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Ecosystem resilience despite large-scale altered hydroclimatic condition

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Climate change is predicted to increase both drought frequency and duration, and when coupled with substantial warming, will establish a new hydroclimatologic paradigm for many regions[1]. Large-scale, warm droughts have recently occurred in North America, Africa, Europe, Amazonia, and Australia, resulting in major impacts on terrestrial ecosystems, carbon balance, and food security[2,3]. Here we compare the functional response of above-ground net primary production (ANPP) to contrasting hydroclimatic periods in the late-20th-century (1975-1998) and drier, warmer conditions in the early 21st century (2000-2009) in the Northern and Southern Hemispheres. We found a common ecosystem water-use efficiency (WUE_e: ANPP/evapotranspiration) across biomes ranging from grassland to forest that indicates an intrinsic system sensitivity to water availability across rainfall regimes, regardless of hydroclimatic conditions. We found higher WUE_e in drier years that increased significantly with drought to a maximum WUE_e (WUE_x) across all biomes; and a minimum native state (WUE_n) that was common across hydroclimatic periods. This indicates biome-scale resilience to the inter-annual variability associated with the early 21st century drought – e.g., the capacity to tolerate low annual precipitation and to respond to subsequent periods of favorable water balance. These findings provide a conceptual model of ecosystem properties at the decadal scale applicable to the wide-spread altered hydroclimatic conditions that are predicted for later this century. Understanding

the hydroclimatic threshold that will break down ecosystem resilience and alter WUE_x may allow us to predict landsurface consequences as large regions become more arid, starting with water-limited, low-productivity grasslands.

Increased aridity and persistent droughts are projected in the 21st century for most of Africa, southern Europe and the Middle East, most of the Americas, Australia, and Southeast Asia[1]. This is predicted to dramatically change vegetation productivity across ecosystems from grasslands to forests[2,4,5] with direct impact on societal needs for food security and basic livelihood[6]. However, model predictions of productivity responses can only provide most-likely scenarios of the impact of climate change, and few experiments have focused on how anticipated changes in precipitation might be generalized across terrestrial ecosystems[9]. Long-term measurements of natural variability in field settings, supported by manipulative experiments, are considered the best approach for determining the impact of prolonged drought on vegetation productivity[6,7].

In field experiments, vegetation productivity is generally measured as the above-ground net primary production (ANPP, or total new organic matter produced above-ground during a specific interval[8]) and vegetation response to changes in precipitation is quantified as rain-use efficiency (RUE), defined as the ratio of ANPP to precipitation over a defined season or year[9]. Using this approach, continental-scale patterns of RUE have been reported for extended periods in the late 20th century[10]. Ecosystem water-use efficiency (WUE_e: ANPP/evapotranspiration[11]) provides additional insight into the ecological functioning of the land surface, where evapotranspiration (ET) is calculated as precipitation minus the water lost to surface runoff, recharge to groundwater and changes to soil water storage[12] (Supplementary Appendix II). Here we compare the functional responses of RUE and WUE_e to local changes in precipitation to document ecosystem resilience – the capacity to absorb disturbances and retain the same function, feedbacks, and sensitivity[13] – during altered hydroclimatic conditions[14].

The objective was to determine how ANPP across biomes responded to altered hydroclimatic conditions forced by the contemporary drought in the Southern and Northern Hemispheres. This study is based on measurementsmade during the period from 2000-2009 at 12 United States Department of Agriculture (USDA) long-term experimental sites in the conterminous United States and Puerto Rico, and 17 similar sites in the Australian continent over a range of precipitation regimes (termed $USDA_{00\text{-}09}$ and $Australia_{01\text{-}09}$, respectively). To contrast productivity under altered hydroclimatic conditions with precipitation variability in the late 20th century, we compared results from the 2000-2009 period with similar analysis of measurements made during the period from 1975-1998[10]. The latter measurements were made primarily at Long-term Ecological Research (LTER) locations, with 14 sites – 12 in North America and 2 in Central and South America - hereafter referred to as the $LTER_{75\text{-}98}$ dataset. For a subset of the $LTER_{75\text{-}98}$ sites, ANPP measurements were continued during the period from 2000-2009 (termed $LTER_{00\text{-}09}$) and these were used for further validation of the results (Supplementary Table A1).

The warm drought during the early 21st century in the US, Europe and Australia has been recognized as a significant change from the climatological variability of the late 20th century[1,15]. Globally, the 2000-2009 decade ranked as the 10 warmest years of the 130-year (1880-2009) record[16]. Global annual evapotranspiration increased on average by 7.1 mm/yr/decade from 1982-1997, and after that, remained at a plateau through 2008[17], thereby revealing the impact of the drought on this important Earth surface process[17]. In the United States, heat waves in 2005, 2006 and 2007 broke all-time records for high maximum and minimum temperatures, and drier than average conditions were reported for over 50% of the conterminous US in 2000-2002 and 2006-2007[18]. In Australia, the widespread 6-year drought from 2001 to 2007 was recorded as the most severe in the nation's history[19]. The mean Palmer Drought Severity Index[20] (PDSI; Supplementary Appendix II) for USDA and Australian sites decreased significantly ($P<0.002$) from 1980-1999 to 2000-2009 (USDA) and 2001-2009 (Australia), declining from -0.06 to -0.81 and from 0.09 to -1.34, respectively, where a reduction in the PDSI indicates an increase in aridity. Furthermore, warm-season temperatures at USDA and Australian sites during the 2000-2009 and 2001-2009 periods, respectively, were significantly higher ($P<0.014$) than 1980-1999 averages, warming by 0.32 and 0.44 ºC, respectively.

The Enhanced Vegetation Index (EVI[21]) satellite observations from the Moderate Resolution Imaging Spectroradiometer (MODIS) were integrated annually (termed iEVI) as an empirical proxy for ANPP at USDA$_{00\text{-}09}$ and Australia$_{01\text{-}09}$ sites (Supplementary Appendix II). There are multiple publications suggesting that this is a robust approximation of collective plant behavior[-23], and here, we quantified the accuracy of this relation for the biomes, years and precipitation patterns of this study. *In situ* estimates of ANPP made with conventional field assessment methods (ANPP$_G$) during the period 2000-2009 were compiled for 10 sites across the United States (Supplementary Table A2) and compared with iEVI measurements for the same site and year (Figure 1). A log-log regression resulted in an equation that was used to estimate ANPP from iEVI values (ANPP$_S$), where $ANPP_S=51.42 \times iEVI^{1.15}$ resulting in a strong correlation between ANPP$_G$ and ANPP$_S$ for this dataset (Figure 1).

Cross-biome WUE$_e$ during altered hydroclimatic condition

The response of plant production to precipitation during the contemporary hydroclimatic conditions of prolonged warm drought showed strong agreement with the ANPP/precipitation relations reported during the late 20th century[10] (Figure 2a). The lowest mean RUE (i.e., slope of the ANPP/precipitation relation) reported for biomes with the highest mean precipitation can be explained largely (though not completely[10]) by the rain water that is not available for plant production due to runoff, groundwater recharge and increased soil water storage. Thus, the increase in water available for vegetation production with increasing precipitation is partially consumed by non-biological components of the hydrologic cycle (i.e., runoff and deep drainage). This is particularly true during entrenched drought due to additional storage-refill capacity[24] of a soil profile that has been depleted of water during prolonged drought. This becomes apparent when production was plotted as a function of evapotranspiration: the mean ecosystem water-use efficiency (WUE$_m$) was constant across the entire precipitation gradient (Figure 2b). Further, there were no significant differences among WUE$_m$ between the three datasets ($P > 0.05$ per homogeneity of regression slope test[25]). Combined, this indicated that all biomes retained their intrinsic sensitivity to water availability during prolonged, warm drought conditions. This fact suggests that the rules governing how species are organized in terms of their tolerance of hydrological stress are robust despite extended perturbation by low precipitation[26].

When water limitations at each site were most severe (for the driest years in each multi-year record), a maximum ecosystem WUE (WUE$_x$) across all biomes was revealed for each of the 3 datasets (Figure 3a). The WUE$_x$ was significantly higher for the Australia$_{01\text{-}09}$ sites (PDSI=-

1.34) than for the $LTER_{75\text{-}98}$ and $USDA_{00\text{-}09}$ sites (PDSI~0 and PDSI=-0.81, respectively) ($P < 0.05$[25], Figure 3a inset). This implies a cross-biome sensitivity to prolonged warm drought where ecosystems sustain productivity in the driest years by increasing their WUE_e. It also indicates that in the driest year of the recent prolonged warm drought, water limitations overshadowed the limitations imposed by other resources even at high-productivity sites. The increase in cross-biome WUE_x with declining PDSI suggests that most biomes were primarily water limited during the driest years of the early 21st century drought.

As a test of ecosystem resilience, a similar comparison was made for the wettest years during mid- to late-drought (2003-2009) and compared to the results for the wettest years during the earlier hydroclimatic conditions from 1975-1998. For the wettest years in both periods, we found a minimum value (WUE_n) that was common to all biomes and similar across both hydroclimatic periods (Figure 3b). The finding that WUE_n did not vary ($P > 0.05$[25]) across different hydroclimatic periods indicates a cross-biome capacity to respond to high annual precipitation, even during periods of warm drought. The decrease from maximum to minimum WUE_e ranged from 14% (for the $USDA_{00\text{-}09}$ and $LTER_{75\text{-}98}$ datasets) to 35% (for the $Australia_{01\text{-}09}$ dataset) and is hypothesized to occur through additional resource constraints that come into play in wet years, including light and nutrient limitations[10,26]. However, it may also be true that mechanistic relationship between the two time-periods is not consistent, where shifts in contemporary species composition as a result of drought influenced this landscape-scale process.

The ability of plants to increase WUE_x and retain historic WUE_n during altered hydroclimatic conditions suggest that the factors controlling these two processes are different with respect to how climate and the vegetation assemblage are changing. During the driest years, there was a cross-biome adjustment in WUE_e that increased with drought intensity, thus sustaining production at near late-20th-century levels during prolonged drought. In the wettest years, the sites exhibited an ability to absorb the disturbances associated with the early 21st century drought and retained the same sensitivity of ANPP to water availability across both hydroclimatic periods. These different responses to precipitation extremes may be due to changes in vegetation structure and function, and plant-soil feedbacks that are not captured in the integrated analysis of either RUE or WUE_e. These must be considered in a full assessment of ecosystem vulnerability or resistance to change.

Ecosystem resilience during altered hydroclimatic condition

In this study, ecosystem resilience was measured as the capacity of ecosystems to absorb disturbances associated with the early 21st century drought and retain late-20th-century sensitivity of ANPP to high annual water availability. Our analyses suggest an intrinsic sensitivity of plant communities to water availability, and a shared capacity to tolerate low annual precipitation but also to respond to high annual precipitation. These findings provide a conceptual model of ecosystem resilience at the decadal scale during the altered hydroclimatic conditions that are predicted for later this century[1] (Figure 4). During the driest years, the high-productivity sites became water limited to a greater extent resulting in higher WUE_e similar to that encountered in less productive, more arid ecosystems. It follows that when all ecosystems are primarily water limited, a cross-biome maximum WUE_e will be reached (WUE_x), and that this cross-biome likely has a maximum value cannot be sustained with further reductions in water availability. Further, we predict that as cross-biome WUE_e reaches that maximum WUE_x value, WUE_n will approach WUE_x because production will be limited largely by water supply and less so by nutrients and light (Figure 4).

With continuing warm drought, the single linear ANPP/ET relation that forms the common cross-biome WUE_e would collapse as biomes endure the significant drought-induced mortality that has been extensively documented over the past decade[2,5]. This loss of resilience associated with dieback would likely occur first for ecosystems that respond most rapidly to precipitation variability (i.e., grasslands[27,28]). Thus, the cross-biome ANPP/ET relation would become non-linear as WUE_x and WUE_n approached zero for the most water-limited, low-productivity sites, while WUE_e values would be less impacted in the high-productivity sites. Subsets of the $LTER_{75\text{-}98}$ (n=4), $USDA_{00\text{-}09}$ (n=5) and $Australia_{01\text{-}09}$ (n=2) datasets limited to grassland sites across a semiarid-to-mesic precipitation gradient were used to corroborate this prediction (Figure 4 inset). During this study period, grassland WUE_x decreased with increasing aridity (decreasing PDSI) indicating an increasing lack of resilience with prolonged warm drought in these biomes, as predicted. This implies that these systems are closer to a threshold which, when crossed, will result in biome reorganization.

Discussion

Here we quantified the impact of the early 21st century drought on ecosystem productivity and resilience across many sites on 2 continents. Cross-biome capacities and sensitivities of production were maintained through prolonged warm drought by increases of WUE_e during the driest years and a resilience during wet years indicated by a common WUE_e across both hydroclimatic periods. The conclusions are particularly compelling because they are based on measurements across multiple biomes with comparisons of multi-year periods of altered hydroclimatic conditions. These findings were extended to predictions that, if warm drought continues, significant mortality, particularly in low-productivity grasslands that are most sensitive to water availability may threaten ecosystem resilience across biomes given the substantial changes in ecosystem structure. The emergence of these patterns at the spatial and temporal scale at which they were derived requires investigation of the supporting ecohydrological mechanisms that underlie the complex plant-soil couplings. Spatially, this work represents broad cross-biome behavior but does not fully represent the complex site-level response to prolonged warm drought. The site-level mechanisms associated with disease, pests, fire, response lags, species replacement and meristem density in forests[2] and grasslands[4,27,29] complicate specific processes maintaining or impacting cross-biome resilience of ecosystem function. Further, there are predictions of a general biogeochemical resetting as increases in carbon dioxide supply affect a multitude of plant and soil processes[30]. Temporally, these predictions of ecosystem resilience were based on behavior at the scale of a decade or longer, including a period of prolonged warm drought. With careful application of this satellite-based metric, it is possible to continue monitoring cross-biome ecosystem resilience at selected cross-continental sites year-by-year into the future as we develop a greater understanding of the physical and biological mechanisms controlling these patterns.

Methods Summary

Daily precipitation and temperature were measured at *in-situ* stations and represented a homogeneous vegetated area of ~2x2 km and no major disturbances (e.g. fires) during the 2000-2009 period. Total and mean annual precipitation were computed from daily values over the study period during the hydrologic year (October – September for the U.S. and May-April for Australia). PDSI values at each location were computed using the corresponding precipitation, temperature and soil water holding capacity data. For the Enhanced Vegetation Index (EVI), images (tiles) from the MODIS website were downloaded to extract a measurement every 16-days at 250m spatial resolution for each site involved. Quality assurance (QA) at the pixel level was applied before window sizes of 9x9 pixels were averaged, including only those pixels that passed the QA control. The resulting time series were smoothed in order to extract more accurate annual integrated EVI values. Estimates of mean annual evapotranspiration were obtained for all the sites by incorporating annual precipitation and percentages of forested and herbaceous cover in a model derived from over 250 catchment-scale measurements from around the world[12].

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Full methods and any associated references are available in the online version of the paper at www.nature.com/nature.

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions GEPC, MSM and AH conceived the study, assembled the data, and produced the preliminary results. The remaining authors collected and analyzed data, and contributed to the interpretation of results. All authors contributed to writing the paper. Statistical analyses were performed by GEPC.

Author information Reprints and permissions information is available at www.nature/com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of this article at www.nature.com/nature. Correspondence and requests for materials should be addressed to GEPC (geponce@gmail.com) or MSM (susan.moran@ars.usda.gov).

Figure Captions:

Figure 1. Relation between ANPP and iEVI. Relation between annual *in situ* estimates of vegetation production ($ANPP_G$) and the corresponding iEVI derived from MODIS data during the 2000-2009 period for 10 selected sites across multiple biomes (Table A2). The solid line represents the linear regression (R^2=0.82, P<0.0001) used to estimate ANPP from iEVI values ($ANPP_S$), where $ANPP_S$=51.42 x $iEVI^{1.15}$. The inset shows the correlation between estimates of $ANPP_S$ and $ANPP_G$ for the 10 sites over multiple years with R=0.94 and root mean squared error (RMSE)=79 g m^{-2}.

Figure 2. Cross-biome sensitivity to precipitation during altered hydroclimatic condition. Relation of plant production to **a)** precipitation and **b)** evapotranspiration (ET) across precipitation regimes during the late 20th century ($LTER_{75-98,}$ green) and during altered hydroclimatic conditions characterized by prolonged, warm drought ($USDA_{00-09}$ and $Australia_{01-09}$, red), showing significant coefficients of determination in best-fit regressions for each dataset (*P*<0.0001). Symbols represent the mean values for each site over the multi-year study period. Three LTER sites with *in situ* estimates of $ANPP_G$ during the 2000-2009 period (black) were included for qualitative validation of results with $ANPP_S$. The Figure 2b inset illustrates differences in mean water-use efficiencies (WUE_m: the slope of the ANPP/ET relation) across hydroclimatic conditions, where PDSI ranged from ~0 to -1.34 and columns labeled with the same letter are not significantly different (*P* >0.05[25]).

Figure 3. **Ecosystem resilience across biomes and hydroclimatic conditions. a)** Maximum (WUE_x) and **b)** minimum (WUE_n) water use efficiency, defined by the slope of the ANPP/evapotranspiration relation in the driest years and wettest years, respectively, based on all sites for each dataset, plus the three $LTER_{00-09}$ validation sites. The insets illustrate the differences in a) WUE_x and b) WUE_n with mean PDSI for the study periods and locations, where columns labeled with the same letter are not significantly different (*P* >0.05[25]) across hydroclimatic conditions.

Figure 4. **A conceptual model of ecosystem resilience during altered hydroclimatic condition. a)** A summary of WUE_e results in this study (solid lines), overlain with the predicted behavior of WUE_x (brown dashed line) and WUE_n (blue dashed line) along a continuum of sites limited primarily by water and by other resources with an arbitrary distinction made here at ET=700 mm yr^{-1} for illustration only (black dashed line). Predictions are based on forecasts of continuing warm drought, resulting in more high-productivity sites that are primarily water limited and an increase in cross-biome maximum WUE_x. When cross-biome WUE_x reaches a maximum that cannot be sustained with further reduction in water availability, minimum WUE_n will also reach a maximum, where WUE_n will approach WUE_x. A non-linear ANPP/ET relation (not shown) will follow as WUE_x and WUE_n approach zero for the most water-limited, low-productivity sites. The inset illustrates the decrease in WUE_x with PDSI for subsets of the

$LTER_{75-98}$ (n=4), $USDA_{00-09}$ (n=5) and $Australia_{01-09}$ (n=2) datasets limited to grassland sites, where columns labeled with the same letter are not significantly different ($P > 0.05$[25]).

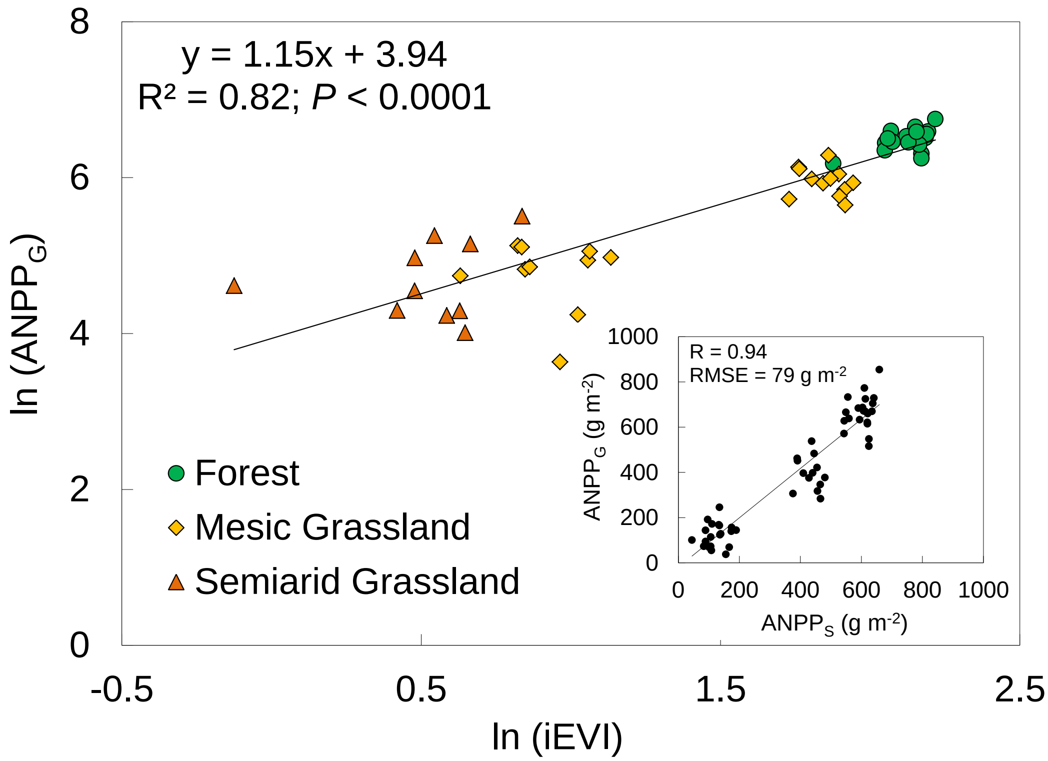
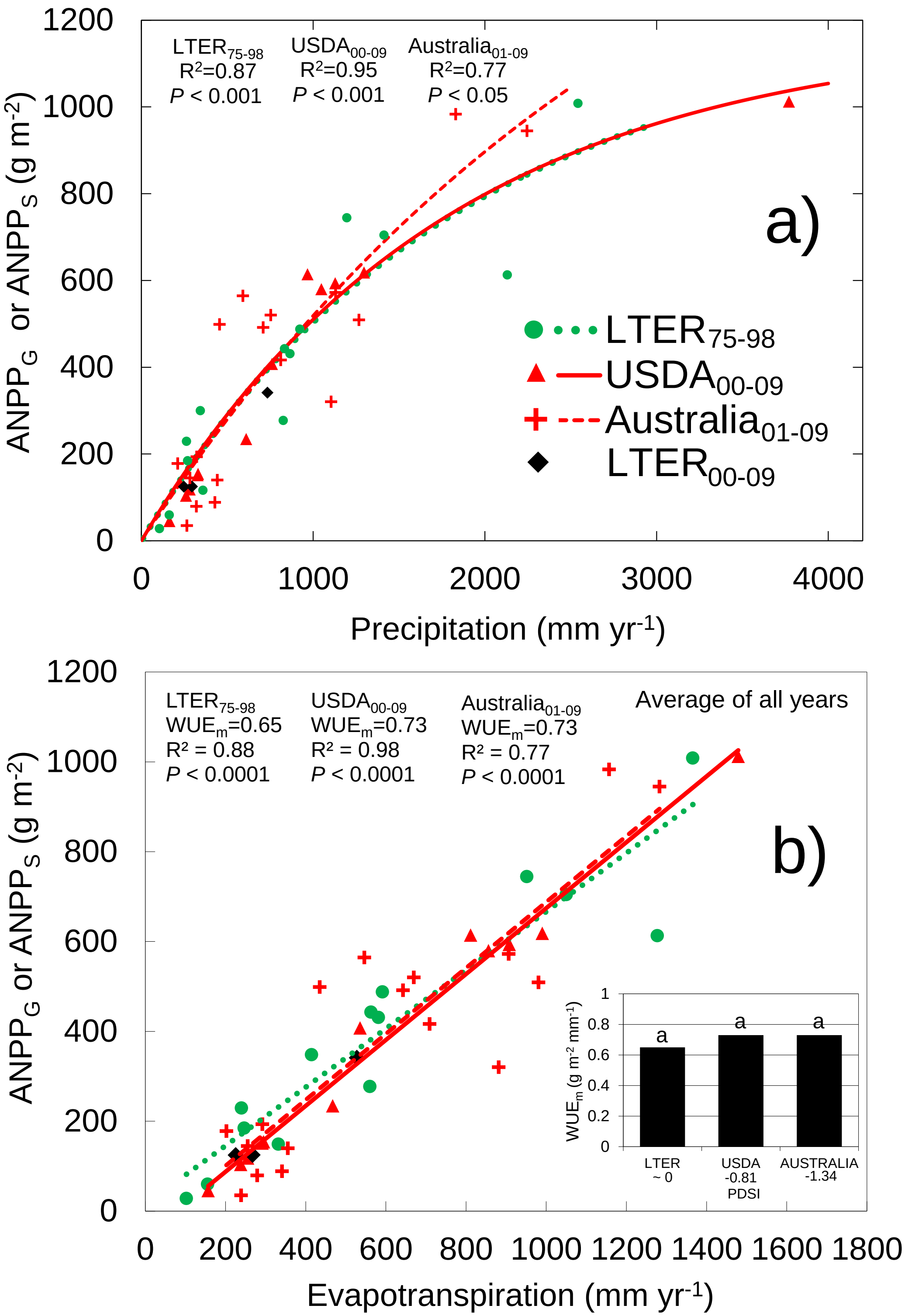
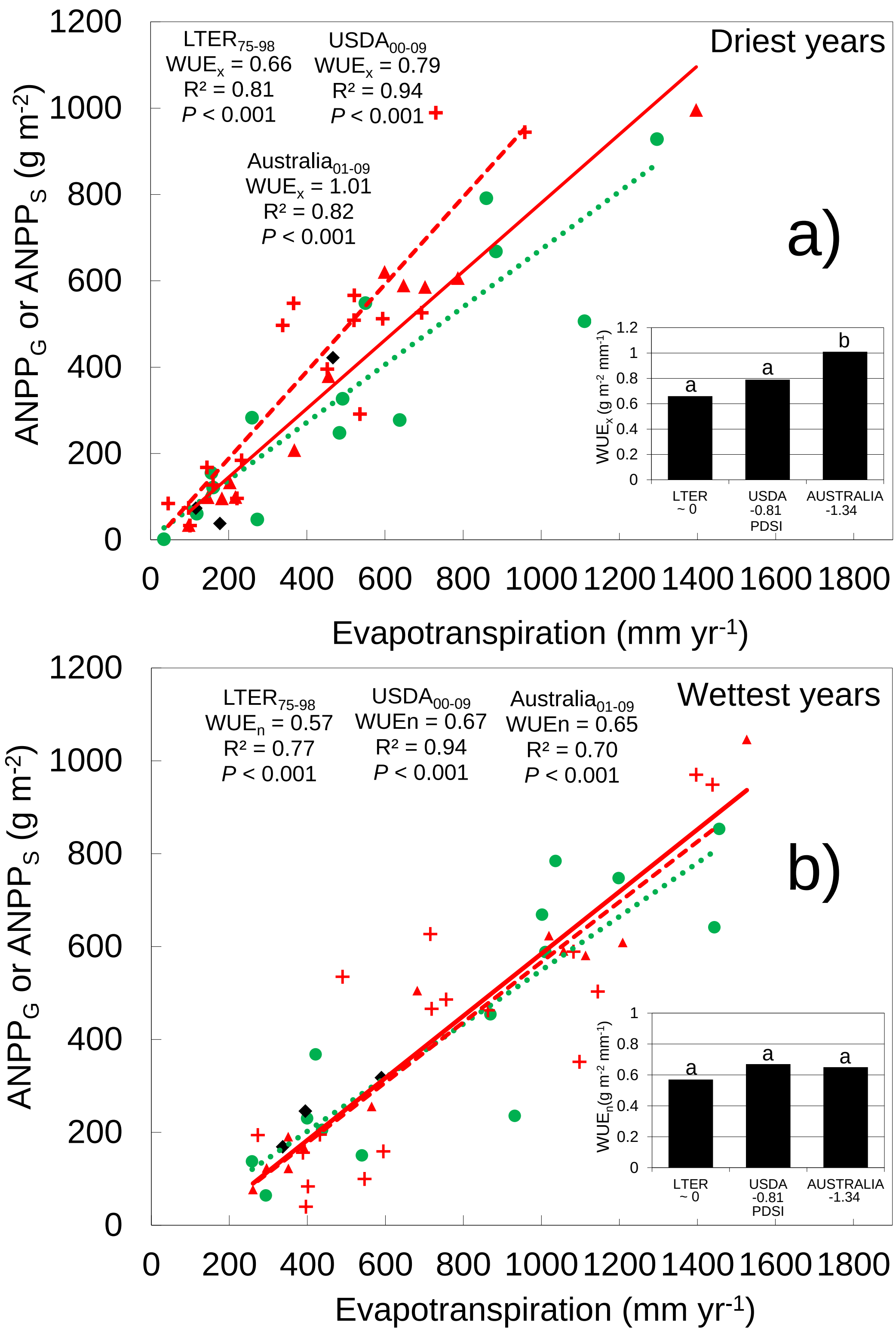

y = 1.15x + 3.94
R² = 0.82; P < 0.0001
Forest
Mesic Grassland
Semiarid Grassland
ln (ANPPG)
ln (iEVI)
R = 0.94
RMSE = 79 g m-2
ANPPG (g m-2)
ANPPS (g m-2)

Figure 1.



LTER75-98
R2=0.87
P < 0.001
USDA00-09
R2=0.95
P < 0.001
Australia01-09
R2=0.77
P < 0.05
a)
LTER75-98
USDA00-09
Australia01-09
LTER00-09
ANPPG or ANPPS (g m-2)
Precipitation (mm yr-1)
LTER75-98
WUEm=0.65
R² = 0.88
P < 0.0001
USDA00-09
WUEm=0.73
R² = 0.98
P < 0.0001
Australia01-09
WUEm=0.73
R² = 0.77
P < 0.0001
Average of all years
b)
WUEm (g m-2 mm-1)
LTER ~ 0
USDA -0.81
AUSTRALIA -1.34
PDSI
Evapotranspiration (mm yr-1)

Figure 2.



$LTER_{75-98}$
$WUE_x = 0.66$
$R^2 = 0.81$
$P < 0.001$
$USDA_{00-09}$
$WUE_x = 0.79$
$R^2 = 0.94$
$P < 0.001$
$Australia_{01-09}$
$WUE_x = 1.01$
$R^2 = 0.82$
$P < 0.001$
Driest years
a)
WUE_x (g m^{-2} mm^{-1})
LTER ~ 0
USDA -0.81 PDSI
AUSTRALIA -1.34
a
a
b
ANPP$_G$ or ANPP$_S$ (g m^{-2})
Evapotranspiration (mm yr^{-1})
$LTER_{75-98}$
$WUE_n = 0.57$
$R^2 = 0.77$
$P < 0.001$
$USDA_{00-09}$
WUEn = 0.67
$R^2 = 0.94$
$P < 0.001$
$Australia_{01-09}$
WUEn = 0.65
$R^2 = 0.70$
$P < 0.001$
Wettest years
b)
WUE_n(g m^{-2} mm^{-1})
LTER ~ 0
USDA -0.81 PDSI
AUSTRALIA -1.34
a
a
a
ANPP$_G$ or ANPP$_S$ (g m^{-2})
Evapotranspiration (mm yr^{-1})

Figure 3.

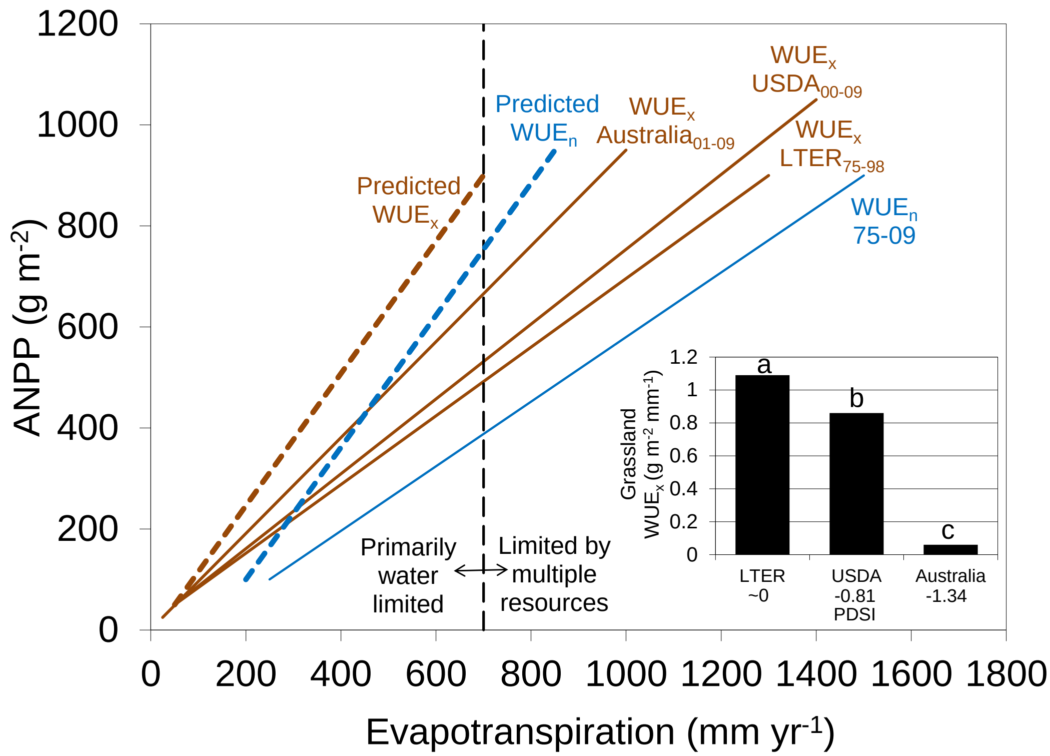

1200
1000
800
600
400
200
0
ANPP (g m-2)
0 200 400 600 800 1000 1200 1400 1600 1800
Evapotranspiration (mm yr-1)
Predicted WUEx
Predicted WUEn
WUEx Australia01-09
WUEx USDA00-09
WUEx LTER75-98
WUEn 75-09
Primarily water limited
Limited by multiple resources
Grassland WUEx (g m-2 mm-1)
1.2
1
0.8
0.6
0.4
0.2
0
a
b
c
LTER ~0
USDA -0.81 PDSI
Australia -1.34

Figure 4.