was 25.

Wind patterns generally were consistent over time and wind borders overall aligned with the grasslands. Boundaries of wind speeds at ≥ 4.5

Table 1

Accuracy, sensitivity (i.e., grassland prediction), specificity (i.e., non-grassland prediction), and variable importance of grassland prediction for different time intervals (5000 = 4900 to 5100 years before present) and random forests and extreme gradient boosting classifiers based on a test set (25% of observations) for modeled training data in central North America.

	5000	1600–1699	1800–1849	1850–1899
<i>random forests</i>				
Accuracy	0.96	0.96	0.97	0.97
Sensitivity	0.97	0.97	0.97	0.97
Specificity	0.94	0.95	0.96	0.96
wind speed	100	100	100	100
vapor pressure	9	22	21	22
soil water content	2	7	5	5
evaporation ratio	10	22	20	19
Precipitation	0	0	0	0
precipitation CV	11	21	19	17
moisture index	10	22	19	19
<i>gradient boosting</i>				
Accuracy	0.96	0.96	0.97	0.96
Sensitivity	0.97	0.97	0.98	0.97
Specificity	0.95	0.96	0.96	0.96
wind speed	100	100	100	100
vapor pressure	14	17	17	18
soil water content	5	1	4	4
evaporation ratio	0	11	1	0
Precipitation	4	0	0	4
precipitation CV	23	18	21	14
moisture index	23	9	19	25

m s^{-1} shifted slightly north over time from 11,000 years before present to recent centuries and also extended into Prairie Peninsula (Fig. 3A). At 11,000 years before present, these wind speeds connected to the Atlantic Coast, similar to the Livneh et al. (2013) model (Fig. 3B). Greater wind speeds of the Global Wind Atlas extended further north; however, that is the direction the wind boundaries shifted over time, while wind speeds were 4 to 4.5 m s^{-1} along the edges, particularly in the Prairie Peninsula (Fig. 3A).

4. Discussion

Based on mapping and modeling, wind may provide an index of the correct conditions for grasslands, in conjunction with flat terrain and moderate, seasonal precipitation. The century-long question of which environmental factors shaped the central grasslands of North America may be answered by mean wind speeds $\geq 4.5 \text{ m s}^{-1}$ at 10 m. Wind speeds between 4 and 4.5 m s^{-1} at 10 m may align with the Prairie Peninsula, with wind being funneled by the rougher topographies of the Ozark Mountains to the south and the Driftless Area to the north (Fig. 3C).

Although there are numerous, complex atmospheric models, the CCSM3 general circulation model, atmospheric reanalysis models, and Global Wind Atlas all displayed similar wind patterns (Collins et al., 2006; Badger and Jørgensen, 2011; Saha et al., 2014; Hersbach et al., 2020). These models rely to some extent on vegetation data because the atmosphere and vegetation interact; for example, the ERA5 atmospheric reanalysis used seasonally varying monthly vegetation information (Hersbach et al. 2020). But these models are intended as wind measures, not vegetation models. Simpler wind models may exist that include only topographic or minimal adjustments. For example, the Livneh et al. (2013) wind dataset was produced by a relatively unadjusted method (Fig. 3B); more adjustment for topography (Fig. 3C) or vegetation may even be required because greater wind speeds extended past the Prairie Peninsula to the Atlantic Ocean, similarly to the wind patterns at 11,000 years before present. More research is required to corroborate evidence for wind control of North American grasslands and determine if winds may affect grassland formation globally.

Since 11,000 years before present, wind boundaries expanded slightly northward and the greater extension of wind boundaries into Canada corresponded with the atmospheric reanalysis models and Global Wind Atlas. Conversely, based on pollen samples, Williams et al. (2009) found that the northern grasslands-forest boundary moved south

from central Saskatchewan about 6000 years ago. Wind patterns overall did not shift much since 11,000 years before present while grasslands may have been more dynamic, with finer scale variation across time and space due to the environmental context of disturbance history and specific site conditions. Movement and changing densities of indigenous people across the landscape may contribute to some of the variation.

Several researchers have noted strong westerly winds in the Great Plains and Prairie Peninsula, but from the climate perspective of precipitation (Borchert, 1950; Delcourt and Delcourt, 1984; Harrington and Harman, 1991; Booth et al., 2006). Delcourt and Delcourt (1993) wrote that grassland vegetation developed by 10,000 years before present in the central and southern Great Plains, due to presence of a relatively dry Pacific air mass. However, modeled precipitation and derived moisture variables and soil moisture were weakly influential in the models compared to wind speed. Mapped precipitation and derived moisture variables did not correspond with grasslands borders, except for demarcation at the southeastern boundary between grasslands and southeastern forests, which receive abundant rainfall from the Gulf Coast. One last climate factor that Transeau (1935) proposed was successive dry and wet periods and their length and intensity; however, analysis of drought severity did not show more change points for grasslands than for eastern forests (e.g., Hanberry et al. 2018a; Hanberry in review). Many precipitation measures encompassing drought remain (e.g., Changnon et al., 2002; although lightning strike density does not align with the Prairie Peninsula, Holle and Murphy, 2015), which could be examined and fit to a classification model, but problems will occur differentiating grasslands solely on precipitation metrics due to overlap in precipitation values with both forests and shrublands. In addition, application of different variations of the Köppen-Trewartha classification system (Trewartha 1968), including evapotranspiration values with modern climate data, indicated no climatic boundary between eastern forests and grasslands (Hanberry and Fraser, 2019).

Every identified climate for grasslands is also climate for closed forests, open forests of savannas and woodlands, and shrubs (Christy, 1892; Sauer, 1950). Prairies are well-suited for tree growth, as evidenced by trees that are present in fire breaks and planted trees that survive, grow, and spread, even during the extreme Dust Bowl drought of the 1930s (Christy, 1892; Wells, 1965). Tree establishment and woodland expansion within the Great Plains grasslands and elsewhere in the U.S. have occurred during dry climate intervals (Ziegler et al., 2008; Shuman et al., 2009; Rogers et al., 2014).

Wind alone is not sufficient to create grasslands, as wind speeds $\geq$

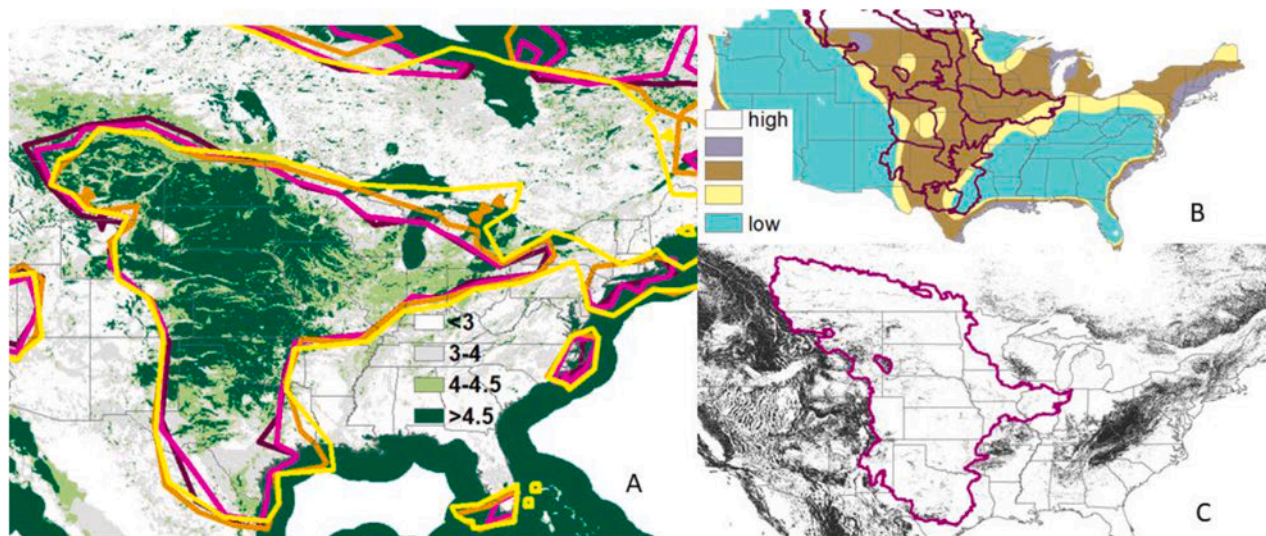


Fig. 3. Wind speeds from the Global Wind Atlas and wind boundaries at $\geq 4.5 \text{ m s}^{-1}$ for years 1600–1950 (purple), 5000 years before present (pink), 10,000 years before present (orange), and 11,000 years before present (yellow; A). The Livneh wind model (B) and areas of greater ruggedness (C; Amatulli et al. 2020). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.5 m s⁻¹ occur in other biomes and the easternmost Prairie Peninsula delineated by wind is now generally forested, where it is not in agriculture. Grasslands are appropriate for either woody vegetation or frequent fire. Fire is the mechanism that favors herbaceous vegetation over trees, while the presence of herbaceous vegetation in turn reinforces fires. From a disturbance perspective, wind carries fire in grasslands due to flat terrain, moderate precipitation to grow plentiful herbaceous fuels, and precipitation variability to cure the fuels and make them available for ignition, particularly with the addition of humans to increase fire probability (Christy 1892). Grasslands globally are located where surface terrain is smooth to rolling and across a range of precipitation and other climate variables, but with dry season intervals during which vegetation cover dries (Sauer 1950).

The boundary between the Great Plains grasslands and eastern forests has been dissolving rapidly under fire exclusion since about 1860 (Christy, 1892; Gleason, 1922; Hanberry and Hansen, 2015). Encroachment by fire-sensitive woody vegetation, such as *Juniperus virginiana*, is one of the few threats that can completely replace grasslands within a few decades (Limb et al. 2010). This process is similar to replacement of fire-dependent open oak and pine forests with a grass-dominated understory by closed forests of fire-sensitive tree species in the eastern U.S. (Hanberry et al. 2018b).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

I thank anonymous reviewers for their time and comments. This research was supported by the USDA Forest Service, Rocky Mountain Research Station. The findings and conclusions in this publication are those of the author and should not be construed to represent any official USDA or U.S. Government determination or policy. The author has no conflicts of interest. The Global Wind Atlas 3.0 is released in partnership with the World Bank Group, utilizing data provided by Vortex, using funding provided by the Energy Sector Management Assistance Program (ESMAP).

References

- Amatulli, G., McInerney, D., Sethi, T., Strobl, P., Domisch, S., 2020. Geomorpho90m, empirical evaluation and accuracy assessment of global high-resolution geomorphometric layers. *Sci. Data* 7, 1–18.
- Anderson, R.C., 2006. Evolution and origin of the Central Grassland of North America: climate, fire, and mammalian grazers. *J. Torrey Bot. Soc.* 133, 626–647.
- Badger, J. and Jørgensen, H.E., 2011. Images from: A high resolution global wind atlas-improving estimation of world wind resources. Danmarks Tekniske Universitet, Risø Nationallaboratoriet for Bæredygtig Energi. Available at: <https://globalwindatlas.info/downloads/gis-files> Accessed 7 January 2021.
- Booth, R.K., Kutzbach, J.E., Hotchkiss, S.C., Bryson, R.A., 2006. A reanalysis of the relationship between strong westerlies and precipitation in the Great Plains and Midwest regions of North America. *Clim. Change* 76 (3–4), 427–441.
- Borchert, J.R., 1950. The climate of the central North American grassland. *Ann. Assoc. Am. Geogr.* 40 (1), 1–39.
- Bruner, W.E., 1931. The vegetation of Oklahoma. *Ecol. Monogr.* 1 (2), 99–188.
- Changnon, S.A., Kunkel, K.E., Winstanley, D., 2002. Climate factors that caused the unique tall grass prairie in the central United States. *Phys. Geogr.* 23 (4), 259–280.
- Christy, M., 1892. Why are the prairies treeless? *Proc. R. Geogr. Soc. Monthly Rec. Geogr.* 14 (2), 78. <https://doi.org/10.2307/1801210>.
- Climate Change Institute, 2021. Images from: the Climate Reanalyzer. Available at: <https://ClimateReanalyzer.org> Accessed 15 January 2021.
- Collins, W.D., Bitz, C.M., Blackmon, M.L., Bonan, G.B., Bretherton, C.S., Carton, J.A., Chang, P., Doney, S.C., Hack, J.J., Henderson, T.B., Kiehl, J.T. et al., 2006. The community climate system model version 3 (CCSM3). *Journal of Climate* 19:2122–2143.
- Davis, A.M., 1977. The prairie-deciduous forest ecotone in the upper Middle West. *Ann. Assoc. Am. Geogr.* 67 (2), 204–213.
- Delcourt, P.A., Delcourt, H.R., 1993. Paleoclimates, paleovegetation, and paleofloras during the Late Quaternary. In: *Flora of North America*. New York: Oxford University Press. Available at: http://beta.floranorthamerica.org/Chapter_4 accessed 24 January 2021.
- Delcourt, P.A., Delcourt, H.R., 1984. Late Quaternary paleoclimates and biotic responses in eastern North America and the western North Atlantic Ocean. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 48 (2–4), 263–284.
- Gleason, H.A., 1922. The vegetational history of the Middle West. *Ann. Am. Assoc. Geogr.* 12 (1), 39–85.
- Global Wind Atlas, 2021. Global Wind Atlas 3.0. Technical University of Denmark (DTU). Available at: <https://globalwindatlas.info/downloads/gis-files> Accessed 7 January 2021.
- Hanberry, B.B., Abrams, M.D., White, J.D., 2018a. Is increased precipitation during the 20th century statistically or ecologically significant in the eastern US? *J. Land Use Sci.* 13 (3), 259–268.
- Hanberry, B.B., Bragg, D.C., Hutchinson, T.F., 2018b. A reconceptualization of open oak and pine ecosystems of eastern North America using a forest structure spectrum. *Ecosphere* 9 (10), e02431. <https://doi.org/10.1002/ecs2.2431>.
- Hanberry, B., Fraser, J., 2019. Visualizing current and future climate boundaries of the conterminous United States: Implications for forests. *Forests* 10 (3), 280. <https://doi.org/10.3390/f10030280>.
- Hanberry, B.B., Hansen, M.H., 2015. Advancement of tree species across ecotonal borders into non-forested ecosystems. *Acta Oecol.* 68, 24–36.
- Harrington, J.A., Harman, J.R., 1991. Climate and vegetation in central North America: natural patterns and human alterations. *Great Plains Q.* 11, 103–112.
- Hart, R.H., Hart, J.A., 1997. Rangelands of the Great Plains before European settlement. *Rangelands Arch.* 19, 4–11.
- He, F., Shakun, J.D., Clark, P.U., Carlson, A.E., Liu, Z., Otto-Bliesner, B.L., Kutzbach, J.E., 2013. Northern Hemisphere forcing of Southern Hemisphere climate during the last deglaciation. *Nature* 494 (7435), 81–85.
- Hengl, T. and Gupta, S., 2019. Data set: Soil water content (volumetric %) for 33kPa and 1500kPa suctions predicted at 6 standard depths (0, 10, 30, 60, 100 and 200 cm) at 250 m resolution. (Version v0.1) Zenodo. DOI:10.5281/zenodo.2784001.
- Hersbach, H., Bell, B., Berrisford, P., Hirahara, S., Horányi, A., Muñoz-Sabater, J., Nicolas, J., Peubey, C., Radu, R., Schepers, D., Simmons, A., Soci, C., Abdalla, S., Abellan, X., Balsamo, G., Bechtold, P., Biavati, G., Bidlot, J., Bonavita, M., Chiara, G., Dahlgren, P., Dee, D., Diamantakis, M., Dragani, R., Flemming, J., Forbes, R., Fuentes, M., Geer, A., Haimberger, L., Healy, S., Hogan, R.J., Hólm, E., Janisková, M., Keeley, S., Laloyaux, P., Lopez, P., Lupu, C., Radnoti, G., Rosnay, P., Rozum, I., Vamborg, F., Villaume, S., Thépaut, J.-N., 2020. The ERA5 global reanalysis. *Q. J. R. Meteorol. Soc.* 146 (730), 1999–2049.
- Holle, R.L., Murphy, M.J., 2015. Lightning in the North American monsoon: An exploratory climatology. *Mon. Weather Rev.* 143, 1970–1977.
- Keeley, J. E. and Rundel, P. W., 2005. Fire and the Miocene expansion of C4 grasslands. *Ecology Letters* 8:683–690.
- Kuhn, M., 2008. Building predictive models in R using the caret package. *J. Stat. Softw.* 28, 1–26.
- Limb, R.F., Engle, D.M., Alford, A.L., Hellgren, E.C., 2010. Tallgrass prairie plant community dynamics along a canopy cover gradient of eastern redcedar (*Juniperus virginiana* L.). *Rangeland Ecol. Manage.* 63 (6), 638–644.
- Liu, Z., Otto-Bliesner, B.L., He, F., Brady, E.C., Tomas, R., Clark, P.U., Carlson, A.E., Lynch-Stieglitz, J., Curry, W., Brook, E., Erickson, D., 2009. Transient simulation of last deglaciation with a new mechanism for Bølling-Allerød warming. *Science* 325, 310–314.
- Livneh, B., Rosenberg, E.A., Lin, C., Nijssen, B., Mishra, V., Andreadis, K.M., Maurer, E. P., Lettenmaier, D.P., 2013. A long-term hydrologically based dataset of land surface fluxes and states for the conterminous United States: update and extensions. *J. Clim.* 26 (23), 9384–9392.
- Lorenz, D. J., Nieto-Lugilde, D., Blois, J. L., Fitzpatrick, M. C., and Williams, J. W., 2016b. Data from: Downscaled and debiased climate simulations for North America from 21,000 years ago to 2100AD. Dryad Dataset. Available at: DOI:10.5061/dryad.1597g Accessed 01 December 2020.
- Lorenz, D.J., Nieto-Lugilde, D., Blois, J.L., Fitzpatrick, M.C., Williams, J.W., 2016a. Downscaled and debiased climate simulations for North America from 21,000 years ago to 2100AD. *Sci. Data* 3, 1–19.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., 2001. Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience* 51 (11), 933. [https://doi.org/10.1641/0006-3568\(2001\)051\[0933:TEOTWA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2).
- R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, USA.
- Rogers, T.R., Russell, F.L., Silman, M., 2014. Historical patterns of oak population expansion in the Chautauqua Hills, Kansas. *J. Biogeogr.* 41 (11), 2105–2114.
- Saha, S., Moorthi, S., Wu, X., Wang, J., Nadiga, S., Tripp, P., Behringer, D., Hou, Y.T., Chuang, H.Y., Iredell, M., Ek M. et al. 2014. The NCEP climate forecast system version 2. *Journal of Climate* 27:2185–2208.
- Sauer, C.O., 1950. Grassland climax, fire, and man. *J. Range Manag.* 3 (1), 16. <https://doi.org/10.2307/3894702>.
- Shantz, B.L. and Zon, R., 1924. Atlas of American Agriculture. Government Printing Office, Washington DC. Available at: <https://ia800809.us.archive.org/4/items/naturalvegetatio00shan/naturalvegetatio00shan.pdf> Accessed 7 January 2021.
- Shuman, B., Henderson, A.K., Plank, C., Stefanova, I., Ziegler, S.S., 2009. Woodland-to-forest transition during prolonged drought in Minnesota after ca. AD 1300. *Ecology* 90, 2792–2807.
- Transeau, E.N., 1935. The prairie peninsula. *Ecology* 16, 423–437.
- Trewartha, G.T., 1968. An Introduction to Climate. McGraw-Hill, New York, NY.

- Wells, P.V., 1965. Scarp woodlands, transported grassland soils, and concept of grassland climate in the Great Plains region. *Science* 148 (3667), 246–249.
- Williams, J.W., Shuman, B., Bartlein, P.J., 2009. Rapid responses of the prairie-forest ecotone to early Holocene aridity in mid-continental North America. *Global Planet. Change* 66 (3–4), 195–207.
- Williams, D. L., 1981. Reconstruction of prairie peninsula vegetation and its characteristics from descriptions before 1860. *Ohio Biological Survey Notes* No. 15: 83–86.
- Ziegler, S.S., Larson, E.R., Rauchfuss, J., Elliott, G.P., 2008. Tree establishment during dry spells at an Oak Savanna in Minnesota. *Tree-Ring Res.* 64 (1), 47–54.