A Review of Modeled Water Use Efficiency of Highly Productive Perennial Grasses Useful for Bioenergy

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Abstract: Whole plant productivity is obviously the ultimate product of leaf photosynthesis and this has led to numerous efforts to relate the two. However, often with perennial grasses, plant productivity is more sink-limited than source-limited, causing the linkage between the photosynthetic rate and productivity to be weak or nonexistent. This has led to a different approach, characterizing plant productivity in terms of the efficiency of intercepted light use in producing biomass, also called radiation use efficiency. Likewise, the efficiency of the use of water to produce plant biomass, or water use efficiency, has been the object of much interest. The use of a simulation model to quantify biomass, using radiation use efficiency in parallel with a daily water balance simulation, allows for the effective calculation of water use efficiency. In this project, the process of determining radiation use efficiency with field data is described, as well as example values for highly productive perennial grasses useful for feedstock for bioenergy. In addition, values of water use efficiency for these grasses are reported and compared with other perennial grasses and common cultivated crops.

Keywords: switchgrass; ALMANAC; water use efficiency (WUE); radiation use efficiency (RUE); biomass

1. Introduction

1.1. General

High-yielding perennial grasses, such as switchgrass (Panicum virgatum L.) and giant miscanthus (Miscanthus × giganteus), have been promoted as promising second-generation biofuel feedstocks in the U.S. and elsewhere. Their ability to produce large fuel loads on marginal sites that are not ideal for row crops with minimal inputs of fertilizer has pushed them to the forefront of bioenergy discussions.

There are numerous simulation models for switchgrass and giant miscanthus plant growth [1–9]. These models simulate plant productivity and also can predict soil erosion and nutrient cycling. Since modeling objectives differ, these models have different functions and details for simulating plant growth. However, these models all have a similar basic functionality. First, all these models simulate the interception of light by the leaf canopy and the conversion of light into biomass. They all partition biomass into the various plant components. Second, these models simulate the dynamics of soil water through precipitation, run-off, and evapotranspiration. Third, the models simulate soil carbon and nitrogen dynamics. Finally, these models simulate drought stress and its impacts on plant growth. Additionally, the Agricultural Land Management Alternatives with Numerical Assessment Criteria (ALMANAC) and Environmental Policy Integrated Climate (EPIC) models simulate other stress effects, including stresses due to high and low temperatures, inadequate nutrients, salinity, low pH, aluminum toxicity and poor soil aeration.
Water requirements for growing switchgrass and giant miscanthus are often an issue. Without adequate water, their biomass yields can be reduced by 45%–80% of total biomass yields [10,11]. Moreover, competition for water with other users makes maximizing water use efficiency vitally important. Again, process-based simulation models are valuable tools since they simulate the dynamics of crop water use based on evaporation of soil water, leaf transpiration, weather, and dynamics of plant communities.

1.2. Quantifying Photosynthetic Performance via Two Approaches: Single Leaf Photosynthesis vs. Radiation Use Efficiency (RUE)

There are many plant simulation models based on single leaf photosynthesis, which is then scaled up to the whole leaf canopy. Such models, such as ORYZA for rice (Oryza sativa L.) [12,13], are based on the assumption that photosynthesis is a major driver and determinant for whole plant productivity. However, frequently grass systems have been shown to be more sink-limited than source-limited. They often rely more on the processes of tiller production, leaf development, and leaf canopy orientation.

Examples:
1. Tall fescue (Festuca arundinacea Schreb.) showed that the productivity of different cultivars are sink-limited (as listed above), not source-limited [14,15].
2. Field-measured leaf CO₂ exchange rate (CER) showed that relatively low productivity sideoats grama (Bouteloua curtipendula (Michaux) Torrey) had higher CER than the much more productive switchgrass, big bluestem (Andropogon gerardii Vitman) and eastern gamagrass [Tripsacum dactyloides (L.) L.] [16].
3. Results under a rainout shelter, showed above ground net primary productivity of nine genotypes of switchgrass was poorly correlated with net photosynthetic rate. The correlation coefficient was only 0.25 [17].

Radiation use efficiency (RUE) or the amount of biomass produced per unit intercepted light, has been adopted by many as a useful alternative for quantifying whole plant productivity. For example, maize had greater biomass accumulation than other grain crops, such as soybean and rice, because maize had a high RUE and needed less nitrogen to grow its leaves [18]. This approach, by simulating leaf expansion via leaf area index (LAI), and light interception by Beer’s Law (with one extinction coefficient value for an ecotype), has been used for a wide range of crops, native plants, and perennial grasses. This system has the advantage of including sink size via LAI and potential biomass productivity. Both of these, when quantified for a perennial grass ecotype under unstressed conditions can be used within a process-based model to simulate productivity with different water, temperature and nutrient stresses. Likewise, by simulating the water balance of a plant system, such a model can quantify the water use efficiency (WUE) via biomass production divided by evapotranspiration or by plant transpiration.

1.3. Quantifying WUE

Water use efficiency (WUE) is the ratio of plant yield, that is, the total biomass yield, economic yield, or CO₂ assimilation, divided by the quantity of water transpired, total water lost (evapotranspiration), including plant transpiration and soil evapotranspiration, or irrigation water at various time scales (e.g., daily, seasonal, etc.) [19,20]. In this paper, we report WUE as the plant dry weight increase divided by the amount of water transpired.

This article is organized as follows: in Section 2, field measurement techniques for values of RUE of some highly productive perennial grasses will be introduced, and then estimation of WUE values with use of the process-based model, ALMANAC, will be described. The simulated WUE values will be validated in Section 3, and examples showing how the model has been validated and applied are also given in Section 3. The study is summarized in Section 4.

2. Methods

2.1. Derivation of RUE for Perennial Grasses

The following is a generalized protocol for sampling plants to determine RUE from field measurements. More detailed information on protocol was available from the Grassland Soil and Water Research
Laboratory website available at https://www.ars.usda.gov/plains-area/temple-tx/grassland-soil-and-water-research-laboratory/docs/193226#Information. The protocol is summarized in Figure 1.

Measurements of photosynthetically active radiation (PAR) intercepted by plants should be made between 10 a.m. and 2 p.m. in clear-sky conditions only, because cloud cover can affect the magnitude of PAR [21]. The location or site name, date and sky conditions are all recorded. Usually, two photos are taken per site: one of the overall landscape with the plot in the center of the frame, and one looking at a single rep showing the quadrat encompassing the target plant. A random sample area for the quadrat is chosen. It is important to walk outside the sample area in order to not trample the stand in front of the area where light measurements will be taken. In a natural setting, if possible, it is best to choose an ungrazed area. In a crop setting, it is important to avoid the edges of the plot, to try to make sure that the sample is taken in the plot interior, and sample midrow to midrow to get a representative sample. Typically, a quadrat 50 cm wide by the length of the light bar is used. Any non-targeted plants in the quadrat must be removed so that only canopy cover from the targeted plant species is obtained. The time, growth stage and plant height are all recorded. PAR readings are taken using a Sunfleck Ceptometer PAR light bar sensor (Decagon Devices Inc., Pullman, WA) or a similar linear sensor that measures PAR. The external sensor is placed on the tripod in direct sunlight near the plots. The light bar is calibrated with the external sensor by taking 10 measurements in direct sunlight. The average of the 10 measurements is recorded. The fraction of PAR intercepted by plants is measured using the light bar. Six or more measurements in each quadrat near the ground are taken. For each measurement the light bar is placed perpendicular to the rows and moved laterally. Within a 50 cm × 50 cm quadrat, measurements are taken every 10 cm. The average is recorded.

When harvesting plants, all plant material in the quadrat is removed and placed in a labeled bag. All replications of each plant species are sampled. In the lab, the whole sample from field is weighed. A subsample will be taken from each of total fresh samples. The subsample is weighed. Each subsample should have a similar proportion of green leaves, dead material, stems and reproductive structure as the whole field sample. After measuring the leaf area of the subsample, the subsample is put back with the whole sample.

Each subsample should be separated into dead material, stems, leaves and reproductive structures and then weighed. The area of each structure is measured using an electronic leaf area meter, such as the LI-3100 leaf area meter (LI-COR Biosciences, Lincoln, NE). The area of the dead material, stems, leaves and reproductive structures must be measured separately. The whole sample is dried in a 66 °C (150 °F) forced air oven until the weight becomes stable.
Figure 1. A generalized protocol for sampling plants to determine radiation use efficiency (RUE) from field measurements. The field protocol pictures are adapted from the Grassland Soil and Water Research Laboratory website available at https://www.ars.usda.gov/ Plains-Area/temple-tx/grassland-soil-and-water-research-laboratory/docs/193226#Information.

2.2. Derivation of RUE Values

The fraction of PAR intercepted (FIPAR) is measured on several dates during the growing season. At least 10 measurements of PAR below the leaf canopy are taken, with the external sensor simultaneously recording each time. Values for intercepted PAR each day are summed for each plot. The slope of the linear regression for aboveground dry biomass as a function of intercepted PAR is the RUE.
2.3. Brief Description of the ALMANAC Model

The model simulates the leaf area growth of the whole canopy, with potential LAI defined for each species/ecotype/variety. Climate and soils often dictate the plant density of forages and, thus, the potential LAI. The proportion of the maximum LAI during the growing season is simulated with a 0.0–1.0 “S” curve. The LAI is simulated as a function of the ratio of current summed degree days/degree days to maturity. This ratio approaches 1.0 near anthesis. This “S” curve defines the potential leaf area during the growing season.

Dry matter accumulation is simulated with the RUE values. The potential dry matter produced each day is calculated from the amount of PAR intercepted by the leaf canopy. The RUE is the dry matter produced per unit of intercepted PAR. Stresses decrease leaf area expansion and decrease dry matter accumulation. ALMANAC simulates different stresses each day. The most severe stress reduces leaf area growth and dry matter accumulation. Leaf area growth is more sensitive to drought than dry matter accumulation is.

ALMANAC simulates drought stress using potential evapotranspiration (PET), calculated using weather variables. The available soil water in the current rooting zone is calculated each day using rainfall, soil infiltration and soil water-holding capacity. When available soil water is insufficient to meet plant demand, the model simulates a drought stress, decreased leaf expansion rates and reduced dry matter accumulation.

The model simulates nutrient stresses that reduce plant growth. These stresses are simulated through a supply and demand approach. Plant N and P uptake is simulated with three parameters defining how nutrient demand changes over the growing season. The optimum fraction of N and P is defined for each species early in plant development, near anthesis and at maturity. These three values are used to simulate the potential nutrient uptake each day. If available N and P are insufficient to meet demand, the model simulates nutrient stress and decreases the dry matter accumulation rate and leaf expansion rate.

High and low temperatures also reduce plant growth in the model. A plant species has a defined base temperature and an optimum temperature. Daily temperatures below the base temperature cause cold temperature stress to occur. Temperatures above the optimum cause high temperature stress to occur.

Using Beer’s law [16], the fraction of PAR intercepted by plants (FIPAR) is:

$$FIPAR = 1.0 - \exp(-k \times LAI).$$

(1)

The light extinction coefficient (k) is calculated as:

$$k = \frac{\log_n (1 - FIPAR)}{LAI}$$

(2)

where log_n = natural log of the number.

Extinction coefficient values have been determined for many grasses [16,22–24]. Accurate simulation of LAI is critical for these equations to describe light interception. This is true during active growth and as leaves senesce.

As described above, biomass growth is simulated with RUE [16,22–24]. The RUE is the dry matter increase per unit of intercepted photosynthetically active radiation (IPAR). Plant dry weight is regressed on summed IPAR and the slope of the regression is the RUE. This regression requires multiple harvest dates during active growth. If only two harvest dates are available, RUE is calculated from differences in the dry matter between the two dates and of summed IPAR between the two dates. Only data from dates showing increases in dry matter should be included. Thus, RUE values need to be calculated for periods of active growth. Sites experiencing drought stress are avoided for RUE calculation. FIPAR is calculated on a daily basis, with values for dates between measurement dates determined by linear interpolation.

ALMANAC simulates water and nutrient competition with a balance sheet approach. Intercepted light for each plant species is computed. Next, potential daily biomass growth is calculated for each species RUE is multiplied by the intercepted PAR to calculate potential biomass growth for a day. Demands for N and P are calculated from the optimum N and P concentrations. When insufficient N and/or P is available, ALMANAC reduces simulated growth rates. ALMANAC simulates variability in root scavenging capacities among competing plant species through differences in the current rooting depth of each species. The potential rooting depths of different plant species are derived from measurements in the literature.
Potential plant transpiration is determined using the potential evapotranspiration and the total community LAI. When soil water is insufficient to meet plant demand, simulated drought stress occurs and limits growth. This occurs for all plant species competing. However, a deeper-rooted plant species can sometimes have access to soil water and nutrients not available to competing shallower-rooted species. In this way, ALMANAC accommodates different rooting depths of species. The deeper-rooted plant species can sometimes have adequate soil water and nutrients, thus avoiding drought and nutrient stresses when a shallower-rooted species is stressed.

2.4. Use of the ALMANAC Model to Derive WUE of Grasses

While water use can be measured directly, it is difficult, involving neutron access tubes, gravimetric measurements of soil moisture with soil cores, or weighing lysimeters. In addition, WUE measurements require plant harvesting to quantify whole plant or grain dry weight. Quantifying WUE over several soils, plant species and climates requires a large amount of resources and time. An efficient alternative is a process-based simulation model that uses equations for water use and for plant growth. Such a model can simulate a diversity of soils, weather data and plant species. Examples of these models include the Environmental Policy Integrated Climate (EPIC) model (originally the Erosion Productivity Impact Calculator) [25], Soil and Water Assessment Tool (SWAT) [4] and Agricultural Land Management Alternatives with Numerical Assessment Criteria (ALMANAC) [2]. These models simulate the water balance while considering such variables as soils, weather and plant species cover. The models simulate leaf area and plant biomass and grain (for crops). These models simulate WUE as the dry weight of plant biomass (or grain) produced per unit of water transpired or per unit of evapotranspiration. For this study, we used the ALMANAC model to calculate perennial grass WUE [26].

3. Results and Discussion

3.1. Representative Values of RUE for Grasses

Values of RUE for different perennial grasses show similar variability as different agricultural crops (Table 1). Using crops as standards, maize (*Zea mays* L.) RUE is 3.5 g per MJ intercepted PAR, grain sorghum (*Sorghum bicolor* (L.) Moench) is 2.8, sunflower (*Helianthus annuus* L.), rice and wheat (*Triticum aestivum* L.) are 2.2, 2.2 and 2.8 [27]. Peanut (*Arachis hypogaea* L.) RUE is 2.0 [28], rice RUE is 2.4 [29] and two-year sugarcane (*Saccharum officinarum* L.) RUE is 2.1 [30].

Values for perennial grasses range from 0.4 g per MJ for prairie sandreed (*Calamovilfa longifolia* (Hook.) Scribn.) in Montana [22] to 4.4 g per MJ for Alamo switchgrass in Texas [28]. Four warm-season native grasses showed the aforementioned value for Alamo switchgrass (4.4), 1.1 for sideoats grama (*Bouteloua curtipendula* (Michaux) Torrey), 1.4 for big bluestem (*Andropogon gerardii* Vitman) and 2.1 for eastern gamagrass (*Tripsacum dactyloides* (L.) [16]. Kiniry et al. [23] measured RUE values of 1.50 for coastal bermudagrass (*Cynodon dactylon* (L.) Pers.), 1.25 for bahiagrass (*Paspalum notatum* Flügge var saureae Parodi), 1.1 for sideoats grama, 1.43 for buffalograss (*Buchloe dactyloides* (Nutt.) Englem.) and 0.63 for blue grama. Kiniry et al. [31] measured values of RUE of 4.35 for Alamo switchgrass, 3.7 for giant miscanthus and Kanlow switchgrass and 3.2 for Cave-in-Rock switchgrass. Kiniry et al. [24] measured values of 1.3 for buffelgrass (*Pennisetum ciliare* (L.) Link) and old world bluestems (*Bothriochloa* Kuntze, *Capillipedium* Stapf and *Dichanthium Willemet*). Kiniry et al. [22] measured values in Montana of 3.5 for threadleaf sedge (*Carex filifolia* Nutt.), 4.0 for needle and thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth), 3.8 for green needlegrass (*Nassella viridula* (Trin.) Barkworth) and the aforementioned 0.4 for prairie sandreed. Kiniry et al. [32] reported a RUE value for tall fescue of 3.2.
### Table 1. Measured radiation use efficiency (RUE) (g/MJ) for annual agricultural crops and perennial grasses.

<table>
<thead>
<tr>
<th>Common Name</th>
<th>Scientific Name</th>
<th>Cultivar</th>
<th>RUE (g/MJ)</th>
<th>Study site</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Annual agricultural crops</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wheat</td>
<td><em>Triticum aestivum</em> L.</td>
<td></td>
<td>2.8</td>
<td>Mexico</td>
<td>[27]</td>
</tr>
<tr>
<td>Grain Sorghum</td>
<td><em>Sorghum bicolor</em> (L.) Moench</td>
<td></td>
<td>2.8</td>
<td>France</td>
<td>[27]</td>
</tr>
<tr>
<td>Maize</td>
<td><em>Zea mays</em> L.</td>
<td></td>
<td>3.5</td>
<td>Texas</td>
<td>[27]</td>
</tr>
<tr>
<td>Peanut</td>
<td><em>Arachis hypogaea</em> L</td>
<td></td>
<td>2.2</td>
<td>Philippines</td>
<td>[27]</td>
</tr>
<tr>
<td>Rice</td>
<td><em>Oryza sativa</em> L</td>
<td></td>
<td>2.4</td>
<td>Texas</td>
<td>[27]</td>
</tr>
<tr>
<td>Sunflower</td>
<td><em>Helianthus annuus</em> L.</td>
<td></td>
<td>2.2</td>
<td>Texas, France</td>
<td>[27]</td>
</tr>
<tr>
<td><strong>Perennial grasses</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Switchgrass</td>
<td><em>Panicum virgatum</em>, L.</td>
<td></td>
<td>4.35, 4.4</td>
<td>Texas</td>
<td>[28], [31]</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3.2</td>
<td>Illinois</td>
<td>[31]</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3.7</td>
<td>Oklahoma</td>
<td>[31]</td>
</tr>
<tr>
<td>Bahiagrass</td>
<td><em>Paspalum notatum</em> Flügge var saurae Parodi</td>
<td></td>
<td>1.25</td>
<td>Texas</td>
<td>[23]</td>
</tr>
<tr>
<td>Big Bluestem</td>
<td><em>Andropogon gerardii</em> Vitman</td>
<td></td>
<td>1.4</td>
<td>Texas</td>
<td>[16]</td>
</tr>
<tr>
<td>Blue Grama</td>
<td><em>Bouteloua gracilis</em> (H.B.K.)</td>
<td></td>
<td>1.43</td>
<td>Texas</td>
<td>[23]</td>
</tr>
<tr>
<td>Buffalograss</td>
<td><em>Buchloe dactyloides</em> (Nutt.) Englem</td>
<td></td>
<td>1.3</td>
<td>Texas</td>
<td>[24]</td>
</tr>
<tr>
<td>Buffelgrass</td>
<td><em>Pennisetum ciliare</em> (L.) Link</td>
<td></td>
<td>1.5</td>
<td>Texas</td>
<td>[23]</td>
</tr>
<tr>
<td>Coastal Bermuda Grass</td>
<td><em>Cynodon dactylon</em> (L.) Pers</td>
<td></td>
<td>2.1</td>
<td>Texas</td>
<td>[16]</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1.1</td>
<td>Texas</td>
<td>[23]</td>
</tr>
<tr>
<td>Giant Miscanthus</td>
<td><em>Miscanthus × giganteus</em></td>
<td></td>
<td>3.7</td>
<td>Illinois</td>
<td>[31]</td>
</tr>
<tr>
<td>Green Needlegrass</td>
<td><em>Nassella viridula</em> (Trin.)</td>
<td></td>
<td>3.8</td>
<td>Montana</td>
<td>[22]</td>
</tr>
<tr>
<td>Needle and Thread</td>
<td><em>Hesperostipa comata</em> (Trin. &amp; Rupr.) Barkworth</td>
<td></td>
<td>4</td>
<td>Montana</td>
<td>[22]</td>
</tr>
<tr>
<td>Plant Name</td>
<td>Scientific Name</td>
<td>Arrhenius Number</td>
<td>Location</td>
<td>Reference</td>
<td></td>
</tr>
<tr>
<td>-----------------------</td>
<td>----------------------------------------</td>
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<td></td>
</tr>
<tr>
<td>Old World Bluestem</td>
<td><em>Bothriochloa Kuntze</em></td>
<td>1.3</td>
<td>Oklahoma</td>
<td>[24]</td>
<td></td>
</tr>
<tr>
<td>Scented-tops</td>
<td><em>Capillipedium Stapf</em></td>
<td>1.3</td>
<td>Oklahoma</td>
<td>[24]</td>
<td></td>
</tr>
<tr>
<td>Bluestem</td>
<td><em>Dichanthium Willemet</em></td>
<td>1.3</td>
<td>Oklahoma</td>
<td>[24]</td>
<td></td>
</tr>
<tr>
<td>Prairie Sandreed</td>
<td><em>Calamovilfa longifolia (Hook.) Scribn.</em></td>
<td>0.4</td>
<td>Montana</td>
<td>[24]</td>
<td></td>
</tr>
<tr>
<td>Sideoats Grama</td>
<td><em>Bouteloua curtipendula (Michaux) Torrey</em></td>
<td>1.1</td>
<td>Texas</td>
<td>[16]</td>
<td></td>
</tr>
<tr>
<td>Tall Fescue</td>
<td><em>Festuca arundinacea Schreb</em></td>
<td>3.2</td>
<td>Montana</td>
<td>[22]</td>
<td></td>
</tr>
<tr>
<td>Threadleaf Sedge</td>
<td><em>Carex filifolia Nutt.</em></td>
<td>3.5</td>
<td>Montana</td>
<td>[22]</td>
<td></td>
</tr>
<tr>
<td>Two-Year Sugarcane</td>
<td><em>Saccharin officinarum L.</em></td>
<td>2.1</td>
<td>Hawaii</td>
<td>[30]</td>
<td></td>
</tr>
</tbody>
</table>
3.2. Examples of Testing ALMANAC’s Simulation of Perennial Grass Biomass

ALMANAC’s simulation of perennial grass biomass has been frequently reported. The model simulated several Texas range sites with native warm season grasses [23,33]. Old world bluestems and buffelgrass were simulated in Oklahoma, Texas and Mexico [18]. The model simulated coastal bermudagrass and bahiagrass in Texas [24]. ALMANAC simulated western grasses in Montana using parameters derived for some common native grasses there [22]. Tall fescue was simulated at several sites where this grass is commonly grown [32]. Finally, the model simulated creosote bush (*Larrea tridentata* (DC.) Cov.) and competing grasses in arid sites in western Texas [34].

Overall, the ALMANAC model [26,35] reasonably predicts grass biomass and can be an effective tool to evaluate management practices that maximize plant productivity, optimize inputs and minimize negative environmental impacts.

3.3. Calculating WUE with the ALMANAC Model

Water use efficiency has been expressed as CO2 assimilation rate per unit water transpired [20] or as plant dry weight increase per unit water used [19]. Plant dry weight is either total above-ground dry weight or crop grain dry weight. Water use includes both the soil water evaporation and transpiration from the leaves during the growth period. WUE values in the literature include 1.0 mmol CO2 per mol of water for big bluestem and 2.6 for indiangrass (*Sorghastrum nutans* (L.) Nash). Accounting for molecular weights, these values are 1.7 and 4.3 mg of carbohydrate (CH2O) per g of water transpired. In an outdoor pot experiment, switchgrass cultivars grown from seeds during the initial 11 weeks of growth had WUE values ranging from 4.3 to 8.5 mg dry weight per g of water used [36]. In another study simulating biomass production and evapotranspiration of fields in Tennessee and Oklahoma [37], switchgrass values were 3.5 to 6.3 mg of CH2O per g of water transpired.

Blue grama (*Bouteloua gracilis* (H.B.K.)) had a WUE value of 4.55 mg per g in a greenhouse study [38]. Likewise, seedlings of Arabian drop-seed grass (*Sporobolus arabisicus*) and bearded sprangletop (*Leptochloa fusca*), when harvested after reaching maximum biomass, had WUE values of 1.0 to 1.4 mg g⁻¹ [39]. Switchgrass WUE in the field in Nebraska had values of 1.0 to 5.5 mg per g [40], similar to switchgrass seedlings in a growth chamber (1.45 to 5.5 mg per g) [41]. A mixture of cool season and warm season grasses (including blue grama) in Colorado had WUE values of 1.0 to 4.5 mg per g [42].

Measuring WUE is valuable for determining areas suitable for large grasses for biofuels because competition with farmland used for food, fiber and feed production has pushed biofuel grass production into areas with less productive soils, where soil water and nutrients are often limited [43]. Limited rainfall and/or the limited capacity of soils to store moisture are important for production of these grasses. However, direct measurements of WUE require labor-intensive procedures involving soil water measurements. Likewise, such calculations of WUE require harvesting to measure plant dry weights. Such direct measurement of WUE for several soils, plant species and climatic conditions requires considerable resources and time. Thus, modeling WUE is critical to increase the efficiency of biofuel feedstock production. As discussed above, the ALMANAC model has been used to efficiently calculate WUE of perennial grasses. In the model, switchgrass WUE was calculated as the plant dry weight increase per unit of water transpired [44,45].

Kiniry et al. [44] simulated plant transpiration and biomass in four study sites: Stephenville, Texas; Mead, Nebraska; Columbia, Missouri and Ames, Iowa. In this study, the WUE of different switchgrass types varied among locations (Table 1). There were four switchgrass types, southern lowland (SL), northern lowland (NL), southern upland (SU) and northern upland (NU) [46]. The WUE values were greatest for lowland types. The highest WUE values in most of TX were the southern lowland types and the greatest WUE values at locations further north were the northern lowland types.

Another study with field-measured biomass [31] compared WUE values for different species and ecotypes. Alamo showed the largest mean each year. Alamo’s values increased from 3.5 mg dry weight per gram of water transpired in year two to 5.6 mg dry weight per gram of water transpired.
in year three. Blackwell and Cave-in-Rock had the lowest values for WUE. Kanlow had the highest WUE value each year, for species and ecotypes other than Alamo. Shawnee was intermediate between Kanlow and Blackwell/Cave-in-Rock. Miscanthus had the lowest WUE in year two but one of the highest in year three.

Extending the work of Kiniry et al. [44] in the northern U.S. and Woli et al. [47] in Mississippi, Behrman et al. [45] parameterized ALMANAC and simulated WUE for the four major switchgrass types in multiple locations across the Great Plains. This study involved 10 sites ranging from northern Missouri to subtropical southern Texas. The sites represented locations anticipated to be primary production areas for biofuel crops. The northern lowland type had the highest WUE in most cases, being greatest for eight of the 14 locations. The southern upland’s values for WUE were greatest at two sites: Booneville, Arkansas and Mead, Nebraska. The northern upland types had the greatest value at Stillwater, Oklahoma.

The WUE values of different switchgrass ecotypes and Miscanthus in these three studies generally ranged from 3 to 6 mg per g. These were within the range of previously reported values that ranged widely and varied among environmental conditions and ecotypes. The WUE of potted switchgrass cultivars had WUE values ranging from 4.3 to 8.5 mg dry weight per g of water used [36]. WUE values of switchgrass in Tennessee and Oklahoma were 3.5 to 6.3 mg CH$_2$O per g of water transpired [37]. Sunburst switchgrass had WUE values ranging from 5.6 to 7.4 mg dry weight per gram of water used [48]. WUE of switchgrass grown in a grassland in Nebraska with little bluestem was 5 mg dry weight per gram of water transpired during the boot or heading stages and dropped to 1 mg g$^{-1}$ during ripening stage [40]. Similar values were reported for switchgrass seedlings in a growth chamber (1.45 to 5.5 mg per g) [41]. The value of WUE for switchgrass ranged from 4.7 to 7.9 during the boot or heading stages when calculated as the ratio of biomass to total water applied and precipitation during the irrigation experiment [49]. The high WUE values for lowland varieties allow for increased yields in southern locations where water is often limiting.

The simulated WUE of the four switchgrass types ranged from 3 to 5 mg per g (Table 2). WUE was usually greatest for the lowland types. However, for the first soil in Ames, this was not true. The highest simulated WUE was for the northern lowland type in most cases in the three northern locations. The highest simulated WUE in Texas was for the southern lowland type for all three soils (Table 2).

<table>
<thead>
<tr>
<th>Location/soil type</th>
<th>SL</th>
<th>NL</th>
<th>SU</th>
<th>NU</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Ames, Iowa</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clarion loam</td>
<td>4</td>
<td>4</td>
<td>5</td>
<td>3.3</td>
</tr>
<tr>
<td>Nicolle loam</td>
<td>4</td>
<td>4.6</td>
<td>3</td>
<td>2.8</td>
</tr>
<tr>
<td>Webster clay loam</td>
<td>5</td>
<td>4.3</td>
<td>4</td>
<td>2.8</td>
</tr>
<tr>
<td><strong>Mead, Nebraska</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yutan silty clay loam</td>
<td>5</td>
<td>5.4</td>
<td>4</td>
<td>3.6</td>
</tr>
<tr>
<td>Tomke silt loam</td>
<td>5</td>
<td>4.9</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Nodaway silt loam</td>
<td>5</td>
<td>4.9</td>
<td>3</td>
<td>3</td>
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<tr>
<td><strong>Columbia, Missouri</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Keswick silt loam</td>
<td>5</td>
<td>4.6</td>
<td>4</td>
<td>3.9</td>
</tr>
<tr>
<td>Mexico silt loam</td>
<td>4</td>
<td>4.5</td>
<td>4</td>
<td>3.2</td>
</tr>
<tr>
<td>Weller silt loam</td>
<td>4</td>
<td>4.3</td>
<td>4</td>
<td>3.2</td>
</tr>
</tbody>
</table>
Stephenville, Texas

<table>
<thead>
<tr>
<th>Soil Type</th>
<th>RUE</th>
<th>WUE</th>
<th>WUE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brackett clay loam</td>
<td>4.3</td>
<td>3.3</td>
<td>3.2</td>
</tr>
<tr>
<td>Altoga clay loam</td>
<td>4.3</td>
<td>3.2</td>
<td>3.1</td>
</tr>
<tr>
<td>Houston Black clay</td>
<td>4.3</td>
<td>3.2</td>
<td>3.1</td>
</tr>
</tbody>
</table>

For high productivity perennial grasses, RUE measured with field data and WUE calculated with a process-based model are valuable and useful means of determining whole plant productivity and water demands. The values given herein can be used to compare to different grasses and to agronomic crops. In addition, the values given for RUE, when incorporated into a process-based model, are useful for many applications, including optimizing management and determining land area required to supply biofuel energy plants. The values for WUE given herein are useful for comparing water requirements and the production of these perennial grasses to other ecological and agronomic systems. This is an important step in optimizing the size and location of such bioenergy production plants. As such, it is also valuable for estimating the environmental and economic impact of large land areas of dedicated energy perennial grasses.

In previous studies, the ALMANAC model that was mostly calibrated by adjusting RUE and WUE values for different ecotypes of switchgrass could provide an accurate estimation of biomass production on different soils and with different weather scenarios [9,50]. Moreover, this model could successfully predict the productivity of these grasses on cropped soils and marginal soils, as well as in wet, normal and dry years for a location [51]. Thus, prior to any expense of building a biofuel facility, cost estimates can be made for the area of land needed for producing biofuel and transportation distances from the growing sites to the facility. Kim et al. [52] has estimated the optimal location of biofuel storage facilities based on the ALMANAC-simulated switchgrass yields across multiple regions in the southern Great Plains of the United States. The accurate prediction of potential biomass production in different locations and years increased the accuracy of cost estimation of transportation (from farm fields to storage facilities and biorefineries) in an agent-based simulation model (ABS) [52].

4. Conclusions

In this study, previously reported values of water use efficiency (WUE) were described for various varieties of switchgrass, calculated with the ALMANAC model. Plant parameters for each switchgrass variety had been developed using measured field data such as height, LAI and RUE. The model was calibrated using measured switchgrass yields collected for multiple years. After the model was successfully calibrated, the values of WUE for switchgrass were compared with measured WUE values in other studies. According to ALMANAC simulation results, the values of WUE for various switchgrass varieties ranged from 1.0 to 5.6 mg dry weight per gram of water used with switchgrass. Our calculated WUE values for switchgrass were similar to the measured values reported in other studies. This demonstrates that the ALMANAC model predicts WUE relatively well for different varieties of switchgrass grown in different locations and years. For further study, this well-calibrated ALMANAC model can be used to estimate the effect of increasing extreme weather events, such as drought and flooding, on switchgrass WUE and its yield, which will provide useful information to overcome the impacts of climate change on biofuel feedstock production. The model will also be useful for predicting the WUE and yield of other highly productive grasses that show promise for bioenergy.

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