Long-term variability of root production in bioenergy crops from ingrowth core measurements

Cheyenne Lei [a,b,c,d]*, Michael Abraha [a,c,d], Jiquan Chen [a,b,c], Yahn-Jauh Su [a,c,d]

[a] Center for Global Change and Earth Observations, Michigan State University, East Lansing, MI 48823, USA

[b] Department of Geography, Environment and Spatial Sciences, Michigan State University, East Lansing, MI, 48824, USA

[c] Great Lakes Bioenergy Research Center, Michigan State University, East Lansing, MI 48824, USA

[d] W. K. Kellogg Biological Station, Michigan State University, Hickory Corners, MI 49060, USA

* Corresponding author
Email: cheyenne@msu.edu
Tel no: + (1) 734-548-2524

This article has been accepted For publication And undergone full peer review but has Not been through the copyediting, typesetting, pagination And proofreading process, which may lead to differences between this
Version And the Version of Record. Please cite this article as doi: 10.1093/jpe/rtab018.

Abstract

Aims

Long-term determination of root biomass production upon land use conversion to biofuel crops is rare. To assess land-use legacy influences on belowground biomass accumulation, we converted 22-year-old Conservation Reserve Program (CRP) grasslands and 50+-year-old agricultural (AGR) lands to corn (C), switchgrass (Sw) and restored prairie (Pr) biofuel crops. We maintained one CRP grassland as a reference (Ref). We hypothesized that land use history and crop type have significant effects on root density, with perennial crops on CRP grasslands having a higher root biomass productivity, while corn grown on former agricultural lands produce the lowest root biomass.

Methods

The ingrowth core method was used to determine in situ ingrowth root biomass, alongside measurements of aboveground net primary productivity (ANPP). Ancillary measurements, including air temperature, growing season length, and precipitation were used to examine their influences on root biomass production.

Important Findings

Root biomass productivity was the highest in unconverted CRP grassland (1716 g m^{-2} yr^{-1}), and lowest in corn fields (526 g m^{-2} yr^{-1}). All perennial sites converted from CRP and AGR lands had lower root biomass and ANPP in the first year of planting but peaked in 2011 for switchgrass and a year later for restored prairies. Ecosystem stability was higher in restored prairies (AGR-Pr: 4.3 ± 0.11; CRP-Pr: 4.1 ± 0.10), with all monocultures exhibiting a lower stability. Root biomass production was positively related to ANPP ($R^2 = 0.40$). Overall, attention should be given to root biomass accumulation in large-scale biofuel production as it is a major source of carbon sequestration.

Keywords: biofuel ecosystems, corn, ingrowth core method, root biomass, restored prairie, switchgrass

Nomenclature: Aboveground Net Primary Production (ANPP); Former Agricultural Lands (AGR); Air Temperature (T_a); Conservation Reserve Program (CRP); Ecosystem Stability (E_S); Growing Season Length (GSL)

1. Introduction

Fine root production constitutes an essential, but often unmeasured, portion of root biomass and hence the carbon budget of ecosystems. Root biomass, along with litter-fall, is a primary source of belowground biomass in terrestrial ecosystems (Chen et al., 2016). While litter-fall is relatively easy to quantify (e.g., through installation of litter traps) (Sayer et al., 2006), accurate determination of root biomass continues to be challenging due to its high spatial (e.g., horizontal and vertical) and temporal (e.g., inter-annual) variations. The amount and dynamics of root biomass are further complicated in managed ecosystems where anthropogenic activities, such as land use change and agronomic management practices (e.g., planting, tillage, fertilization, irrigation, harvesting, etc.) in agricultural lands can have direct, significant, and lasting effects on root development and accumulation (Frank et al., 1995). The relative magnitude of the changes in root biomass may also be significant in agricultural ecosystems compared with other natural ecosystems due to management intensity, frequency and establishment of systems (Deal et al., 2013). Moreover, crop types within agricultural systems may significantly vary in their root biomass production (e.g., Monti and Zatta, 2009). This study was stimulated to fill these knowledge gaps through empirical endeavors to quantify dynamics of root biomass.

Quantifying root biomass remains difficult due partially to a lack of standardized methods (Cairns et al., 1997; Milchunas and Lauenroth, 2001; Gill et al., 2002; Chen et al., 2014), variable microclimatic conditions that limit sampling and retrieval, and assessment of roots in a laboratory that is time consuming (Steingrobe et al., 2001; Thum et al., 2017). Conventionally, root biomass has been quantified using in situ root biomass sampling (Ni, 2001; Deal et al., 2013; Reth et al., 2005; Sierra et al., 2007; Ma et al., 2008; Andreasson et al., 2016), ecosystem modeling, or remote sensing (O'Connell et al., 2015). In situ measurements provide direct estimates of root biomass production and comparison between sites or treatments temporally (Makkonen and Helmisaari, 1999; Li et al., 2012).

Biofuel crops are promoted to provide climate mitigation benefits through renewable liquid transportation fuel source (Robertson et al., 2017). Substantial land area is required to meet expected biofuel target productions (USDOE, 2016), which may come through conversion of uncultivated land or diversion of current crop lands with implications to root biomass accumulation and soil carbon sequestration. In the USA, corn is one of the major biofuel crops, and yet perennial cellulosic biofuel crops such as switchgrass and restored prairie sequester more carbon through their extensive belowground biomass and provide greater climate and ecological benefits (Asbjornsen et al., 2014; Robertson et al., 2017; Abraha et al., 2019). In addition, perennial biofuel crops provide climate mitigation benefits through higher canopy reflectance (e.g., albedo) (Robertson et al., 2017). While climate mitigation potential of such bioenergy crops is well studied (e.g., Abraha et al., 2019; Sciusco et al., 2020), their root biomass accumulations nonetheless remains understudied. The biophysical mechanisms on root biomass in croplands are still poorly understood, with many factors known to affect spatial and temporally (Deal et al., 2013). In brief, studies have indicated that root production can vary by vegetation type (Tufekcioglu et al., 1998) and with aboveground net primary productivity (ANPP) (Du et al., 2019). These results point to the fact that temporal variation in root biomass production is essential for estimating root variations and productivity (Fukuzawa et al., 2013). Hence, accurate estimates of root biomass and their spatiotemporal variation is crucial for taking the long-term carbon dynamics and storage into account, and ultimately essential for understanding ecosystem functions.

Here, we investigated belowground root biomass production and dynamics of three bioenergy crops with two contrasting land use histories — conventional agriculture (AGR) versus Conservation Reserve Program (CRP) grasslands — and an unconverted CRP grassland dominated by smooth brome grass (*Bromus inermis Leyss*) over an 8-year period (2010–2017). We focus on the spatial and temporal changes of ingrowth root cores and their dependencies on environmental variables (i.e., air temperature, precipitation, growing season length) as well as aboveground net primary productivity (ANPP). We hypothesize that: 1) land use history plays a lasting role in determining root density, with crops on former CRP grasslands producing higher root biomass compared to crops on former AGR lands; and 2) the growth and productivity of root biomass of crops is influenced by air temperature and growing season length. We quantified ecosystem stability (E_S) to emphasize the treatment effect size using variance components in lieu of significance tests.

2. Methods

2.1. Study Area

Experimental study sites were established as part of the Great Lakes Bioenergy Research Center (GLBRC) at the W.K. Kellogg Biological Station (42° 24′ N, 85° 24′ W, 288 m a.s.l.) of the Michigan State University, MI, USA. The climate is humid continental temperate with a 30-year (1981–2010) average annual air temperature of 9.9 °C and average annual precipitation of 1027 mm (NCDC, 2013). Soils within the study sites are well-drained *Typic Hapludalfs* developed on glacial outwash (Thoen, 1990), with the water table approximately 12–14 meters beneath the surface.

Two contrasting land use histories – CRP and AGR – were used in this study. CRP lands included three sites (11–17 ha) that were managed as CRP grasslands for 22 years before conversion to soybean in 2009 and to no-till continuous corn (CRP-C), switchgrass (CRP-Sw), or restored prairie (CRP-Pr) from 2010 onwards. CRP is an incentive program that encourages farmers to remove environmentally sensitive lands from agricultural production and rent them to the USDA to be primarily converted to perennial grasslands for a minimum of 10 years in order to improve the soil, water, and environmental quality of land (USDA-FSA, 2017). AGR lands also included three sites (11–14 ha) that were managed as conventionally tilled corn-soybean croplands for 50+ years prior to conversion to soybean in 2009, and to no-till continuous corn (AGR-C), switchgrass (AGR-Sw), or restored prairie (AGR-Pr) from 2010 onwards (Figure 1). An additional CRP grassland was maintained under smooth brome grass — a cool season C3 grass of Eurasian origin — to serve as a historical reference (denoted as CRP-Ref; Figure 2). The soil carbon and nitrogen contents were significantly higher in former CRP grasslands compared to former agricultural lands, with pH for all sites ranging from 5.8 to 6.4 (Table 1).

2.2. In Situ Measurements

Root biomass (diameter < 5 mm) were measured using the ingrowth core method (Neill, 1992; Tufekcioglu et al., 1999). At each site, ten soil cores (7 cm diameter) were removed in 15 cm increments using a soil auger, cleaned for any plant matter, and placed in mesh bags 30 cm long. The bags were then reinserted into the soil. Any surface organic material initially removed to access the soil cores was returned on top of the bag. Samples were inserted prior to the growing season (i.e., just before snow melt) and left for 12 months. After extraction, samples were stored in a freezer until processing. The samples were carefully washed in a chamber-based structure, which involved separating roots from stones and soil. Ingrowth roots were retrieved using 2-mm sieves, labelled and dried using a Thermo Fisher laboratory drying oven (ThermoFisher Scientific, Grand Island, NY, USA) at 65°C to 70°C for 48 hours before weighing. For all sites, aboveground biomass was measured from ten 1-m^2 quadrats at peak standing biomass to determine ANPP (http://glbrc.kbs.msu.edu/protocols/117; https://lter.kbs.msu.edu/).

2.3. Environmental Factors

Air temperature and precipitation were continuously measured at each site. Air temperature and precipitation measurements were taken daily from the eddy covariance tower situated inside each site and averaged for the growing season to give the best estimate micrometeorological conditions. Growing season lengths (GSL) was determined using net ecosystem exchange (NEE) of CO_2 where NEE $\leq$ -1.0 g C m^{-2} for three consecutive days indicated ecosystem carbon uptake and signaled the start of the growing season and NEE $\geq$ 1.0 g C m^{-2} for three consecutive days indicated the end of the growing season (e.g., Abraha et al., 2016; Shao et al., 2017).

2.4. Spatial and Temporal Relationships

Since our objective was to study *in situ* root systems over a large area, a total of ten root biomass samples were collected at each of the seven sites for a total of 70 cores annually. Sampling plots were geographically referenced using a handheld global positioning system (GPS) unit for easy identification. Our annual samples of root biomass were then analyzed in order to understand the spatial changes in root production after the conversion of a landscape. We employed a bar chart to compare inter-annual variations and by temporally aggregating subsamples of all root biomass for each site in RStudio v. 1.2.5033 (R Core Team, 2020).

Root biomass in each year (2010–2017) was then evaluated through the least squares-based linear models (LMs) tests for multiple comparisons using the R-package ‘agricolae’ (R Development Team, 2013), with GSL and ANPP as the independent variables. This enabled a relationship comparison between annual root biomass and ANPP by site. These effects were tested with analysis of variance (ANOVA) and a post hoc Tukey to see whether difference in the LSM of root biomass production among sites. Standard error of the mean (SEM) in annual root production at each site and between CRP and AGR land use histories were quantified for their contributions to root production.

The inter-annual changes (i.e., temporal variability) and variations among the study sites were quantified using linear models with potential explanatory variables of GSL, ANPP, precipitation, and air temperature. This spatial-temporal separation method was explored by first investigating annual temporal differences over the study period by site, and then exploring the relationship between the two variables pooled across the entire study period (Biederman et al., 2017).

Finally, ecosystem stability (E_S) of root biomass production for each site over the study period was computed to determine proportional change of root biomass temporally.

$$E_S = \frac{\mu}{\sigma} \tag{1}$$

where μ is the mean total root biomass produced over 2010–2017, and σ is the mean temporal standard deviation over the same time period. E_S measures the degree of constancy relative to its derived mean. A greater E_S indicates a lower temporal change in the annual production of root biomass and consequently a higher stability over time (Tilman, 1996; Tilman et al., 2006). Finally, a Pearson's correlation coefficient was determined to measure the strength of linear association between the root production and E_S.

3. Results

3.1. Spatial Variability of Root Biomass

Root production from samples at each site showed large variation in subplot root production during 2011- 2014 (Figure 3). After sites were established in 2010, spatial variability within a site decreased. Between the two perennials sites, other than 2011, switchgrass site seemed to have a reduced variability compared to restored prairies sites. No root biomass data was retrieved from the two Corn sites in 2013 due to failure to plant corn around buried root bags.

3.2. Temporal Root Biomass Establishment, Productivity and ANPP

No clear trend was observed in root biomass production in the corn fields throughout the study period, with both CRP-C and AGR-C lands producing similar root biomass (~620 g m^{-2}) from 2010 to 2017 (Figure 4). Significantly lower ANPP was observed in 2012 (CRP-C =1370.36 g m^{-2} yr^{-1}; AGR-C = 913.59 g m^{-2} yr^{-1}) in comparison to the overall mean of 1706 g m^{-2} yr^{-1} at CRP-C and 1399 g m^{-2} yr^{-1} at AGR-C.

ANPP and root biomass production of switchgrass were higher in the former CRP lands compared to those in the former AGR lands, except from 2012 to 2014 when root production was higher on former AGR land than that on former CRP land. Root biomass production in both switchgrass fields was low during the planting year of 2010 (CRP-Sw = 728 g m^{-2}; AGR-Sw = 710 g m^{-2}) and peaked in 2011 as crops were established (CRP-Sw = 1525 g m^{-2}; AGR-Sw = 1680 g m^{-2}). By 2012 both switchgrass fields showed a reduced root biomass of 863 g m^{-2} (CRP-Sw) and 1277 g m^{-2} (AGR-Sw) and then remained similar throughout the study period. ANPP also peaked in 2013, averaging 1323 g m^{-2} yr^{-1} (CRP-Sw) and 1076 g m^{-2} yr^{-1} (AGR-Sw) and remained similar afterwards.

Restored prairie fields showed a peak root biomass in 2012 (CRP-Pr = 1783 g m^{-2}; AGR-Pr = 1253 g m^{-2}), one year later than the switchgrass fields. From 2013 onwards, root production in these plots remained statistically similar throughout. ANPP for both restored prairies was relatively low, averaging 620 g m^{-2} yr^{-1}.

The CRP reference site had the highest annual average root biomass production (CRP-Ref = 2508 g m^{-2} yr^{-1} in 2011) that decreased over time to ~778 g m^{-2} yr^{-1} by 2017. CRP-Ref also showed the highest variability in root biomass (SEM = ±318 g m^{-2}), while its ANPP was more or less constant over the study period (~600 g m^{-2} yr^{-1}), with small dips in 2014 and 2015.

3.3. Environmental Factors and Root Growth

Air temperature was observed to range between 15°C in the beginning of the growing season, and peaked up to 25°C, with an average temperature of 19.7°C, which is within the optimal range for root growth. Air temperature and precipitation did not have a significant effect on the average root biomass production, with both location-specific and site-average values (Figure 5 a, b).

Growing season lengths (GSL) varied from week 15 (late April) to week 40 (early October) from 2010 through 2017 (Figure 5c). The GSL for all crop types across land use histories was similar, with annual corn averaging around 100 days, while switchgrass and restored prairie had an average of ~130 days (Figure 5, 6). Site-level root biomass was highly correlated with GSL ($p<0.05$, adj. $R^2 = 0.62$) at the AGR-Sw site. This trend was positive for all perennials, specifically for prairie (CRP-Pr $R^2 = 0.24$; AGR-Pr $R^2 = 0.20$), but negative for corn at both AGR and CRP lands.

A negative correlation was observed between root biomass production and ANPP with an average bias of 1593 g m^{-2} yr^{-1} (adj. $R^2 = 0.40$, $p<0.05$). ANPP varied between 400 g m^{-2} to 800 g m^{-2} for perennials, with much higher ANPP for the corn sites (Figure 5e). However, after the bioenergy crops were established, there appeared no significant correlation between ANPP and root biomass production among the sites ($p>0.05$).

AGR lands exhibited a higher overall E_S with rank order as follows: restored prairie (4.3±0.11), switchgrass (3.4±0.08) and corn (3.1±0.08). The CRP lands had slightly lower E_S, with restored prairie the highest (4.1±0.10) and reference grassland the lowest (2.7±0.06) (Figure 6).

4. Discussion

4.1. Root Growth and Land Use Effects

Roots serve as a key mediator to connect aboveground and belowground ecological processes. Overall, former CRP lands exhibited similar average belowground root biomass but a higher aboveground plant biomass compared to former AGR lands over the study period. This could be due to higher soil organic matter, soil carbon and soil nitrogen arising from pre-conversion land use (Deal et al., 2013; Abraha et al., 2016). Our switchgrass and restored prairie fields had large root biomass that is similar to grasslands reported by Zan et al. (1997, 2001) who found root biomass production of in switchgrass (1100 g m^{-2} yr^{-1}) and corn (790 g m^{-2} yr^{-1}), and by Ma et al. (2008) who reported an average root biomass of 775 g m^{-2} yr^{-1} for grasslands including meadow (1385 g m^{-2} yr^{-1}), typical (688 gm^{-2} yr^{-1}) and desert steppe (300 g m^{-2} yr^{-1}).

Land use conversions and crop type could also have profound effects on above- and belowground production. On average, the corn fields, regardless of land use history, exhibited the highest ANPP but the lowest root biomass production; in contrast, the unconverted CRP-Ref had the lowest ANPP but the highest root biomass. All converted perennials showed lower root biomass production and ANPP during the initial planting year in 2010. Root biomass production peaked in the second year and third year after planting for switchgrass and restored prairie, respectively, and became more or less constant afterwards at a reduced level ($p<0.05$, Figures 3,4). Finally, ANPP peaked in 2013 for most of the perennials and was steady thereafter. Similar results were reported by Makkonen and Helmisaari (1999) who found that roots were still expanding into the ingrowth cores up to the third year of establishment of a managed forest, before an equilibrium was observed. Other studies reported that perennial grass could increase root biomass by a factor of four after establishment (Propheter et al., 2010). Peaking of root biomass production in the early years after planting and of ANPP in the later years indicates preferential shift in carbon allocation to below- and above-ground biomass over the lifetime of the perennials (Asbjornsen et al., 2014).

Restored prairie fields exhibited a higher E_S compared to all other sites. This is likely due to higher species diversity in the restored prairie fields compared to the corn, switchgrass and smooth brome grass monocultures. A similar result was reported by Tilman et al. (2006) where E_S increased with increasing plant diversity. Thus, identifying changes in root production at the spatial and temporal scale in different bioenergy crops provides a useful insight into soil carbon accumulation benefits.

4.2. Variation in Root Biomass Production and Biophysical Conditions

During the 2012 drought year, ANPP was drastically reduced at all sites except the reference site. The root biomass production for the same year declined as well at all converted sites except the restored prairie fields — likely due to the high number of species (Abraha et al., 2016) and high E_S. The CRP-Pr site contained more C_3 and less C_4 species than the AGR-Pr site despite both being planted with the same species, which may have caused a higher root production at the CRP-Pr than at the AGR-Pr during the drought. Precipitation amount and its distribution are crucial as proportional root allocation in grasslands is usually inversely correlated with mean annual precipitation where water is the predominant factor limiting plant growth (Hui and Jackson, 2006; Cleland et al., 2019). In 2015, a dry spring followed by a cool summer reduced precipitation amount which may have affected root biomass within AGR lands (Figure 4).

Growing season length is an important indicator that has been highly overlooked in understanding the productivity of root biomass. The growing seasons for corn sites in both land use histories were much shorter than those for perennials, with corn being planted long after perennials have emerged. This may explain why the growing season length and root biomass were negatively correlated for corn (Figure 5c), i.e., corn is planted much later and does not need as long a growing period to mature and produce roots. Perennials, on the other hand, with longer growing seasons and deeper root systems throughout the seasons, potentially yield a higher resistance (e.g., E_S) for lower growing temperatures (e.g., Propheter et al., 2010; Robertson et al., 2011). The ANPP at the corn fields was higher than that at the perennial fields, likely due to corn being more intensively managed for high aboveground production. However, the late planting of the perennials in 2010 may have contributed to the short growing season observed in that year.

Root biomass production has been found to vary in relation with crop characteristics (i.e., crop species, air temperature, precipitation, geographical location) that can be affected by soil properties and elevation (Vogt et al., 1986, Cairns et al., 1997, Chen et al., 2004). However, the crop type, alongside air temperature and precipitation, did not explain the variation in total root biomass production, indicating that our hypothesis was nullified. Most previous studies found the aforementioned relationships to be weak, with environmental characteristics ranging within very narrow values.

Carbon allocated belowground dominates root biomass production, but can be highly affected by higher temperatures that can affect the water use efficiency of the crop through water loss, including evapotranspiration. For example, corn covers less surface area due to being planted in rows, compared to dense switchgrass and restored prairie sites. This can lead to much higher water loss from exposed soil due to evaporation from the soil, and increased water loss in leaves due to transpiration (Abraha et al., 2016). Abraha et al. (2015, 2016) analyzed carbon and water exchanges within our study sites from 2010 to 2013 and observed that landscape dynamics, alongside climate changes (i.e. drought in 2012) can affect yield and grassland ecosystems. This proof alongside our study can be applied at larger scales, where decreases/increases in root biomass productivity over long term could potentially alter microclimatic conditions and yield of perennial biofuel cropping systems.

4.3. Limitations and Future Recommendations

We found that a proportion of the variation in root biomass production can be explained by crop type, land use history and environmental variables. Taking data from ingrowth cores has been shown to be a good resource in studying the dynamics of root production within ecosystems. The approach is particularly suitable for estimating the potential of root biomass production. Our study has identified some limitations and potentials of the method and recommendations for future study. Firstly, as roots grow into the cores, the necessary for a stabilization period for crops as well as the need for minimum disturbance to the soil can be limiting factors. This was mitigated as much as possible by reducing the disturbance to roots and the rooting environment through small ingrowth core samples, and installing them before the onset of each root growing period. This allowed roots to regain a new equilibrium within the ingrowth core annually and has been proven with other research to be effective (Ostonen et al., 2005). We also suggest the use of other stable relative methods, such as sequential coring, to compare the different approaches for retrieving and analyzing root biomass. However, exploring the effectiveness and suitability of multiple methods was beyond the scope of this study, and future research efforts would be needed to identify these changes in root biomass production. Secondly, in this study we did not account for the effects of land surface characteristics (i.e., vegetation properties, leaf area index, soil moisture) on spatiotemporal variation of root biomass production. Vegetation cover and their unique canopies can directly affect water use efficiency of crops by the amount of water which is evaporated from leaves as well as the ground subsurface. Future effects will be needed to quantify these differences, through the use of remote sensing, and continuous measurements of evapotranspiration and soil moisture. Lastly, by investigating multiple components of land use legacy common to the Midwest in USA, we found that differences in root biomass production are dominated by crop types. Future studies are needed to further understand root biomass distribution over longer time periods in order to explore extreme climatic events that may occur. Other belowground processes at microscales may also be needed (e.g., microtopography, soil structure and aggregates, etc.) (Augusto et al., 2015; Andreasson et al., 2016).

Acknowledgments

Support for this research was provided by the Great Lakes Bioenergy Research Center, U.S. Department of Energy, Office of Science, Office of Biological and Environmental Research (Awards DE-SC0018409 and DE-FC02-07ER64494) at the Kellogg Biological Station, and by Michigan State University AgBioResearch. We acknowledge the help and support of laboratory colleagues in the Landscape Ecology and Ecosystem Science (LEES) Laboratory at Michigan State University, the Kellogg Biological Station and the Great Lakes Bioenergy Research Center for help in acquiring data. We also thank Dr. Qian and Dr. Maowei Liang for advice and guidance in statistical R code and Mrs. Kristine Blakeslee for her feedback on the manuscript before resubmission. Finally, we also thank our anonymous reviewers for their insightful comments and suggestions.

References

Abraha, M., Chen, J., Chu, H., Zenone, T., John, R., Su, Y. J., Hamilton, K., & Robertson, G. P. (2015). Evapotranspiration of annual and perennial biofuel crops in a variable climate. *Global Change Biology: Bioenergy*, 7(6), 1344-1356. https://doi.org/10.1111/gcbb.12239

Abraha, M., Gelfand, I., Hamilton, S. K., Shao, C., Su, Y.-J., Robertson, G. P., & Chen, J. (2016). Ecosystem water-use efficiency of annual corn and perennial grasslands: Contributions from land-use history and species composition. *Ecosystems*, 19(6), 1001–1012. https://doi.org/10.1007/s10021-016-9981-2

Abraha, M., Gelfand, I., Hamilton, S. K., Chen, J., & Robertson, G. P. (2019). Carbon debt of field-scale Conservation Reserve Program grasslands converted to annual and perennial bioenergy crops. *Environmental Research Letters*, 14, 024019 1–10. https://doi.org/10.1088/1748-9326/aafc10

Abraha, M., Hamilton, S. K., Chen, J., & Robertson, G. P. (2018). Ecosystem carbon exchange on conversion of Conservation Reserve Program grasslands to annual and perennial cropping systems. *Agricultural and Forest Meteorology*, 253, 151–160. https://doi.org/10.1016/j.agrformet.2018.02.016

Abraha, M., Hamilton, S. K., Chen, J., & Robertson, G. P. (2020). Long-term evapotranspiration rates for rainfed corn versus perennial bioenergy crops in a mesic landscape. *Hydrological Processes*, 34, 810-822.

Andreasson, F., Gonzalez, M., Augusto, L., & Bakker, M. R. (2016). Comparison of ingrowth cores and ingrowth meshes in root studies: 3 years of data on *Pinus pinaster* and its understory. *Trees*, 30(2), 555–570. https://doi.org/10.1007/s00468-015-1256-6

Asbjornsen, H., Hernandez-Santana, V., Liebman, M., Bayala, J., Chen, J., Helmers, M., Ong, C.K. & Schulte, L. A. (2014). Targeting perennial vegetation in agricultural landscapes for enhancing ecosystem services. *Renewable Agriculture and Food Systems*, 29(2), 101–125. https://doi.org/10.1017/S1742170512000385

Augusto, L., De Schrijver, A., Vesterdal, L., Smolander, A., Prescott, C., & Ranger, J. (2015). Influences of evergreen gymnosperm and deciduous angiosperm tree species on the functioning of temperate and boreal forests. *Biological Reviews*, 90(2), 444–466. https://doi.org/10.1111/brv.12119

Betts, R. A. (2001). Biogeophysical impacts of land use on present- day climate: Near-surface temperature change and radiative forcing. *Atmospheric Science Letters*, 2(1- 4), 39–51. https://doi.org/10.1006/asle.2001.0037

Biederman, J. A., Scott, R. L., Bell, T. W., Bowling, D. R., Dore, S., Garatuza- Payan, J., Thomas, K. E., Krishnan, P., Krofcheck, D. J., Litvak, M. E., Maurer, G. E., Meyers, T. P., Oechel, W. C., Papuga, S. A., Ponce-Campos, G. E., Rodriguez, J. C., Smith, W. K., Vargas, R., Watts, C. J., Yepez, E. A., & Goulden, M. L. (2017). CO_2 exchange and evapotranspiration across dryland ecosystems of southwestern North America. *Global Change Biology*, 23(10), 4204–4221. https://doi.org/10.1111/gcb.13686

Cairns, M. A., Brown, S., Helmer, E. H., & Baumgardner, G. A. (1997). Root biomass allocation in the world's upland forests. *Oecologia*, 111(1), 1–11. https://doi.org/10.1007/s004420050201

Chen, J., John, R., Sun, G., McNulty, S., Noormets, A., Xiao, J., Turner, M. G., & Franklin, J. F. (2014). Carbon fluxes and storage in forests and landscapes. In *Forest Landscapes and Global Change* (pp. 139–166). Springer, New York, NY. https://doi.org/10.1007/978-1-4939-0953-7_6

Chen, S., Lin, S., Reinsch, T., Loges, R., Hasler, M., & Taube, F. (2016). Comparison of ingrowth core and sequential soil core methods for estimating belowground net primary production in grass-clover swards. *Grass and Forage Science*, 71(3), 515–528. https://doi.org/10.1111/gfs.12214

Chen, W., Zhang, Q., Cihlar, J., Bauhus, J., & Price, D. T. (2004). Estimating fine-root biomass and production of boreal and cool temperate forests using aboveground measurements: A new approach. Plant and Soil, 265(1-2), 31-46. https://doi.org/10.1007/s11104-005-8503-3

Cleland, E. E., Lind, E. M., DeCrappeo, N. M., DeLorenze, E., Wilkins, R. A., Adler, P. B., ... & Firn, J. (2019). Belowground biomass response to nutrient enrichment depends on light limitation across globally distributed grasslands. *Ecosystems*, 22(7), 1466-1477. https://doi.org/10.1007/s10021-019-00350-4

Deal, M. W., Xu, J., John, R., Zenone, T., Chen, J., Chu, H., Mayer, C. (2013). Net primary production in three bioenergy crop systems following land conversion. *Journal of Plant Ecology*, 7(5), 451–460. https://doi.org/10.1093/jpe/rtt057

Denman, K. L., Menon, S., Brasseur, G., Chidthaisong, A., Ciais, P., Cox, P. M, Holland, E. (2007). Couplings between changes in the climate system and biogeochemistry. *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the*

Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. https://www.ipcc.ch/pdf/assessment-report/ar4/wg1/ar4-wg1-chapter7.pdf

Du, H., Liu, L., Su, L., Zeng, F., Wang, K., Peng, W., ... & Song, T. (2019). Seasonal changes and vertical distribution of fine root biomass during vegetation restoration in a karst area, Southwest China. *Frontiers in Plant Science*, 9, 2001. https://doi.org/10.3389/fpls.2018.02001

ESRI, R. (2011). ArcGIS desktop: release 10. Environmental Systems Research Institute, CA.

Frank, A. B., Tanaka, D. L., Hofmann, L., & Follett, R. F. (1995). Soil carbon and nitrogen of Northern Great Plains grasslands as influenced by long-term grazing. *Rangeland Ecology & Management*, 48(5), 470–474.

Finér, L., Ohashi, M., Noguchi, K., & Hirano, Y. (2011). Factors causing variation in fine root biomass in forest ecosystems. *Forest Ecology and Management*, 261(2), 265-277. https://doi.org/10.1016/j.foreco.2010.10.016

Gelman, A. (2005). Analysis of variance? Why it is more important than ever. *The Annals of Statistics*, 33(1), 1–53. https://doi.org/10.1214/009053604000001048

Gill, R., Kelly, R., Parton, W., Day, K., Jackson, R., Morgan, J., et al. (2002). Using simple environmental variables to estimate belowground productivity in grasslands. *Global Ecology and Biogeography*, 11(1), 79–86. https://doi.org/10.1046/j.1466-822X.2001.00267.x

Howarth, R. W., Bringezu, S., Martinelli, L. A., Santoro, R., Messem, D., & Sala, O. E. (2009). Introduction: Biofuels and the environment in the 21st century. *Cornell University Library's Initiatives in Publishing (CIP)*. http://cip.cornell.edu/biofuels/ https://doi.org/10.1111/j.1469-8137.2005.01569.x

Hui, D., & Jackson, R. B. (2006). Geographical and interannual variability in biomass partitioning in grassland ecosystems: A synthesis of field data. *New Phytologist*, 169(1), 85–93.

Jørgensen, U., & Schelde, K. (2001). Energy crop water and nutrient use efficiency. *International Energy Agency Bioenergy Task*, 17, Short Rotation Crops.

Kell, D. B. (2012). Large-scale sequestration of atmospheric carbon via plant roots in natural and agricultural ecosystems: Why and how. Philosophical transactions of the royal society: *Biological Sciences*, 367(1595), 1589–1597. https://doi.org/10.1098/rstb.2011.0244

Lark, T. J., Meghan Salmon, J., & Gibbs, H. K. (2015). Cropland expansion outpaces agricultural and biofuel policies in the United States. *Environmental Research Letters*, 10(4), 044003. https://doi.org/10.1088/1748-9326/10/4/044003

Lenton, T. M. and Vaughan, N. E.: The radiative forcing potential of different climate geoengineering options. *Atmospheric Chemistry and Physics*, 9, 5539–5561, https://doi.org/10.5194/acp-9-5539-2009, 2009.

Li, X., Zhu, J., Lange, H., & Han, S. (2012). A modified ingrowth core method for measuring fine root production, mortality and decomposition in forests. *Tree Physiology*, 33(1), 18–25.

Luyssaert S., Jammet M., Stoy P. C. et al. (2014) Land management and land-cover change have impacts of similar magnitude on surface temperature. *Nature Climate Change*, 4, 389–393.

Ma, W., Yang, Y., He, J., Zeng, H., & Fang, J. (2008). Above- and belowground biomass in relation to environmental factors in temperate grasslands, Inner Mongolia. *Life Sciences*, 51(3), 263–270. https://doi.org/10.1007/s11427-008-0029-5

Makkonen, K., & Helmisaari, H. S. (1999). Assessing fine-root biomass and production in a Scots pine stand–comparison of soil core and root ingrowth core methods. *Plant and soil*, 210(1), 43–50. https://doi.org/10.1023/A:1004629212604

McMillen, R. T. (1988). An eddy correlation technique with extended applicability to non-simple terrain. *Boundary-Layer Meteorology*, 43(3), 231–245. https://doi.org/10.1007/BF00128405

Milchunas, D. G., & Lauenroth, W. K. (2001). Belowground primary production by carbon isotope decay and long-term root biomass dynamics. *Ecosystems*, 4(2), 139–150. https://doi.org/10.1007/s100210000064

Monti, A., & Zatta, A. (2009). Root distribution and soil moisture retrieval in perennial and annual energy crops in northern Italy. *Agriculture, Ecosystems and Environment*, 132, 252–259.

NCDC (National Climate Data Center). 2013. Summary of Monthly Normal 1981–2010 (MI, USA: Gull Lake Biology Station). www.ncdc.noaa.gov/cdo-web/search

Neill, C. (1992). Comparison of soil coring and ingrowth methods for measuring belowground production. *Ecology*, 73(5), 1918–1921. https://doi.org/10.2307/1940044

Ni, J. (2001). Carbon storage in terrestrial ecosystems of China: estimates at different spatial resolutions and their responses to climate change. *Climatic Change*, 49(3), 339–358. https://doi.org/10.1023/A:1010728609701

Odum, E. P. (1984.) Properties of agroecosystems. In *Agricultural Ecosystems*: *Unifying Concepts*, ed. by R. Lowrance, B. R. Stinner, and G. J. House (pp. 5–11). John Wiley, New York, USA.

O'Connell, J., Byrd, K., & Kelly, M. (2015). A hybrid model for mapping relative differences in belowground biomass and root:shoot ratios using spectral reflectance, foliar N and plant biophysical data within coastal marsh. *Remote Sensing*, 7(12), 16480–16503. https://doi.org/10.3390/rs71215837

Ostonen, I., Lõhmus, K., & Pajuste, K. (2005). Fine root biomass, production and its proportion of NPP in a fertile middle-aged Norway spruce forest: Comparison of soil core and ingrowth core methods. *Forest Ecology and Management*, 212(1-3), 264–277. https://doi.org/10.1016/j.foreco.2005.03.064

Post, W. M., & Kwon, K. C. (2000). Soil carbon sequestration and land- use change: Processes and potential. *Global Change Biology*, 6(3), 317–327. https://doi.org/10.1046/j.1365-2486.2000.00308.x

Propheter, J. L., Staggenborg, S. A., Wu, X., & Wang, D. (2010). Performance of annual and perennial biofuel crops: yield during the first two years. *Agronomy Journal*, 102(2), 806–814. https://doi.org/10.2134/agronj2009.0301

Qian, S. S., Craig, J. K., Baustian, M. M., & Rabalais, N. N. (2009). A Bayesian hierarchical modeling approach for analyzing observational data from marine ecological studies. *Marine Pollution Bulletin*, 58(12), 1916–1921. https://doi.org/10.1016/j.marpolbul.2009.09.029

Qian, S. S., Stow, C. A., & Borsuk, M. E. (2003). On Monte Carlo methods for Bayesian inference. *Ecological Modelling*, 159(2), 269–277. https://doi.org/10.1016/S0304-3800(02)00299-5

Quamen, F. R., & Naugle, D. E. (2007). Benefits of the Conservation Reserve Program to Grassland Bird Populations in the Prairie Pothole Region of North Dakota and South Dakota. *Final Report to the US Department of Agriculture Farm Service Agency,* RFA OS-IA-04000000-N34. www.fsa.usda.gov/Internet/FSA_File/grassland_birds_fws.pdf.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

R Development Team (2013). R foundation for statistical computing. Vienna, Austria, 3(0).

Reth, S., Reichstein, M., & Falge, E. (2005). The effect of soil water content, soil temperature, soil pH-value and the root mass on soil CO_2 efflux – A modified model. *Plant and Soil*, 268(1), 21–33. https://doi.org/10.1007/s11104-005-0175-5

Robertson, G. P., Dale, V. H., Doering, O. C., Hamburg, S. P., Melillo, J. M., Wander, M. M., ... & Duke, C. S. (2008). Sustainable biofuels redux. *Science*, 322(5898), 49–50.

Robertson, G. P., Hamilton, S. K., Del Grosso, S. J., & Parton, W. J. (2011). The biogeochemistry of bioenergy landscapes: carbon, nitrogen, and water considerations. *Ecological Applications*, 21(4), 1055–1067. https://doi.org/10.1890/09-0456.1

Robertson, G. P., Hamilton, S. K., Barham, B. L., Dale, B. E., Izaurralde, R. C., Jackson, R. D., Tiedje, J. M. (2017). Cellulosic biofuel contributions to a sustainable energy future: Choices and outcomes. *Science*, 356(6345). https://doi.org/10.1126/science.aal2324

Sayer, E. J., Tanner, E. V., & Cheesman, A. W. (2006). Increased litterfall changes fine root distribution in a moist tropical forest. *Plant and Soil*, 281(1-2), 5–13. https://doi.org/10.1007/s11104-005-6334-x

Sciusco, P., J. Chen**,** M. Abraha, C. Lei, Z. Ouyang, R. Zhang, G. P. Robertson, G. Shirkey, R. John, and R. Lafortezza. (2020). Spatiotemporal variations of albedo in managed agricultural landscapes: Inferences to global warming impacts (GWI). *Landscape Ecology,* 35, 1385–1402

Shao, C., Chen, J., Chu, H., Lafortezza, R., Dong, G., Abraha, M. Qi, J. (2017). Grassland productivity and carbon sequestration in Mongolian grasslands: The underlying mechanisms and nomadic implications. *Environmental Research*, 159, 124–134. https://doi.org/10.1016/j.envres.2017.08.001

Sierra, C. A., Harmon, M. E., Moreno, F. H., Orrego, S. A., & Del VALLE, J. I. (2007). Spatial and temporal variability of net ecosystem production in a tropical forest: Testing the hypothesis of a significant carbon sink: Variability of NEP in tropical forests. *Global Change Biology*, 13(4), 838–853. https://doi.org/10.1111/j.1365-2486.2007.01336.x

Sprunger, C. D., & Robertson, G. P. (2018). Early accumulation of active fraction soil carbon in newly established cellulosic biofuel systems. *Geoderma*, 318, 42–51. https://doi.org/10.1016/j.geoderma.2017.11.040

Steingrobe, B., Schmid, H., & Claassen, N. (2001). The use of the ingrowth core method for measuring root production of arable crops–influence of soil and root disturbance during installation of the bags on root ingrowth into the cores. *European Journal of Agronomy*, 15(2), 143–151. http://dx.doi.org/10.1016/S1161-0301(01)00100-9

Suyker, A. E., & Verma, S. B. (2012). Gross primary production and ecosystem respiration of irrigated and rainfed maize–soybean cropping systems over 8 years. *Agricultural and Forest Meteorology*, 165, 12–24. https://doi.org/10.1016/j.agrformet.2012.05.021

Tilman, D. (1996). Biodiversity: population versus ecosystem stability. *Ecology*, 77(2), 350–363. https://doi.org/10.2307/2265614

Tilman, D., Reich, P. B., & Knops, J. M. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, 441(7093), 629. https://doi.org/10.1038/nature04742

Thoen, G. F. (1990). *Soil Survey of Barry County, Michigan*. The Service. p 286

Thum, T., MacBean, N., Peylin, P., Bacour, C., Santaren, D., Longdoz, B., Ciais, P. (2017). The potential benefit of using forest biomass data in addition to carbon and water flux measurements to constrain ecosystem model parameters: Case studies at two temperate forest sites. *Agricultural and Forest Meteorology*, 234–235, 48–65. https://doi.org/10.1016/j.agrformet.2016.12.004

Tufekcioglu, A., Raich, J. W., Isenhart, T. M., & Schultz, R. C. (1998). Fine root dynamics, coarse root biomass, root distribution, and soil respiration in a multispecies riparian buffer in Central Iowa, USA. *Agroforestry Systems*, 44(2-3), 163-174. https://doi.org/10.1023/A:1006221921806

Tufekcioglu, A., Raich, J. W., Isenhart, T. M., & Schultz, R. C. (1999). Root biomass, soil respiration, and root distribution in crop fields and riparian buffer zones. *Agroforest Systems.*, 44, 163-174.

United States Department of Agriculture Farm Services Agency (USDA-FSA) (2017). Conservation Reserve Program. https://www.fsa.usda.gov/programs-and-services/conservation-programs/conservation-reserve-program/index.

U.S. Department of Energy (USDOE) (2016). 2016 Billion-Ton Report: Advancing domestic resources for a thriving bioeconomy, Volume 1: Economic availability of feedstocks. Langholtz, M.H., Stokes, B.J., & Easton, L.M. (Leads), ORNL/TM-2016/160. Oak Ridge National Laboratory, Oak Ridge, TN.

Vogt, K. A., Grier, C. C., & Vogt, D. J. (1986). Production, turnover, and nutrient dynamics of above-and belowground detritus of world forests. In *Advances in Ecological Research* (Vol. 15, pp. 303–377). Academic Press. https://doi.org/10.1016/S0065-2504(08)60122-1

Wagle, P., Kakani, V. G., & Huhnke, R. L. (2016). Evapotranspiration and ecosystem water use efficiency of switchgrass and high biomass sorghum. *Agronomy Journal*, 108(3), 1007–1019. https://doi.org/10.2134/agronj2015.0149

Webb, E. K., Pearman, G. I., & Leuning, R. (1980). Correction of flux measurements for density effects due to heat and water vapour transfer. *Quarterly Journal of the Royal Meteorological Society*, 106(447), 85–100. https://doi.org/10.1002/qj.49710644707

Wu, Z., Dijkstra, P., Koch, G. W., Peñuelas, J., & Hungate, B. A. (2011). Responses of terrestrial ecosystems to temperature and precipitation change: a meta- analysis of experimental manipulation. *Global Change Biology*, 17(2), 927–942. https://doi.org/10.1111/j.1365-2486.2010.02302.x

Zan, C. S., Fyles, J. M., Girourard, P. and Samson, R. A. 2001. Carbon sequestration in perennial bioenergy, annual corn, and uncultivated systems in southern Quebec. *Agriculture, Ecosystems & Environment.,* 86: 135–144. https://doi.org/10.1016/S0167-8809(00)00273-5

Zan, C., Fyles, J., Girouard, P., Samson, R., & Doan, M. (1997). Carbon storage in switchgrass and short-rotation willow plantations. In Making a business from biomass in energy, environment, chemicals, fibers, and materials. *Proceedings of the Third Biomass Conference of the Americas: Energy, Environment, Agriculture, and Industry.* August 24e29, Montreal, Qúebec, Canada. New York: Pergamon (pp. 355–361).

Zenone, T., Chen, J., Deal, M. W., Wilske, B., Jasrotia, P., Xu, J., Philip Robertson, G. (2011). CO_2 fluxes of transitional bioenergy crops: effect of land conversion during the first year of cultivation. *Bioenergy*, 3(5), 401–412. https://doi.org/10.1111/j.1757-1707.2011.01098.x

Zeri, M., Hussain, M. Z., Anderson- Teixeira, K. J., DeLucia, E., & Bernacchi, C. J. (2013). Water use efficiency of perennial and annual bioenergy crops in central Illinois. *Journal of Geophysical Research: Biogeosciences*, 118(2), 581–589. https://doi.org/10.1002/jgrg.20052

Table 1: Soil physical and chemical properties of seven scale-up study sites in 2009. Means followed by the same letters are not significantly different by t-test (P<0.05). CEC = Cation Exchange Capacity. Source: https://lter.kbs.msu.edu/datatables/372. Means with the same letter are not significantly different ($p < 0.05$).

Site	Area (ha)	Sand ($g.kg^{-1}$)	Silt ($g.kg^{-1}$)	Clay ($g.kg^{-1}$)	Soil (pH)	CEC [meq $(100\ g)^{-1}$]	Bulk Density ($g.m^{-3}$)	Nitrogen ($g.kg^{-1}$)	Carbon ($g.kg^{-1}$)
CRP-Ref	9.1	600.1^{a}	52.5^{b}	347.4^{a}	6.2^{a}	6.50^{ab}	1.41^{c}	2.69^{ab}	30.60^{a}
CRP-Sw	17.9	700.1^{a}	32.5^{b}	267.4^{a}	5.9^{a}	6.00^{ab}	1.42^{c}	2.03^{cd}	23.76^{b}
CRP-Pr	13.1	684.9^{a}	47.5^{b}	267.6^{a}	6.2^{a}	5.46^{b}	1.34^{c}	2.27^{bc}	26.40^{ab}
CRP-C	19.5	670.0^{a}	60.1^{ab}	269.1^{a}	6.1^{a}	6.02^{ab}	1.41^{c}	2.79^{a}	30.94^{a}
AGR-Sw	14.1	624.9^{a}	42.6^{b}	332.5^{a}	6.4^{a}	7.07^{ab}	1.73^{a}	1.34^{c}	13.71^{c}
AGR-Pr	23.0	535.2^{a}	102.4^{a}	362.4^{a}	5.8^{a}	8.60^{a}	1.61^{b}	1.62^{dc}	16.38^{c}
AGR-C	11.2	642.5^{a}	52.6^{ab}	304.9^{a}	6.4^{a}	8.08^{ab}	1.55^{b}	1.32^{c}	14.21^{c}

Table 2: Growing season averages (and standard deviations) of air temperature (T_a), precipitation (Precip) and growing season days (GSL) for all sites during 2010 – 2017.

	Year	Air Temp º F	Precip mm	GSL Days
CRP-Ref	2010	22.5 (±2.4)	382.5	90
	2011	18.3 (±3.5)	450.7	111
	2012	19.1 (±3.9)	168.4	98
	2013	16.4 (±2.1)	270.7	84
	2014	17.8 (±4.4)	351.0	113
	2015	16.4 (±1.6)	633.0	119
	2016	19.7 (±4.3)		89
	2017	18.5 (±4.1)		88
CRP-Sw	2010	22.7 (±1.5)	177.8	51
	2011	18.3 (±3.4)	457.8	146
	2012	20.9 (±4.7)	222.9	148
	2013	18.2 (±5.0)	442.5	145
	2014	17.4 (±4.6)	536.7	159
	2015	16.8 (±3.8)	688.0	139
	2016	18.2 (±5.6)		149
	2017	17.8 (±4.6)		128
CRP-Pr	2010	23.4 (±2.0)	182.9	63
	2011	21.7 (±2.7)	457.8	145
	2012	22.9 (±4.9)	222.9	148
	2013	20.3 (±3.8)	476.0	155
	2014	18.9 (±3.5)	492.5	162
	2015	21.1 (±2.2)	707.0	137
	2016	21.8 (±2.7)		137
	2017	19.1 (±3.2)		154
CRP-C	2010	24.1 (±2.1)	347.2	85
	2011	23.4 (±3.3)	286.7	95
	2012	23.5 (±5.2)	178.7	116
	2013	21.3 (±2.7)	261.4	92
	2014	20.9 (±2.5)	354.8	107
	2015	22.4 (±2.2)	464.0	98
	2016	22.2 (±2.5)		84
	2017	19.9 (±3.3)		86
AGR-Sw	2010	21.5 (±6.8)	283.5	106
	2011	21.2 (±4.9)	510.4	157
	2012	22.1 (±4.6)	222.9	148
	2013	20.5 (±3.0)	434.8	129
	2014	20.3 (±2.7)	420.6	131
	2015	19.5 (±3.5)	658.0	129
	2016	21.3 (±2.8)		127
	2017	19.5 (±3.6)		135
AGR-Pr	2010	25.0 (±1.7)	182.9	63
	2011	21.1 (±4.4)	457.8	146
	2012	21.8 (±4.6)	222.9	148
	2013	20.1 (±3.4)	442.5	145

	2014	19.4 (±2.6)	453.6	136
	2015	19.2 (±1.9)	623.0	127
	2016	20.8 (±3.7)		134
	2017	18.6 (±4.3)		132
AGR-C	2010	15.4 (±4.3)	380.2	89
	2011	16.8 (±4.4)	293.8	95
	2012	13.5 (±4.2)	178.7	117
	2013	14.6 (±4.0)	297.9	96
	2014	16.2 (±3.6)	354.8	102
	2015	14.4 (±4.6)	441.0	90
	2016	17.5 (±5.3)		98
	2017	16.4 (±5.2)		97

Figure Legends

Figure 1. Location of sampling plots at the Kellogg Biological Station (KBS). One meter DEM (shown in greyscale). Black dots indicate sampling sites for root biomass. Average root biomass production is shown with a circle diameter. World Imagery basemap credits: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community.

Figure 2. Land use history and conversions at the study site. Lands managed under Conservation Reserve Program (CRP) and under conventionally tilled corn-soybean rotation agricultural (AGR) croplands were converted to soybean in 2009, and to switchgrass (Sw), restored prairie (Pr) and corn (C) from 2010 onwards. One CRP grassland was maintained in smooth brome grass as a reference.

Figure 3. Bar charts showing comparison of root biomass production within each site during 2010 to 2017. Black circles represent each of the 10 samples taken from the site, solid line represent the average root biomass production annually. Any present whiskers represent the lower and upper limits of the 95% family-wise confidence level. No root biomass data was retrieved at corn sites in 2013

Figure 4. (a-g) Bar graph of temporal changes in root biomass production and aboveground net primary production (ANPP) for each site. Analysis of variance with multiple comparison Tukey test was used to compare among years. (h) Bar graph of average root biomass production and ANPP between different crop types, and between land use histories. Analysis of variance with multiple comparison Tukey test was used to compare the differences by crop type and land use history. Average root biomass production is indicated by dark grey color, while ANPP is

indicated by light grey color. Standard error of the mean (SEM) for root biomass production and ANPP are indicated by error bars. Root biomass production was not collected in 2013 at the two corn sites. Sites and years with the same letter indicate no significant difference.

Figure 5. (a-d) Statistical analysis of variance based on linear model with root biomass production as a dependent variable. The red lines show relationships among sites, while black lines show within site relationships. Dashed and solid lines indicate insignificant and significant relationships, respectively ($p<0.05$). Open symbols indicate AGR lands, and closed symbols indicate CRP lands.

Figure 6. Ecosystem Stability (unitless) for each site from 2010–2017. The ratio of mean plot root biomass to its temporal standard deviation is displayed as points. Errors bars indicate ± 1 standard deviation (SD) for ecosystem stability.

Figure 1. Location of sampling plots at the Kellogg Biological Station (KBS). One meter DEM (shown in greyscale). Black dots indicate sampling sites for root biomass. Average root biomass production is shown with a circle diameter. World Imagery basemap credits: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community.

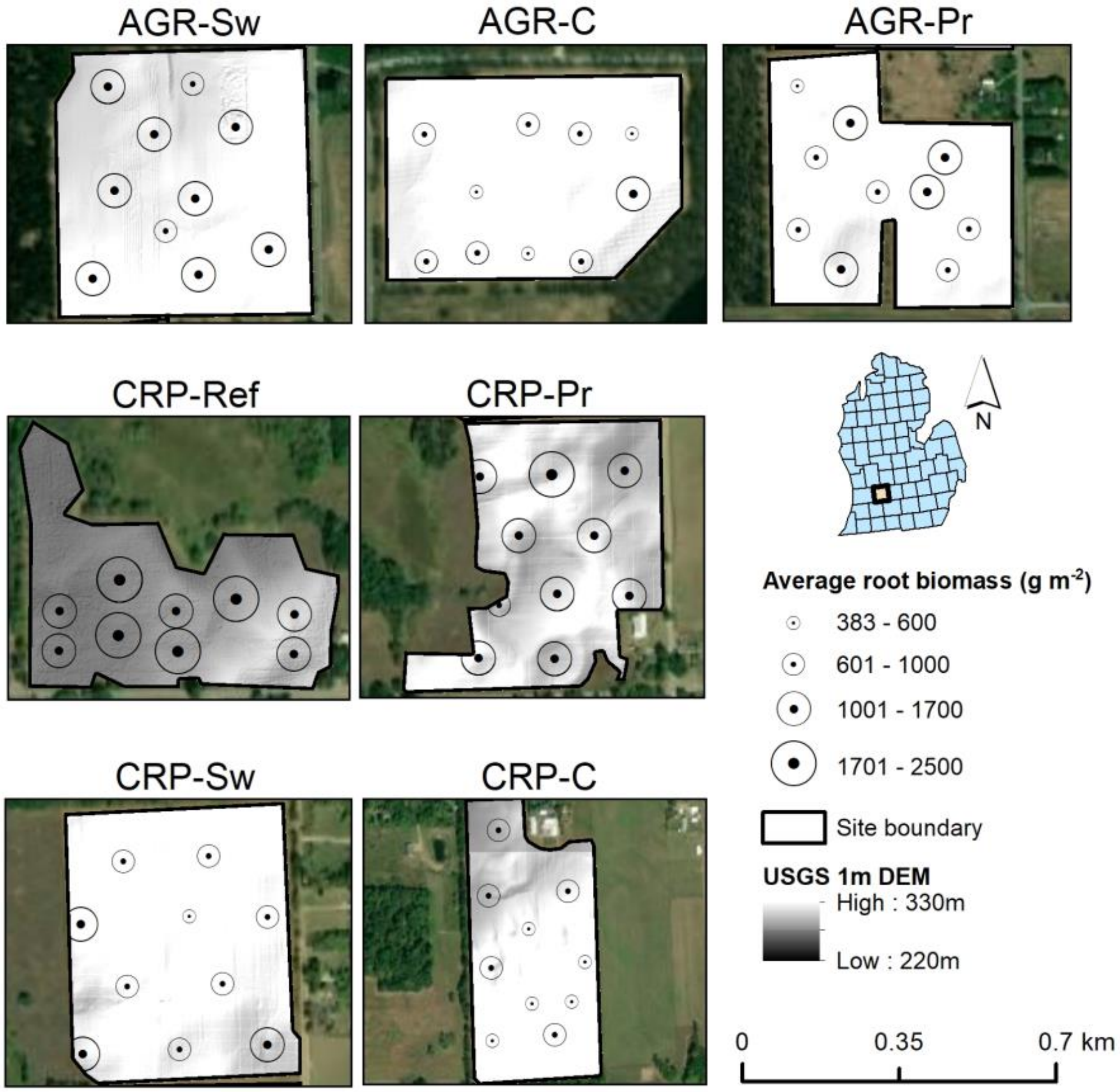
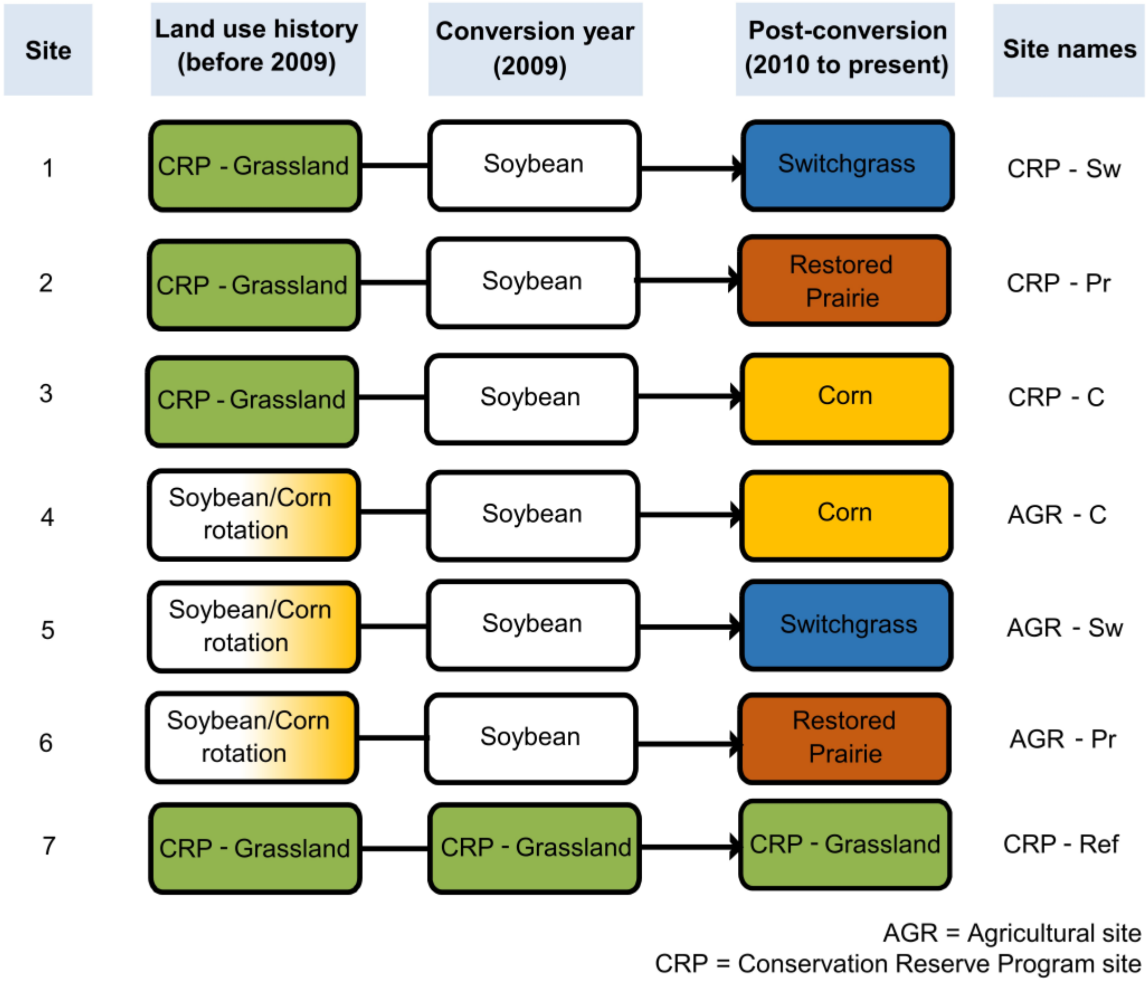


Figure 2. Land use history and conversions at the study site. Lands managed under Conservation Reserve Program (CRP) and under conventionally tilled corn-soybean rotation agricultural (AGR) croplands were converted to soybean in 2009, and to switchgrass (Sw), restored prairie (Pr) and corn (C) from 2010 onwards. One CRP grassland was maintained in smooth brome grass as a reference.



Site	Land use history (before 2009)	Conversion year (2009)	Post-conversion (2010 to present)	Site names
1	CRP - Grassland	Soybean	Switchgrass	CRP - Sw
2	CRP - Grassland	Soybean	Restored Prairie	CRP - Pr
3	CRP - Grassland	Soybean	Corn	CRP - C
4	Soybean/Corn rotation	Soybean	Corn	AGR - C
5	Soybean/Corn rotation	Soybean	Switchgrass	AGR - Sw
6	Soybean/Corn rotation	Soybean	Restored Prairie	AGR - Pr
7	CRP - Grassland	CRP - Grassland	CRP - Grassland	CRP - Ref

AGR = Agricultural site
CRP = Conservation Reserve Program site

Figure 3. Bar charts showing comparison of root biomass production within each site during 2010 to 2017. Black circles represent each of the 10 samples taken from the site, solid line represent the average root biomass production annually. Any present whiskers represent the lower and upper limits of the 95% family-wise confidence level. No root biomass data was retrieved at corn sites in 2013.

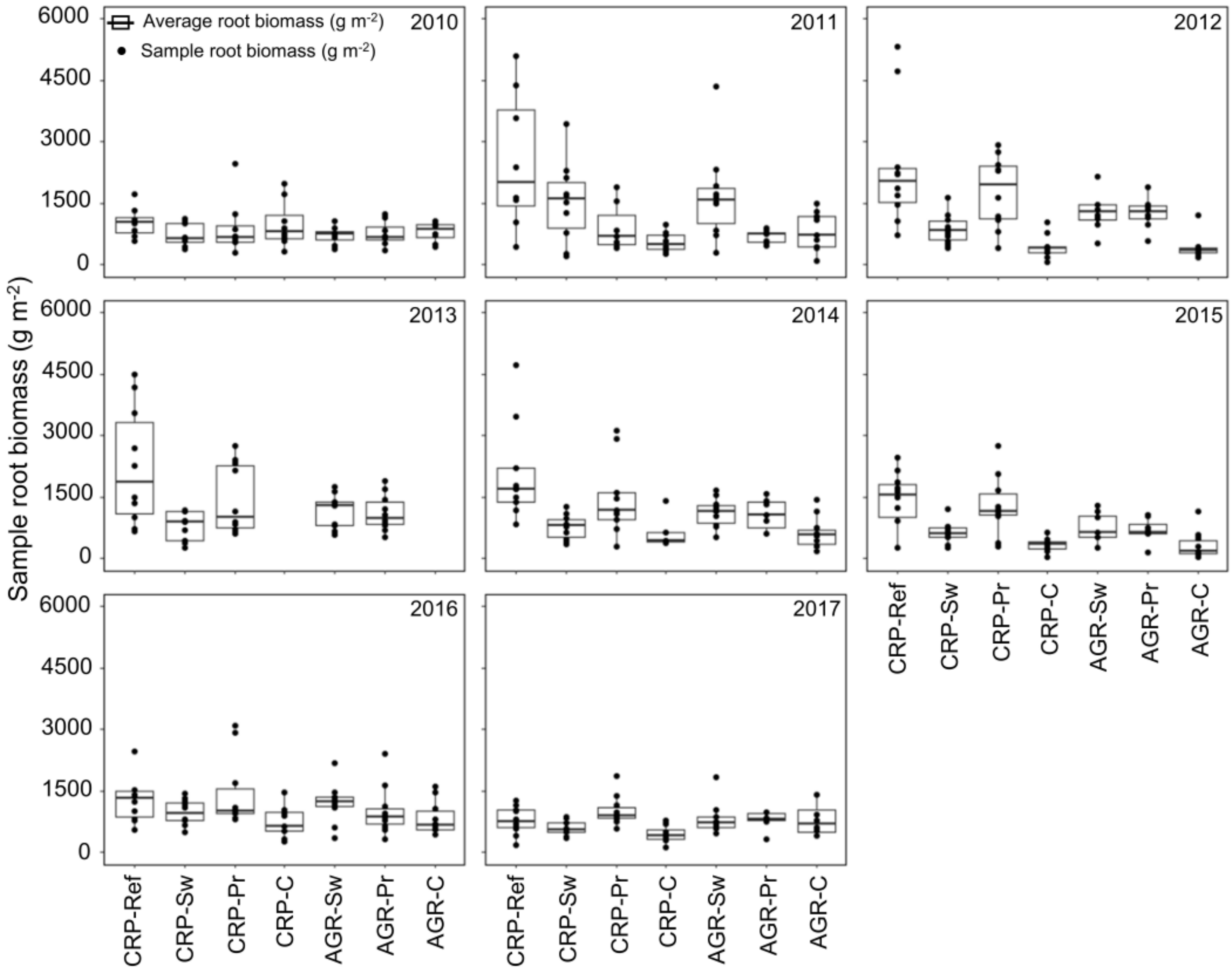


Figure 4. (a-g) Bar graph of temporal changes in root biomass production and aboveground net primary production (ANPP) for each site. Analysis of variance with multiple comparison Tukey test was used to compare among years. (h) Bar graph of average root biomass production and ANPP between different crop types, and between land use histories. Analysis of variance with multiple comparison Tukey test was used to compare the differences by crop type and land use history. Average root biomass production is indicated by dark grey color, while ANPP is indicated by light grey color. Standard error of the mean (SEM) for root biomass production and ANPP are indicated by error bars. Root biomass production was not collected in 2013 at the two corn sites. Sites and years with the same letter indicate no significant difference.

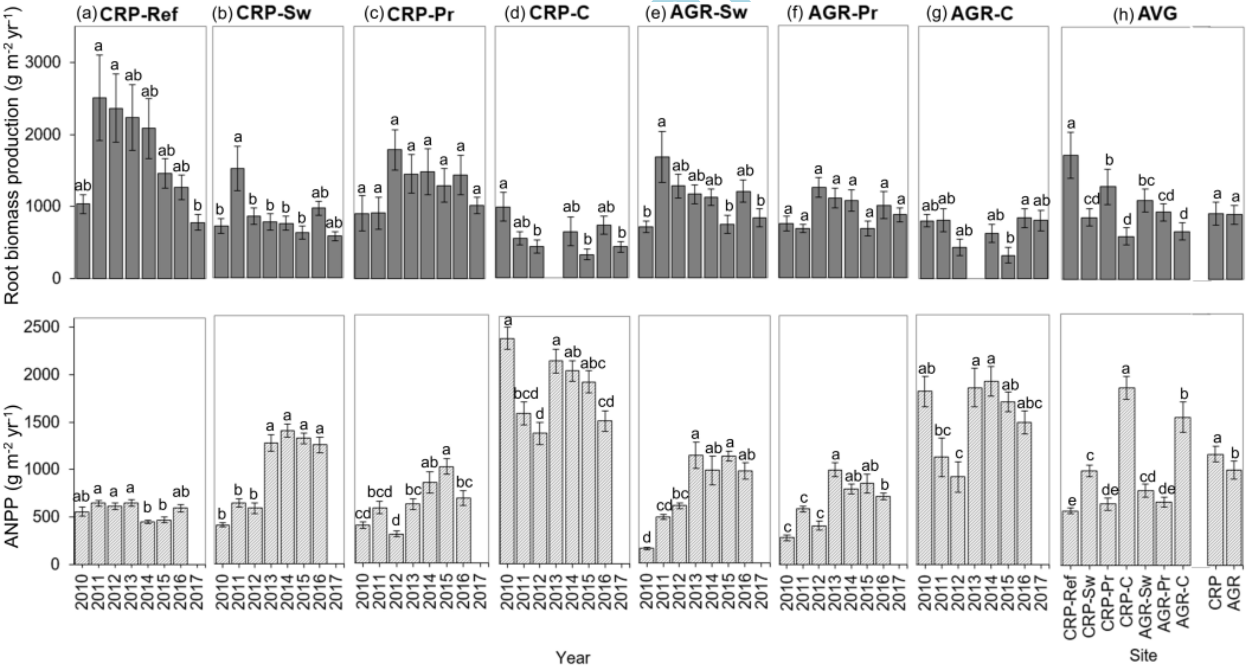


Figure 5: (a-d) Statistical linear model with root biomass production as a dependent variable. The red lines show relationships among sites, while black lines show within site relationships. Dashed and solid lines indicate insignificant and significant relationships, respectively ($P < 0.05$). Open symbols indicate AGR lands, and closed symbols indicate CRP lands.

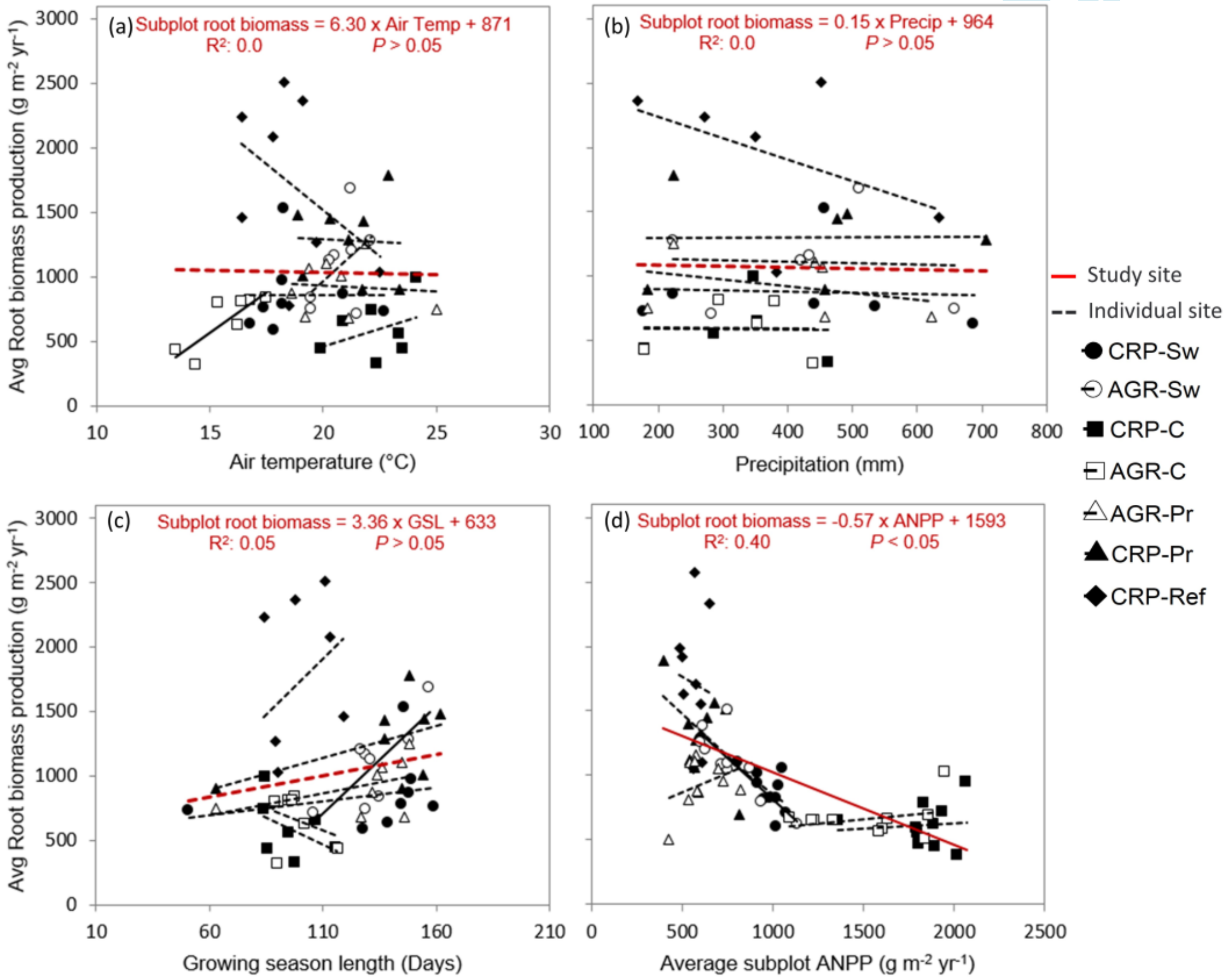


Figure 6. Ecosystem Stability (unitless) for each site from 2010–2017. The ratio of mean plot root biomass to its temporal standard deviation is displayed as points. Errors bars indicate ± 1 standard deviation (SD) for ecosystem stability.