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The Shifting Role of mRUE for Regulating Ecosystem Production

David E. Reed,* Jiquan Chen, Michael Abraha, G. Philip Robertson, and Kyla M. Dahlin

Michigan State University, East Lansing, Michigan 48823, USA

ABSTRACT

To create a comprehensive view of ecosystem resource use, we integrated parallel resource use efficiency observations into a multiple-resource use efficiency (mRUE) framework using a dynamic factor analysis model. Results from 56 site-years of eddy covariance data and mRUE factors for a site in the US Midwest show temporal dynamics and coherence (using Pearson's R) among resources are associated with interannual variation in precipitation. Loading factors are derived from mRUE observations and quantify how strongly data are connected to the underlying ecosystem state. Water and light resource use loading factors are coherent at annual timescales (Pearson's R of 0.86), whereas declining patterns of carbon use efficiency loading factors highlight the ecosystem's trade-off between carbon uptake and respiration during the growing season. At annual and monthly timescales, influence decreases from ~ 85 to $\sim 65\%$ for loading factors for carbon use, while influence of light use loading factors peaks to $\sim 60\%$ at growing season timescales. Quantifying variation in ecosystem function provides novel insights into the temporal dynamics of changing importance of multiple resources to ecosystem function.

Key words: multiple-resource use efficiency; ecosystem production; eddy covariance; dynamic factor analysis; carbon cycling; ecosystem function.

HIGHLIGHTS

- A framework for multiple-resource use efficiency shows coherence among resource uses.
- Loading factors for carbon use were highest at annual timescale ($\sim 85\%$), while light loading factors peaked during the growing season ($\sim 60\%$).
- Growing season carbon uptake is prioritized at the expense of respiration loses.

INTRODUCTION

In an effort to study complex systems, ecosystem scientists often attempt to quantify mechanisms to isolate parts of a larger whole (Chapin and others 2002). Mechanisms in ecosystems are the means by which organisms acquire resources—energy and materials in the environment—that are required for growth and maintenance (Field and others 1992). However, these mechanisms can be difficult to directly observe at ecosystem or landscape scales, and thus, information is often indirectly inferred. For example, gross primary productivity at the landscape scale via partition modeling is estimated based on net carbon observations (Baldocchi and

others 2001; Reichstein and others 2005), or on remotely sensed satellite images (Running and others 2004). Alternatively, multiple-resource observations can be used to quantify mechanisms and determine how efficiently ecosystems utilize resources. This approach has been used to quantify changes to individual mechanisms (Carmo-Silva and others 2015), by single species or assemblages of species within an ecosystem (Funk and Vitousek 2007), and at multiple spatiotemporal scales (Gill and Finzi 2016).

de Wit (1992) introduced the conceptual framework of ecosystem resource use efficiency (RUE) as carbon production per unit resource. For example, light use efficiency is calculated as the ratio of gross primary productivity (GPP) to incoming radiation (Campbell and Norman 2012). The RUE concept can also inform many ecosystem processes. For example, Carmo–Silva and others (2015) showed how the Rubisco function can be improved via the linkages between Rubisco regulation and light, nutrient and water use efficiencies. One reason invasive species can out-perform natives by using limiting resources more efficiently on short time-scales (Funk and Vitousek 2007). Gill and Finzi (2016) demonstrated in forested ecosystems that the primary limitation on productivity transitions from belowground resources at high latitudes to aboveground resources at low latitudes using biome-scale estimates of resource use efficiency. The RUE concept has also been used in agricultural systems for: (i) showing that corn (*Zea mays*) has the greatest biomass growth rate arising from a high radiation use efficiency compared to soybean and rice (Sinclair and Horie 1989), (ii) showing that the development of molecular technology, plant breeding and genetics may increase the yield and resource use efficiency of wheat, leading to greater food security (Parry and Hawkesford 2010) and (iii) ranking biofuel crop sustainability based on efficient use of land, water, nitrogen and energy resources (de Vries and others 2010). Recently, RUE has been used to directly quantify water (for example, Abraha and others (2016)), light (for example, Wu and others (2012)) and carbon (for example, Bradford and Crowther (2013)) uses in terrestrial ecosystem studies.

In an attempt to unify the RUE concept across multiple ecosystem types and temporal scales, Hodapp and others (2019) suggested extending RUE to more than one nutrient or resource. A framework for multiple RUE (mRUE) was advanced by Han and others (2016) using structural equation modeling—similar to other types of ecological analysis, where time-series data are summed or averaged to annual timescales, regressed against another time series, binned over similar environmental conditions or otherwise treated to remove the observations from the time series. With this approach, information from the time series itself pertaining to summer-high–winter-low phenological patterns is lost, potentially resulting in a biased conclusion (Brillinger 1981; Reed and others 2018b). Fortunately, this information loss can be avoided by using appropriate time-series frequency analysis methods, such as Fourier transforms, spectral analysis or wavelet analysis (Legendre and Legendre 2012). An emphasis of these approaches is that the dynamic results are derived and quantified from the information connecting discrete data points, not the data points themselves—providing glimpses into patterns beyond the observations. In a recent example, wavelet analysis was used to highlight common time periods of variation within a time series (Reed and others 2018a). In a contrasting example, ecological observation data (for example, carbon and water fluxes, radiation, air temperature) are commonly summed to annual timescales in which all information pertaining to summer-high–winter-low phenological patterns is lost. The review by Hodapp and others (2019) concluded there is a lack of literature incorporating temporal dynamics of RUE or, in this case, several RUEs analytically combined into one mRUE. In this study, we use new analytical approaches that maintain the intrinsically time-series-based nature of mRUE data and quantify the connectedness of these time-series observations to ecosystem function in order to provide novel insights into the mRUE temporal dynamics of the underlying ecosystem state. The end result provides insight into the controls of ecosystem function that are dynamic in time.

We use 30-min measurements of net ecosystem exchange of carbon, water and radiative fluxes over multiple years to calculate three RUEs, which in turn are used in a dynamic factor analysis to quantify ecosystem function as a single unit-less time series. This time series allows us to quantify ecosystem function variations and ultimately connect ecosystem function to mRUEs. Using 56 site-years of eddy covariance data (8 years from seven sites and five land-cover types), the first objective of this work is to quantify the temporal changes in net ecosystem productivity (NEP) at seven sites representing different annual and perennial cropping systems. Then, the data are used to constrain a dynamic factor analysis where loading factors for water, light and carbon quantify the connection between the observed RUE and an undefined

ecosystem state time series. This leads to the second objective, connecting variations in RUE information to environmental state variables in order to reveal the regulatory mechanisms of ecosystem production. Finally, our third objective is to identify the relative importance of individual RUEs for NEP at multiple temporal scales.

MATERIALS AND METHODS

Study Sites

The study area is located in southwest Michigan (42°24′N, 85°24′W, 288 m a.s.l.) at the Great Lakes Bioenergy Research Center of the W. K. Kellogg Biological Station's Long-term Ecological Research site. The climate is humid and continental, with a 30-year mean annual air temperature of 9.9 °C, and monthly averages from − 4.2 °C in January to 22.8 °C in July. Mean annual precipitation is 1027 mm, of which 523 mm falls during the growing season (May–September). Although most years of the study period (2009–2016) received near average precipitation, the year 2012 was dry, with ∼ 60% of annual precipitation and ∼ 65% of normal precipitation during the growing season. The years 2013 and 2015 were wet during the spring and into the growing season, both with months of more than 250% precipitation (National Climatic Data Center 2018). Soils at the research site are well-drained sandy loam, classified as a Typic Hapludalf (Bhardwaj and others 2011). Other details on the site history can be found in Zenone and others (2011).

Of the seven agricultural fields used in this study, three were managed as corn–soybean rotation agricultural land for 50+ years and four as USDA Conservation Reserve Program grasslands since 1987 (Abraha and others 2015). Six of the fields were converted to no-till soybean (*Glycine max*) in 2009. In 2010, two fields were planted to no-till continuous corn, two to switchgrass (*Panicum virgatum*) and two to mixed grass/forb restored prairie. Corn was planted and harvested each year since 2010, and fields with perennial vegetation were harvested post-senescence every autumn from 2011 onwards. The seventh site was left as a grassland reference site and has remained uncut since 2009. Corn was fertilized with ∼ 180 kg N ha^{-1} year^{-1} and switchgrass at ∼ 56 kg N ha^{-1} year^{-1}, whereas restored prairie and reference fields were not fertilized. None of the fields received irrigation. Additional site details can be found at Abraha and others (2015). For this study, land-cover type was defined as soybean for six sites in 2009 (6 site-years), corn, switchgrass or prairie for each of two sites from 2010–2016 (14 site-years each) and grassland for the reference site from 2009 to 2016 (8 site-years).

Eddy Covariance Data and Processing

An eddy covariance tower was established at each of the seven sites starting in November 2008, each with an LI-7500 open-path infrared gas analyzer (LI-COR Biosciences, Lincoln, NE, USA) and a CSAT3 three-dimensional sonic anemometer (Campbell Scientific Inc., Logan, UT, USA). The LI-7500s were calibrated every 4–6 months, and eddy covariance observations were sampled and logged at 10 Hz using a Campbell CR5000 data logger. Flux sensors were positioned 1.5–2.0 m above the average canopy height. CO_2 and H_2O fluxes were processed following standard AmeriFlux guidelines, with 30-min average NEP computed using EdiRe (Clement 1999), and then partitioned into gross primary production (GPP) and ecosystem respiration (R_{eco}) using nighttime methods of Wutzler and others (2018) in REddyProc. The u^* filtering was done following Papale and others (2006), with an average u^* threshold of 0.11 m/s between all site-years, which removed 25.3% of the observations. Non-gap-filled 30-min data were averaged to daily timescale only if more than 60% of the 24-h period observations were available. Between all site-years, there was an average of 17% missing data at the daily timescale. When averaging from the daily to the longer timescales (monthly, growing season or annual), no more than 20% of the days of each timescale were missing.

Ecosystem RUEs were calculated as ratios of GPP to each resource on a daily scale (Figures 1, 2), with ± 3-day running mean values to reduce noise in the time series. We used evapotranspiration (ET) observations to calculate water use efficiency (WUE, Figure 1A):

$$\mathrm{WUE} = \frac{\mathrm{GPP}}{\mathrm{ET}} \tag{1}$$

We used incoming solar radiation observed above the canopy to calculate light use efficiency (LUE, Figure 1B) as:

$$\mathrm{LUE} = \frac{\mathrm{GPP}}{\mathrm{Light}} \tag{2}$$

We used ecosystem respiration (R_{eco}) flux observations to calculate carbon use efficiency (CUE, Figure 1C) as:
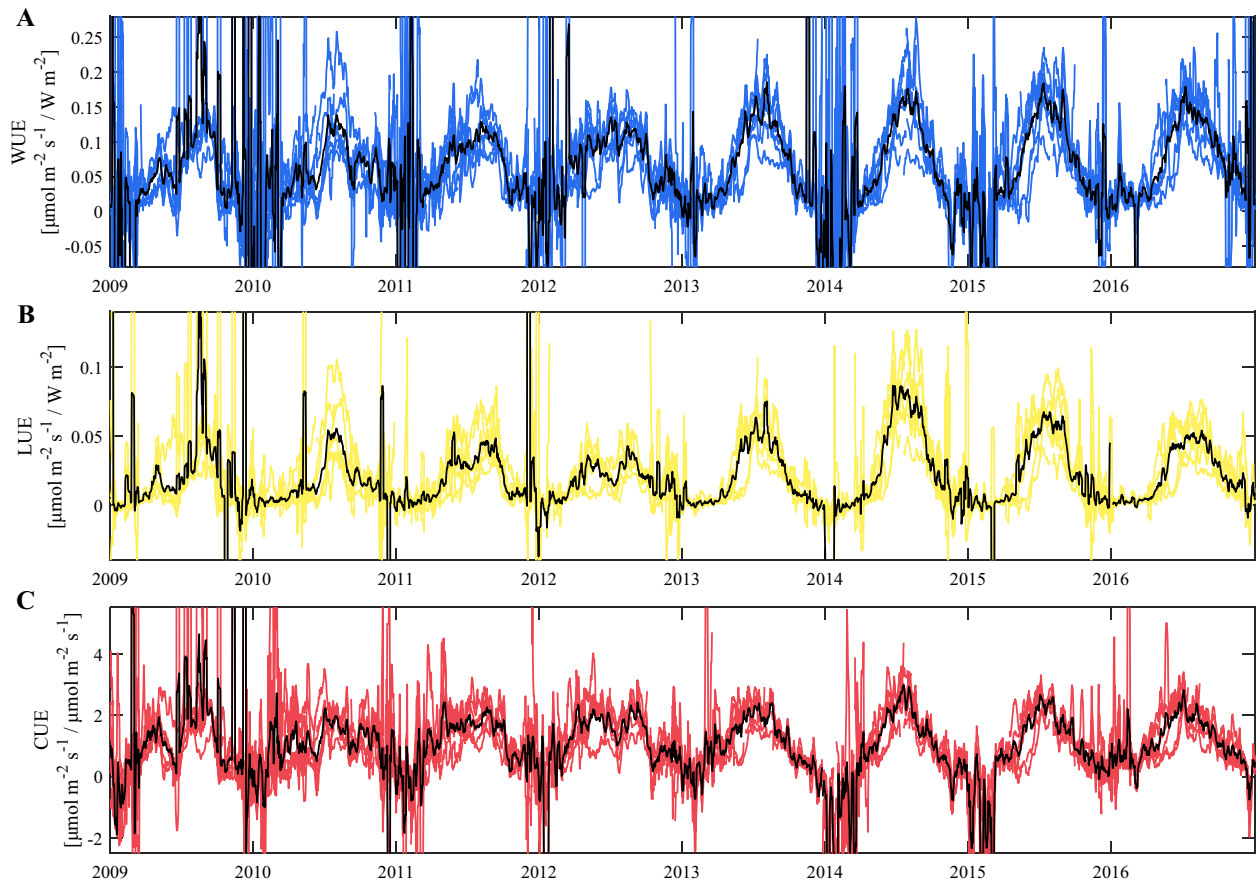
Figure 1. Three-day running means of water (**A**, blue), light (**B**, yellow) and carbon (**C**, red) resource use efficiencies for each of the seven sites, with average values between all sites in black (Color figure online).

$$CUE = \frac{GPP}{R_{eco}} \qquad (3)$$

All resource use efficiencies were rescaled to values of -5 to 5 to compare the differences caused by unit of ET, solar radiation and R_{eco}. MATLAB (The MathWorks, Inc., R2017a) was used for eddy covariance time-series processing and analysis.

Dynamic Factor Analysis

Dynamic factor analysis (DFA) has gained increasing attention from ecologists as a tool for examining the multivariate time-series datasets (Zuur and others 2003a), and broadly speaking is comparable to principal component analysis, but for time-series datasets. DFA has been used extensively in fisheries analysis (Zuur and others 2003b) and more recently in forestry (Linares and Camarero 2012), phenology (Gordo and Sanz 2005) and climate (Friedland and Hare 2007). We used the R MARSS package (Holmes and others 2012) to identify un-

known, common underlying time-series trends from the observational time series of three resource use efficiencies (equations 1–3), following the approach of Zuur and others (2003a):

$$y_{(t)} = Zx_{(t)} + a + v_{(t)} \qquad (4)$$

where $y_{(t)}$ are the three observational mRUE time series, modeled as a linear combination of $x_{(t)}$, the hidden underlying ecosystem state time series and Z are the loading factors that indicate how strongly the mRUE data is connected to the underlying ecosystem state (Figure 2, negative Z values show a negative relationship), a are offsets between observations and modeled state and $v_{(t)}$ are the errors drawn from a multivariate normal distribution with a variance–covariance matrix that is diagonal with equal variances. Each loading factor does not have a direct ecological meaning, but reflects the amount of broadly defined holistic ecosystem processes that are connected to a RUE time series, and could be used to describe ecosystem functioning in a variety of fashions. Here, we
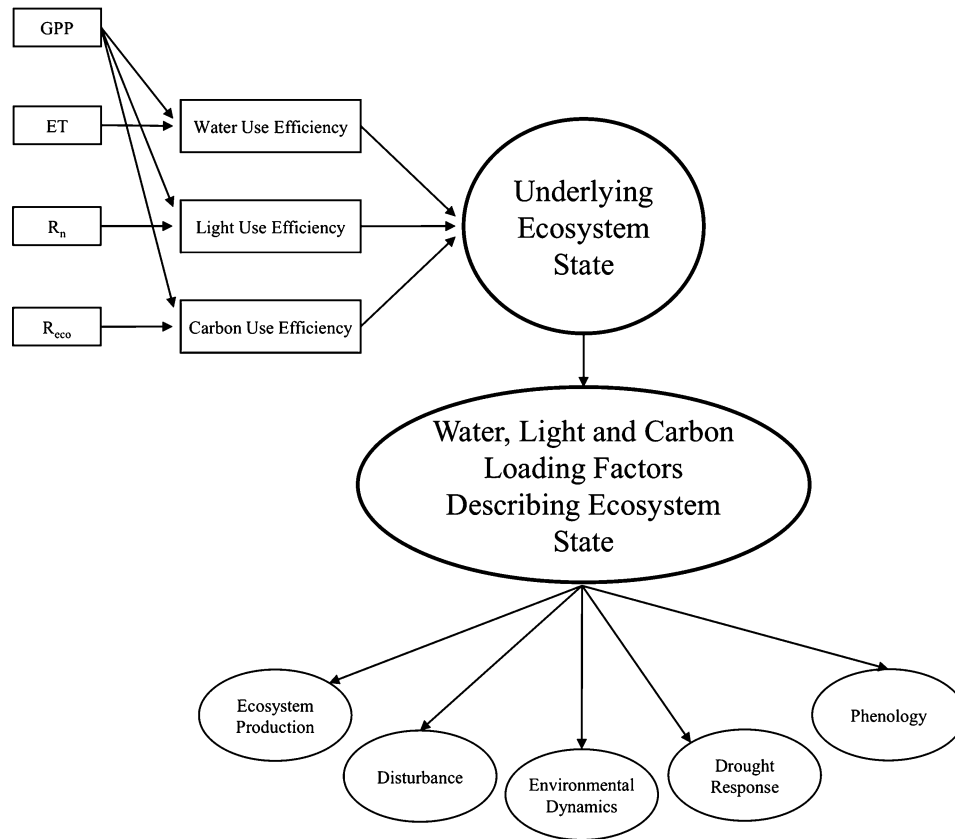
Figure 2. Conceptual framework that ecosystem evapotranspiration, solar radiation, ecosystem respiration (R_{eco}), along with gross primary productivity (GPP), are integrated as three resource use efficiencies (water, light and carbon) that in turn are used to understand unseen ecosystem processes through dynamic factor analysis. The model output is loading factor time series, one for each resource, that describes the state functioning of the ecosystem from the aspect of each resource. The multiple-resource use efficiency model can be used to assess ecosystem function from different points of view and at multiple temporal scales, including in this case, ecosystem production.

choose to use the loading factors to describe the ecosystem state in the context of ecosystem production.

We ran the DFA model (Figure 2) using the three RUE time-series data from each site-year for annual and growing season periods with each of the seven sites treated as a replicate. The growing season was defined as days above the 90% maximum GPP value for each site-year. To capture the seasonal changes, the DFA model was also run for each site-year, with all seven sites averaged on a monthly basis for 8 years. The DFA model produced time series of three loading factors for each site-year that described the underlying ecosystem state, and all output grouped across all seven sites for annual and seasonal analyses across 8 years. Model output was screened if the model run contained missing values greater than 20% timescale-dependent threshold (i.e., 73 days out of a single year, 24 days out of the growing season, or 6 days a month). The relative weights of loading factors were calculated by month for each loading factor as the percent of the sum of all loading factors. Differences between DFA loading factors were determined with Student's T-test. Time-series coherence was defined as the Pearson correlation coefficient or Pearson's R of two time series.

RESULTS

The weights for mRUE loading factors were dynamic and changed daily. Loading factors for water, light and carbon at annual and growing season scales were binned across all site-years (Figure 3A) and loading factors were higher on average at the growing season scale, relative to the annual or monthly timescale. For an individual set of loading factors at the growing season timescale, light use loading factors ranked the highest, signifying a higher degree of connection between light use and ecosystem function. Growing season light use loading factors tracked annual precipitation
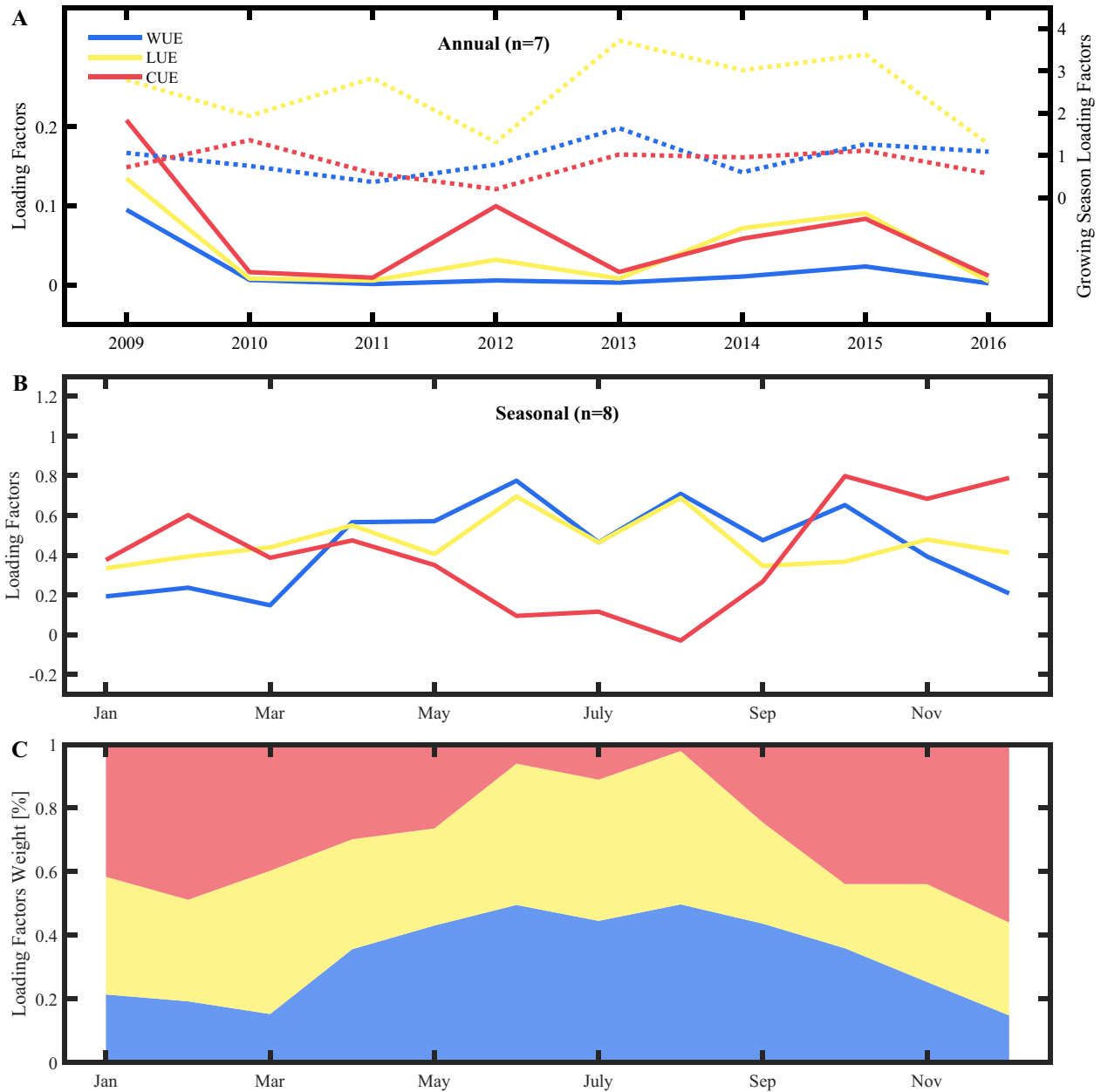
Figure 3. Changes in dynamic factor analysis (DFA) for water, light and carbon use efficiencies for annual timescales (solid line, left axis) and for the growing season only (dotted line, right axis) (**A**). Monthly loading factors shown for each resource use efficiency (**B**) and normalized weights of each loading factor (**C**).

amounts well ($p < 0.05$), with 2012 having the lowest and 2013 and 2015 having the highest values. This pattern was not significant for water or carbon use loading factors at the growing season timescale, nor for any loading factors at the annual timescale. At annual scales, water use loading factors were the lowest, with a considerable covariance noted between light and carbon use loading factors.

Although all RUEs show a clear summer-high and winter-low pattern (Figure 1), similar seasonal patterns emerged only for water and light use loading factors when the DFA model was run on a monthly basis (Figure 3B). However, carbon use loading factors show divergent behaviors, with a decreasing trend throughout the year until late summer, after which a large increase happens during the early fall. When weighted against each other, the average growing season carbon use loading factor is lower relative to water and light use loading factors in the growing season, particularly in the middle of summer (Figure 3C).

The restored prairie sites had higher water use loading factors among the land-cover types (Figure 4A). Light use loading factors appear high in both the reference grassland site and the soybean sites (Figure 4B). Due to the experimental design (i.e., six fields planted to soybean in 2009), it is difficult to determine whether the soybean land-cover type or the year (2009) had higher light use loading factors. A slightly higher carbon use loading factors is noted for the reference grassland (Figure 4C).

We also find clear temporal coherence (Pearson's R) between the mRUE loading factors. Average coherence between annual loading factors was 0.89, with coherence loading factor between water and light (0.86, $p = 0.006$), water and carbon (0.79, $p = 0.002$) and light and carbon (0.83, $p = 0.003$) significant. However, at the growing season timescale, coherence between loading factors was not significant (average $p = 0.37$). Coherence of normalized differences between annual and growing season timescales (Figure 4D) was significant (average $p = 0.01$) and appeared similar to the coherence at the annual timescale, with an average value of 0.83.

Loading factors also exhibit interdependent behavior and covary at multiple temporal scales. In order to probe the interdependence of loading factors, we show proportions of loading factors summed to 100% on ternary plots. First, we show monthly data from all site-years (Figure 5A), with a seasonal pattern of increasing light use loading factors from winter into summer, from ~ 30 to $\sim 50\%$ in June to $\sim 30\%$ in winter. Water use loading factors decrease from $\sim 70\%$ in winter to $\sim 50\%$ in summer and then bounce back to $\sim 70\%$ by the end of the year. Carbon use is high in winter ($\sim 80\%$) and decreases to $\sim 50\%$ in summer. We also directly compared model results across timescales. Average water use loading factors reach their base during the growing season, decreasing from $\sim 65\%$ at annual and monthly timescales to $\sim 40\%$ at growing season timescale (Figure 5B), whereas carbon use loading factors show a decreasing trend with smaller timescales, with $\sim 85\%$ at annual timescales and $\sim 65\%$ at monthly scales. Light use loading factors peak in the growing season at $\sim 60\%$, with values of $\sim 35\%$ at other timescales.

DISCUSSION

The first objective of this study was to quantify the temporal dynamics of ecosystem resource use efficiency derived from DFA loading factors, high-lighted as a gap in the literature (Hodapp and others 2019). We demonstrate that the loading factors for water and light use follow annual summer-high–winter-low trends, similar to environmental drivers (for example, air temperature, solar radiation) and net carbon flux measurements (Baldocchi and others 2001; Noormets 2009). Although loading factors describe the amount of influence each RUE has on ecosystem function as a function of time, high loading factors are connected to ecosystem function in a holistic fashion. This matches the results of Shi and others (2014) who reported differences in light and water use efficiencies between summer and winter due, in part, to changing sensitivities to the atmospheric vapor pressure deficit. Here, high water and light use loading factors values during the summer show that water and light are relatively more important to ecosystem functioning in the summer.

Carbon use loading factors show a different trend, with high values during winter declining throughout the growing season, only to increase again in the fall. To explain these changes, we hypothesize that agricultural ecosystems are prioritizing carbon uptake at the expense of increased respiration during the growing season. That is, plants may be expressing low carbon use efficiencies in order to prioritize carbon allocation to belowground storage for grassland and prairie fields or growth of seeds for corn and soybean fields. Additionally, high summer air and soil temperatures increase respiration at the ecosystem level across multiple land-cover types (Law and others 2002), which would act to reduce carbon use efficiencies. The agricultural ecosystems in this study show decreases in loading factors of carbon use during the growing season, with a negative loading factor value found in August when the plant canopy is fully established. Kikuzawa (1995) reports that simultaneous leaf emergence, such as in agricultural systems, maximizes carbon efficiency, which would cause a large and sudden shift from respiration to net carbon accumulation. However, in August, there would be the highest amount of self-shading within the canopy, net respirations rates would be high due to temperature, all while maximizing energy partitioning into fruits, seeds or storage for next season.

To probe the connection between RUE information and regulatory mechanisms for our second objective, we combine the time-series nature of the loading factor results with the land-cover information. Although long resource use efficiency time series are rare in the literature, Tarvainen and others (2015) used data from a 3-year study to
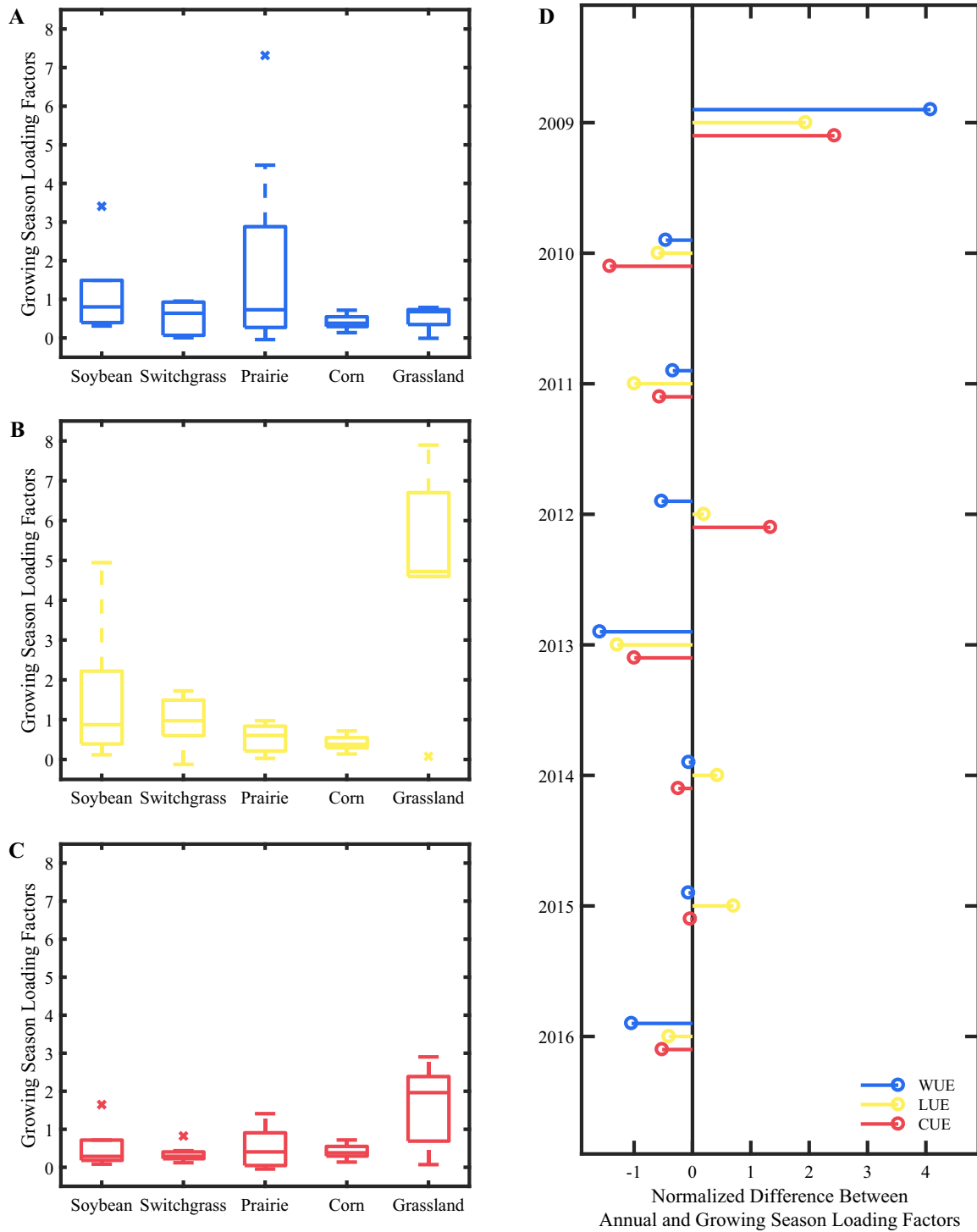
Figure 4. **A–C** Box plots (box defined as median, 25th and 75th percentiles of data, whiskers out to last data point within ± 2.7σ, outliers denoted with x's outside of whiskers) of water (**A**), light (**B**) and carbon (**C**) loading factors for the five land-cover types. **D** Stem plot of normalized differences of water, light and carbon loading factors between annual and growing season timescales.

build multiple regression models and showed water, light and nitrogen resource use efficiencies having time-dependent peaks. They found that

water use efficiency of Norway spruce (*Picea abies*) peaked in spring, nitrogen use efficiency peaked in summer and light use efficiency reached its highest
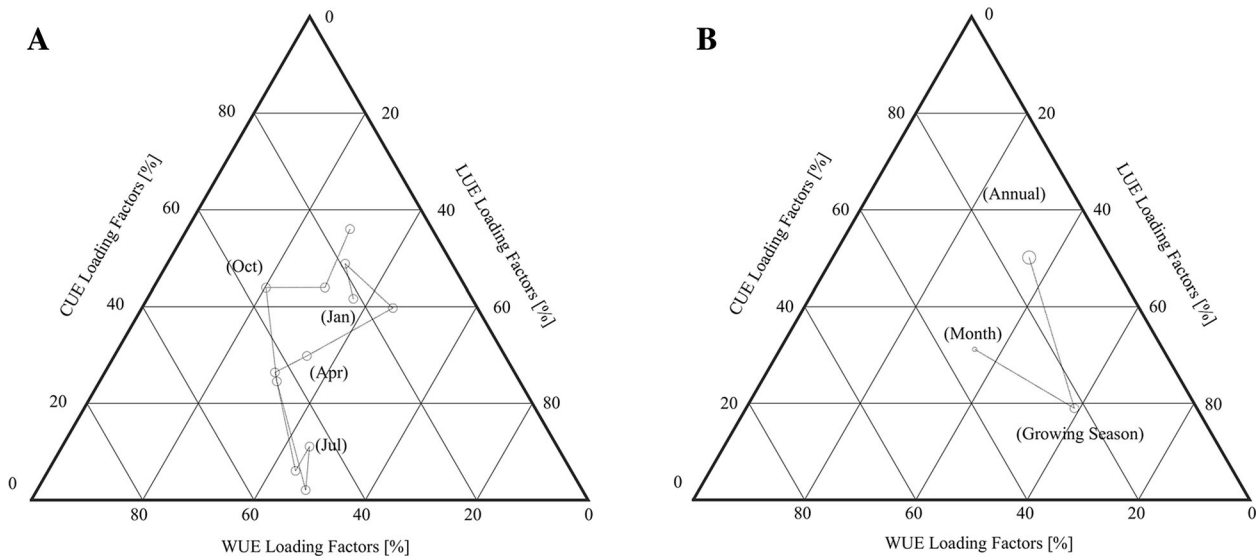
Figure 5. Ternary plots of normalized water, light and carbon use loading factors annually for each month (**A**) and loading factors for model timescales of annual, growing season and monthly lengths (**B**).

point in fall. We found that light use loading factors peaked in summer at our sites, whereas water and carbon use loading factors both peaked later during winter (Figure 5A). This indicates ecosystem function being connected to light use efficiency during the summer, whereas water use and carbon use efficiencies share importance during the non-growing season. Tarvainen and others (2015) showed within canopy variation of resource use efficiencies in their relatively deep spruce canopies. In our study, this variation is type dependent: Water use loading factors are high in the restored prairie, light use loading factors in soybean, and light and carbon use loading factors in the reference grassland. This is in contrast to other agriculture light use efficiency results, such as Sinclair and Horie (1989) who showed corn having higher light use efficiency relative to other crops. However, our work combines multiple-resource use efficiencies, whereas Sinclair and Horie (1989) used separate resource efficiencies.

Our third objective is identifying key RUEs at multiple temporal scales, and at the annual time-scales, carbon use appears the most influential factor to ecosystem function, with water use being second (Figure 5B). Although the DFA results only quantify ecosystem function in a holistic sense, one interpretation of these findings is that light use efficiency, when aggregated to the annual time-scale, might be a proxy for growing season length or at least the sum of available light over the year. Previous work on growing season lengths has shown that Michigan growing seasons are more

stable than that of other states (Kunkel and others 2004). Generally, across the Upper Midwest recent climate change has been impacting summer relative humidity and annual precipitation, and not growing season length (Motew and Kucharik 2013). Furthermore, from 1948 to 2007, the Upper Midwest saw an increase in net carbon uptake due to a reduction in soil moisture stress as well as decreased stomatal conductance resulting from the increase in humidity (Motew and Kucharik 2013). A second interpretation of carbon being the most influential factor is that the ecosystem is carbon limited on annual timescales. When results include the winter season and the carbon respiration signal during winter, soil respiration increasingly dominates the carbon flux signal and therefore the carbon use efficiencies at the annual timescale. Combined, these findings show Midwest ecosystem function being influenced more by carbon and water use efficiencies and less by growing season length and light use efficiency, which have been shown to be relatively stable in time.

Environmental science is quickly becoming more data rich, which facilitates new and novel analytical approaches. Methods that employ annual, monthly or weekly sums or averages from time series ultimately sacrifice information (Reed and others 2018b). For example, a mature forest and a mesic grassland could both be carbon-neutral on an annual timescale, but examining the two intra-annual time series would show large difference in the daily and seasonal magnitude of carbon fluxes between sites (Reichstein and others 2007; Yi and

others 2010). We use the DFA to pull information from the time series itself, quantifying the connections and data between discrete observations, instead of focusing on the absolute values of the observations. In this way, we are able to show interdependence of resource use and their dynamics.

DFA is an underutilized method to quantify drivers of time-series observations and can be a powerful tool for analyzing ecosystem dynamics, here with a focus on carbon cycling and resource use efficiencies. We show for these sites that water and light use efficiencies have expected seasonal patterns and are connected to the amount of growing season rainfall, while carbon use efficiency shows a trade-off between carbon uptake at the expense of higher respiration. We also find the importance of water use efficiency increases over smaller timescales, demonstrating that annual sums of precipitation are less significant to carbon cycling than monthly precipitation. DFA can also be applied in other ecosystems and with other datasets in order to quantify ecosystem dynamics in a more comprehensive method. In sum, the three resource uses co-limited ecosystem function at varying degrees at multiple timescales.

A holistic framework for modeling ecosystem functions remains an open challenge. Combining multiple-resource use efficiencies via DFA loading factors allows multiple regulating processes to be incorporated into one framework. Taking the advantages of this framework, additional work could add yearly or irregular data such as annual yield or disturbances (for example, fertilizer applications, irrigation, tillage and so on) to examine temporal effects between data at multiple frequencies and scales. Changes in regulating processes during disturbances could be quantified, or irregular units such as phenology or growing season lengths could be incorporated in an inclusive fashion. The mRUE concept can help answer a fundamental question in ecosystem science: how important are different resources to carbon assimilation and use?

ACKNOWLEDGEMENTS

DATA ACCESSIBILITY STATEMENT

Data used for this project are available in the Michigan State University Landscape Ecology & Ecosystem Science Lab data repository (http://lees.geo.msu.edu/research/NASA_carboncycle/) and the Climate Science Research Group data repository (https://sites.google.com/view/climate-science-lab/data-and-code), while analysis code is availed at https://github.com/ClimateScienceResearchGroup/mRUE. When accepted for publication, data and code will be available at Dryad.

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