The Challenge of Lignocellulosic Bioenergy in a Water-Limited World

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It is hoped that lignocellulosic sources will provide energy security, offset carbon dioxide enrichment of the atmosphere, and stimulate the development of new economic sectors. However, little is known about the productivity and sustainability of plant cell-wall energy industries. In this study, we used 16 global circulation models to project the global distribution of relative water availability in the coming decades and summarized the available data on the water-use efficiency of tree- and grass-based bioenergy systems. The data on bioenergy water use were extremely limited. Productivity was strongly correlated with water-use efficiency, with C_4 grasses having a distinct advantage in this regard. Our analysis of agroclimatic drivers of bioenergy productivity suggests that relative water availability will be one of the most important climatic changes to consider in the design of bioenergy systems.

Keywords: climate change, lignocellulosic bioenergy, water availability, drought, sustainability

The sharply increasing demand for energy raises concerns over our continued reliance on fossil fuels because of the uncertainty of future supply and the environmental externalities associated with fossil energy production (Campbell and Laherrerre 1998, Heinberg 2005, Solomon et al. 2007). Of the available alternatives, nonfood plant biomass (cell-wall based, or *lignocellulosic* biomass) is seen as a key bridging technology to a low-carbon economy because of its compatibility with existing agronomic practices, materials handling, and energy-production systems. There is also the oft-cited potential to stimulate local economic development (Mathews 2007), energy security (Ragauskas et al. 2006), and the capacity to restore soil properties or other ecological aspects of degraded landscapes (Tilman et al. 2006, Semere and Slater 2007, Bhardwaj et al. 2010). In a recent process-based modeling analysis, Beringer and colleagues (2011) estimated the future global bioenergy production potential using all available sources of biomass to be 130–270 exajoules per year, equal to 15%–25% of the projected global demand, with dedicated energy crops supplying 20%–60% of this, depending on land availability and irrigation. Importantly, priority was given to food production and biodiversity protection in determining land availability for bioenergy production, and productivity potentials accounted for changes in growing conditions due to projected climate change. Although industrial-scale bioenergy production has been questioned on economic, ecological, and energetic grounds (Giampietro et al. 1997, Evans and Cohen 2009, Gerbens-Leenes et al. 2009), it appears that dedicated energy farming with lignocellulosic crops has the capacity to supply a significant fraction of future energy demand with the associated potential for changes in land use (Njakou Djomo and Ceulemans 2012). Where and how such energy production systems are managed must be carefully considered with respect to growing conditions, socioeconomic considerations, and market forces.

Industrial-scale production of energy from lignocellulosic sources will require large amounts of water, largely from evapotranspiration from biomass production, and the prospect of even greater human appropriation of available surface freshwater raises concerns of sustainability and ecological impacts (Berndes 2002, Pimentel et al. 2004, Varis 2007, Evans and Cohen 2009, Gerbens-Leenes et al. 2009, Bhardwaj et al. 2010, Robertson et al. 2011). Estimates of current evapotranspiration for agricultural crop production range from 2500 to 7500 cubic kilometers per year (Postel et al. 1996, Postel 1998, Rockström et al. 1999, Rost et al. 2008), and recent modeling analyses (Berndes 2002, Beringer et al. 2011) suggest that bioenergy-crop production of the scale needed to meet future projections (Nakićenović et al. 1998, Beringer et al. 2011) could double this amount. Such an increase in evaporative water loss, if it is not offset by increased water-use efficiency, might decrease the rates of groundwater recharge, which would exacerbate the rapid drop in water tables occurring in many regions of the world. Clearly, as we come to rely more heavily on the ecosystem service of energy supply, it will be

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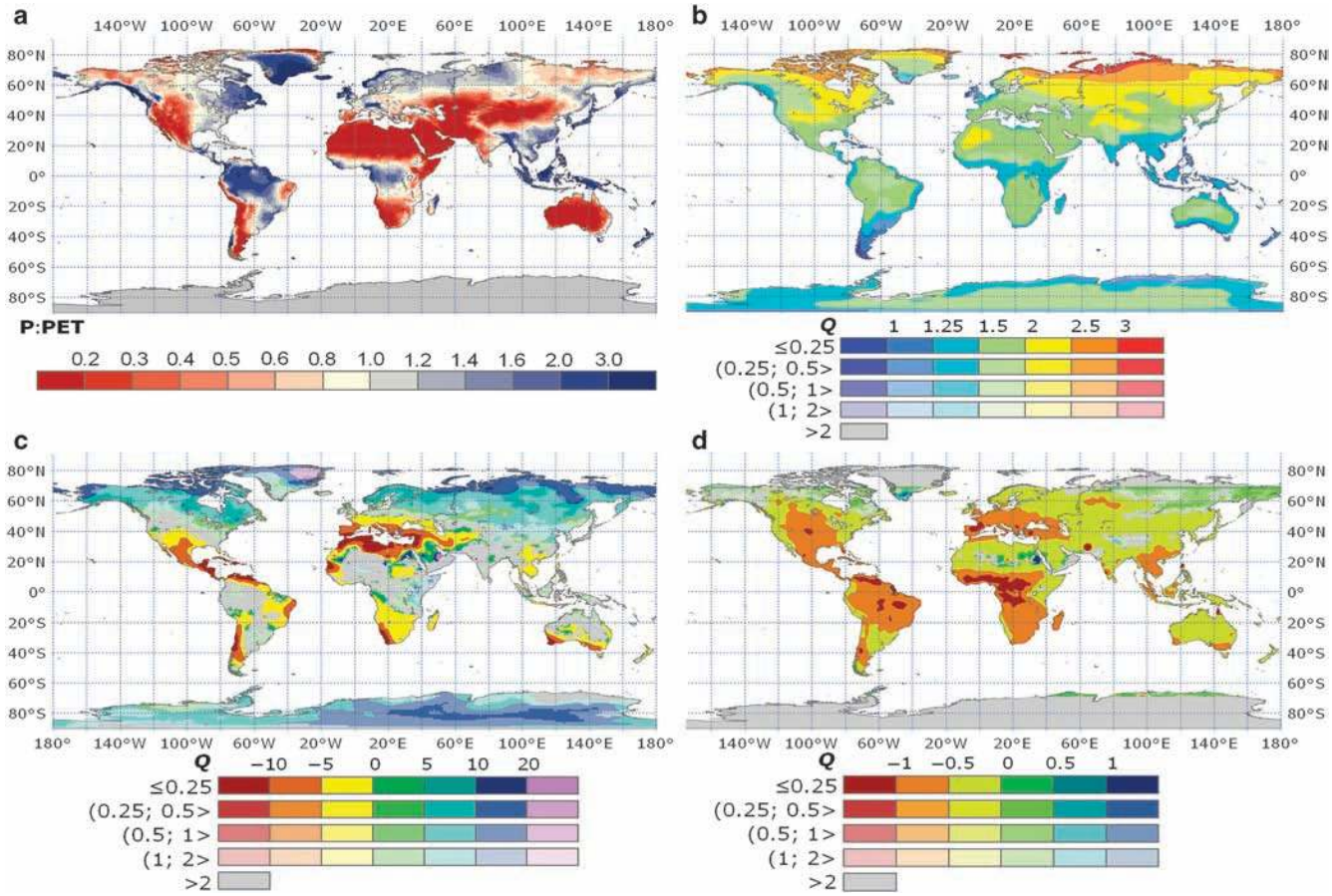

Figure 1. (a) The ratio (P:PET) of mean annual precipitation (P) to mean annual potential evapotranspiration (PET) for the period of 1980–2009, calculated from the Climatic Research Unit Global 0.5° Monthly Time Series 3.1 data set. The original climate data that were used to derive figure 1 are available at* http://badc.nerc.ac.uk/view/badc.nerc.ac.uk__ATOM__dataent_1256223773328276. *(b) Changes in mean annual temperature (in degrees Celsius) over the period of 2035–2064 compared with the 1980–2009 baseline. (c) The percentage change of the mean annual sum of precipitation and (d) of the mean annual relative Palmer Z-index (rZIND) for the same periods as that in panel (b). The color depicts the change of the mean of the given climatological variable, the color shade distinguishes intermodel agreement expressed as an uncertainty factor,* Q *(i.e., the ratio of the standard deviation of the predicted change to the median of the 16 data points for the given grid). Areas with* Q > 2 *(signaling no agreement between the projections) are colored in gray.

crucial to engineer and manage bioenergy-cropping systems to be as water efficient as possible, more so because future changes in climate are expected to increase drought stress over most of the world's land surface (figure 1; Beringer et al. 2011, Trnka et al. 2011).

To date, most analyses of the potential impact of bioenergy production on water resources have been global-scale syntheses, some using process-based ecosystem modeling derived from limited data on energy-crop water use (e.g., Berndes 2002, Gerbens-Leenes et al. 2009, Beringer et al. 2011). Such analyses are useful for considering the potential effects of bioenergy production in a global context and for evaluating changes in resource availability and climate. However, concerns have been raised over drawing inferences from such a limited data base (Giampietro and Mayumi 2009, Maes et al. 2009). Furthermore, in order to match appropriate crops to prevailing agroclimatic conditions (Trnka et al. 2011), to design bioenergy-cropping systems with high water-use efficiency, and to improve future model parameterizations, detailed knowledge of the ecophysiology and water relations of the major bioenergy crops under realistic field conditions is crucially needed. We argue that plant ecophysiology must move from the realm of theoretical to applied science, and more research at appropriate field scales is needed to inform the development and management of bioenergy-cropping systems. Accordingly, our objectives in this article are to survey the literature to determine the availability of data on the water relations of representative nonfood lignocellulosic tree and grass energy crops, to identify information gaps, and to make recommendations for future research. In addition, we provide examples of the kind of research needed to advance our understanding of the ecohydrologic implications of industrial-scale bioenergy production.

Agroclimatic and ecophysiological considerations for bioenergy-cropping systems

The relative availability of water in the environment to support plant growth depends on the seasonal progression of precipitation (expressed here as P) and temperature, which, in turn, determines the evaporative demand of the atmosphere. A reference potential evapotranspiration (PET) can be calculated simply as a meteorological heat sum (Thornthwaite 1948) or can incorporate climatic influences and physiological control of water loss by plants in response to a vapor-pressure deficit, temperature, drought, elevated atmospheric carbon dioxide (CO_2), or other factors (e.g., Allen et al. 1998). The regional water balance can be calculated as the ratio of P to PET (P:PET). When this ratio is higher than 0.4–0.5, the area is considered suitable for rain-fed production, whereas below this threshold, irrigation becomes necessary to sustain growth in some parts of the season. The P:PET ratio (figure 1a) helps to indicate areas that are potentially suitable for rain-fed production and those in which biomass production would require irrigation. In our climate-modeling study, the goal was to summarize the current distribution of plant-available water on the basis of widely available empirical data, and for this, measured P and PET were superior to the estimated actual evapotranspiration (AET). This approach facilitates comparisons with global estimates of future changes in temperature (figure 1b) and drought stress (figure 1c) and avoids confusion with the calculated AET that we determined from the empirical data on plant physiological processes (tables 1a–2d). In most regions, P is greater than AET, which ensures that our approach is conservative (e.g., ecosystems do not use more water than is available); however, there are regions in which AET greatly exceeds P. Agriculture in such regions necessarily depends on maintaining adequate soil water content through irrigation or through farming in floodplains or other hydrologically favorable physiographic settings. This effectively decouples the plant physiological responses that determine water-use efficiency from the prevailing climate and represents a special case (beyond the scope of this article). The United Nations Food and Agriculture Organization has developed a tool—CropWat (*www.fao.org/nr/water/infores_databases_cropwat.html*)—for estimating irrigation demand in such regions on the basis of soil, climatic, and plant-physiology data for most of the major agricultural crops grown in these regions, although the bioenergy-crop species of the present study are not represented.

Agroclimatic conditions define the physical limits of the design, distribution, and productivity of the bioenergy-production systems of the future. In continental settings of high latitudes (e.g., greater than 50 degrees [°]), P may be low because of the low water-holding capacity of cold air, but P:PET can still be favorable because of the low evaporative demand of the atmosphere. At lower latitudes, the increased water-holding capacity of warm air allows for greater P, especially in the maritime settings favored by onshore ocean currents and prevailing winds, mountainous regions, or the intertropical convergence zone, but higher temperatures result in much greater PET. The lowest water availability occurs where P is low and PET high, along the western regions of North and South America, in northern and southern Africa, in the Middle East, in Central Asia, and in Australia. Using the threshold of 0.4, one can identify areas that are climatically suitable for rain-fed production, and in general, this estimate agrees rather well with multicriteria assessments of rain-fed crop suitability (Fischer et al. 2002, 2005).

In the present study, the global P:PET ratio (figure 1a) is based on the Climatic Research Unit (CRU) Global 0.5° Monthly Time Series (TS) 3.1 data set produced by CRU at the

Table 1a. Plant-level physiology and stand-level productivity of representative tree crop species with potential for lignocellulosic bioenergy production using short-rotation coppice culture, from the peer-reviewed literature survey.

Taxa	Mean photosynthesis[a]	Mean stomatal conductance[b]	Mean instantaneous water-use efficiency[c]	$\delta^{13}C$	Mean ANPP
Acer pseudoplatanus	6.5	165.2	0.039		1.2
Acer rubrum	7.7	175.2	0.044		1.3
Alnus	7.9	81.0	0.097	–28.8	9.0
Eucalyptus	16.8	396.0	0.042	–27.3	17.5
Larix	7.0	56.0	0.125	–26.4	1.0
Liquidambar	8.6	280.0	0.031	–27.4	4.4
Liriodendron	8.9	102.1	0.087		0.9
Pinus	4.7	99.0	0.047	–27.3	5.0
Platanus	9.5	286.5	0.033		5.5
Populus, pure spp.	13.7	303	0.045	–28.0	10.1
Populus hybrids	12.7	343	0.037	–28.1	8.1
Quercus	10.4	185.5	0.056	–27.8	7.2
Robinia	9.7	296.7	0.033	–24.3	8.8
Salix, pure spp.	13.7	316.0	0.043	–27.9	8.4
Salix hybrids	20.6	378.0	0.054		8.0

Note: For further information, see the supplemental material, available online at *http://dx.doi.org/10.1525/bio.2013.63.2.6.*
Abbreviations: ANPP, aboveground net primary production, in megagrams per hectare per year; $\delta^{13}C$, carbon isotope discrimination of leaf biomass, in parts per thousand.
[a]In micromoles (μmol) per square meter (m^2) per second. [b]In millimoles (mmol) per m^2 per second. [c]In μmol per mmol.

Table 1b. Stand-level water use and meteorological conditions of representative tree crop species with potential for lignocellulosic bioenergy production using short-rotation coppice culture, from the peer-reviewed literature survey.

Taxa	Mean understory evapotranspiration[a]	Mean stand overstory transpiration[a]	Mean stand water-use efficiency[b]	Bioenergy water-use efficiency at the farm gate[c]	Mean annual temperature[d]	Mean annual precipitation[e]	Ratio of mean annual precipitation to actual evapotranspiration
Acer pseudoplatanus					10.0	877	
Acer rubrum					9.2	1186	
Alnus	230.0	538.0	16.8	28.1	11.3	1305	1.7
Eucalyptus		1054.0	16.5	27.7	20.5	1309	
Larix	62.0	101.0	6.3	10.6	–8.7	230	1.4
Liquidambar	205.0	462.5	9.4	15.8	15.7	1304	1.9
Liriodendron					13.0	1692	
Pinus	251.8	410.0	12.3	20.5	16.6	1145	1.7
Platanus		293.8	18.9	31.5	18.4	1019	
Populus, pure spp.	117.0	419.2	24.0	40.2	11.4	607	1.1
Populus hybrids	142.5	439.1	18.5	30.9	10.2	753	1.3
Quercus		294.8	24.3	40.6	13.6	913	
Robinia	370.0	204.5	43.2	72.2	10.9	700	1.2
Salix, pure spp.	240.1	403.8	20.7	34.6	5.7	661	1.0
Salix hybrids	119.4	324.9	24.5	41.1	6.6	703	1.2

Note: For further information, see the supplemental material, available online at *http://dx.doi.org/10.1525/bio.2013.63.2.6.*
[a]In millimeters (mm) per year. [b]In kilograms per mm. [c]In megajoules per cubic meter. [d]In degrees Celsius. [e]In mm.

Table 2a. Plant-level physiology and stand-level productivity of C_4 grass species considered for lignocellulosic bioenergy, from the peer-reviewed literature survey.

Taxa	Mean photosynthesis[a]	Mean stomatal conductance[b]	Mean instantaneous water-use efficiency[c]	$\delta^{13}C$	Mean ANPP
Miscanthus	26.0	220	0.118		21.7
Panicum virgatum	17.5	210	0.083	–13.5	10.1
Pennisetum	20.2	296	0.068		12.4
Spartina	18.4	227	0.081	–13.0	10.6

Note: For further information, see the supplemental material, available online at *http://dx.doi.org/10.1525/bio.2013.63.2.6.*
Abbreviations: ANPP, aboveground net primary production, in megagrams per hectare per year; $\delta^{13}C$, carbon isotope discrimination of leaf biomass, in parts per thousand.
[a]In micromoles (μmol) per square meter (m^2) per second. [b]In millimoles (mmol) per m^2 per second. [c]In μmol per mmol.

Table 2b. Stand-level water use and meteorological conditions of C_4 grass species considered for lignocellulosic bioenergy, from the peer-reviewed literature survey.

Taxa	Mean stand overstory transpiration[a]	Mean stand water-use efficiency[b]	Bioenergy water-use efficiency at the farm gate[c]	Mean annual temperature[d]	Mean annual precipitation[e]	Ratio of mean annual precipitation to actual evapotranspiration
Miscanthus	537	29.8	54.7	17.2	493	0.9
Panicum virgatum	457	22.8	42.2	20.1	461	1.0
Pennisetum	495	27.5	44.3	9.1	424	0.8
Spartina				13.0	775	

Note: For further information, see the supplemental material, available online at *http://dx.doi.org/10.1525/bio.2013.63.2.6.*
[a]In millimeters (mm) per year. [b]In kilograms per mm. [c]In megajoules per cubic meter. [d]In degrees Celsius. [e]In mm.

Table 2c. The plant-level physiology, productivity, and water use of C_3 grass species considered for lignocellulosic bioenergy, from the peer-reviewed literature survey.

Taxa	Mean photosynthesis[a]	Mean stomatal conductance[b]	Mean instantaneous water-use efficiency[c]	$\delta^{13}C$	Mean ANPP
Arundo	22.8	180	0.126	–26.2	25.6
Phalaris arundinaceae	10.3	200	0.051		8.4
Phragmites spp.	15.2	235	0.064		10.1
High-diversity mixed prairie	17.1	455	0.037	–28.0	4.6

Note: For further information, see the supplemental material, available online at *http://dx.doi.org/10.1525/bio.2013.63.2.6.*
Abbreviations: ANPP, aboveground net primary production, in megagrams per hectare per year; $\delta^{13}C$, carbon isotope discrimination of leaf biomass, in parts per thousand.
[a]In micromoles (µmol) per square meter (m^2) per second. [b]In millimoles (mmol) per m^2 per second. [c]In µmol per mmol.

Table 2d. The stand-level water use of C_3 grass species considered for lignocellulosic bioenergy, from the peer-reviewed literature survey.

Taxa	Mean stand water-use efficiency[a]	Bioenergy water-use efficiency at the farm gate[b]	Mean annual temperature[c]	Mean annual precipitation[d]	Ratio of mean annual precipitation to actual evapotranspiration
Arundo	40.5	71.2	16.5	859	1.3
Phalaris arundinaceae	19.6	34.5	9.9	693	1.0
Phragmites spp.	12.6	23.7	11.1	812	1.0
High-diversity mixed prairie	9.5	16.7	13.4	859	1.7

Note: For further information, see the supplemental material, available online at *http://dx.doi.org/10.1525/bio.2013.63.2.6.*
[a]In kilograms per mm. [b]In megajoules per cubic meter. [c]In degrees Celsius. [d]In mm.

University of East Anglia (Mitchel and Jones 2005). The PET values available as part of the CRU TS 3.1 data set were based on the grass reference evapotranspiration equation (Ekström et al. 2007). Figure 1b–1d is based on the results of 16 global circulation models, which were run with the assumption of the emission scenario known as SRES-A2 (Nakićenović and Swart 2000) with a CO_2 level in 2050 of around 533 parts per million compared with 361 parts per million in the middle of the baseline period (1995). Figure 1b and 1c show the expected changes in the mean annual temperature and relative changes in the mean annual temperature calculated as a difference between the periods of 2035–2064 and 1980–2009 averaged over a 1-degree (°) grid. The changes in drought levels (figure 1d) were analyzed using the relative Palmer *Z*-index (rZIND) introduced by Dubrovský and colleagues (2009). Calculating the rZIND made it possible to assess drought changes even in situations in which only monthly temperature and P data were available, as in our case. The rZIND calculation required data on available soil water content, and therefore, we used the soil-texture-based water-holding capacity global data developed by Webb and colleagues (1993). Note that figure 1a is based on annual data, so in some regions, the water balance during the growing season might be more favorable than is suggested (e.g., throughout the Indian subcontinent).

The expected changes in global climate will inevitably alter the agroclimatic conditions throughout the major agricultural areas, as was shown for Europe by Trnka and colleagues (2011). The change in the global mean annual temperature calculated as a difference between the periods 2035–2064 and 1980–2009 for 16 global circulation models is more than 1.5 degrees Celsius (°C; figure 1b). The global circulation models also agree on the regional distribution of these changes, with the smallest increments expected in the tropical and coastal regions and the largest concentrated north of 50 degrees north (°N). The global circulation models show much lower agreement in terms of P patterns (figure 1c), with many areas (shown in gray in the figure) showing conflicting projections. Interestingly, the agreement is stronger in areas in which a decrease in P is to be expected rather than in those in which an increase in P is more likely. It should be noted that changes in annual P totals are, in general, much smaller than those projected for individual seasons and months and that in many regions, greater variability of water availability within and between individual growing seasons is expected (Trnka et al. 2011).

Increasing temperatures will result in a potentially longer growing season (especially in latitudes greater than 50°), but it is also associated with higher evaporative demand. The increase in P annual sums will mostly occur north of

50°N, whereas elsewhere, either there is no agreement in the projections or a decrease in P is expected. This could lead to a higher risk of drought events. In order to assess likely changes in drought patterns, we applied the rZIND calculation, for which negative values signal increasing dryness. This analysis shows an almost universal trend for lower rZIND values—that is, a relatively drier climate around 2050 compared with the baseline (figure 1d). This is especially relevant for those regions in which the P:PET ratio under the baseline climate is lower than 1, which can be considered regions in which rain-fed production of biomass might be decreased because of low water availability. These regions include the central United States and the Mediterranean but also eastern Brazil and Central Europe northeast of the Alps.

Understanding plant ecophysiological controls over water-use efficiency is the starting point of designing climatically appropriate bioenergy production systems. At a broad scale, the use of energy-crop species in climates similar to that of their provenance seems prudent (Lewandowski et al. 2003); however, the degree of variation in water-use traits between species and between genotypes within a species is very poorly understood, which masks opportunities to increase water-use efficiency and sustainability. Grasses of tropical origin using the C_4 photosynthetic pathway evolved in hot and dry climates and generally have very high water-use efficiency because of specialized anatomy that concentrates CO_2 at the site of carboxylation, which decreases photorespiration and allows reduced stomatal conductance per unit of carbon fixed (Sage and Monson 1999). Plants of the C_3 photosynthetic pathway, which includes all tree species, transport water through an integrated hydraulic system, the chief resistances of which occur at the soil–root and stomata–air interfaces. Stomatal control of water loss from leaf surfaces provides a primary means of regulating water stress in response to prolonged changes in vapor pressure and soil moisture, and a decreased stomatal conductance under elevated atmospheric CO_2 may also confer higher water-use efficiency (Berry et al. 2010). The carbon-isotopic composition of plant tissue ($\delta^{13}C$) is thought to correlate with water-use efficiency, which possibly provides a quantitative trait useful in crop-screening and -improvement programs (Chamaillard et al. 2011, Dillen et al. 2011). Recently, it has been recognized that some tree species exert tight stomatal control over water loss to maintain (more or less) constant leaf water potential, thereby avoiding catastrophic stem hydraulic failure (*cavitation*) in response to water deficits, which is termed *isohydry* (Hoffman et al. 2011). Other species, more profligate in their water use (termed *anisohydry*), may have high productivity but are thought to be more susceptible to water stress. Other mechanisms of drought avoidance or tolerance include drought deciduousness, osmotic adjustment (especially in halophytes), deep rooting, and stem capacitance in large trees (Kramer and Boyer 1995, Pallardy 2008). Because water-use efficiency is a complex or composite trait, the degree to which it is under genetic control is not well understood, and therefore, its use in bioenergy-crop-improvement programs has been limited, although this is beginning to change (Chamaillard et al. 2011, Dillen et al. 2011, Fichot et al. 2011).

Literature survey and bioenergy water-use efficiency calculation

To determine the availability of ecophysiological data needed to design water-efficient bioenergy-cropping systems, we surveyed the peer-reviewed scientific literature (up to 2011), using academic Internet search engines with access to all major databases in the natural sciences (e.g., AGRICOLA, CAB, Plant Science, Ecology Abstracts, BIOSIS, Environmental Science and Pollution Management, JSTOR, the Web of Science), with the objectives of summarizing the available data, illustrating how to apply the data in the design of climatically robust bioenergy-crop systems, and identifying knowledge gaps and future research needs. We restricted our survey to the representative species of the major groups (grasses, trees) of so-called "second generation" bioenergy crops, those based on cell-wall or lignocellulosic technologies to avoid food versus fuel issues, and to provide consistent comparisons of bioenergy water-use efficiency across crop types on the basis of the most commonly available data (physiological process rates, rates of biomass production and water use). In addition, the diverse array of bioenergy types and the associated energy conversion processes (e.g., first and second generation ethanol, biodiesel, cocombustion, combined heat and power, bagasse, gasification, pyrolysis) each has different water requirements with varying levels of data availability (and therefore varying reliability of their final water-use efficiency estimates). An analysis of the water requirement of different components of bioenergy production chains in the context of life cycle analysis showed that water transpired to grow the crop is often the largest water requirement by far of the entire process (Berndes 2002, Evans and Cohen 2009). Our analysis is of the water-use efficiency of the bioenergy-cropping system at the farm gate—that is, the yield of energy (in megajoules [MJ] per hectare [ha]) produced per unit of water lost to evapotranspiration per year. Assembling the available data on the bioenergy water-use efficiency of the primary lignocellulosic crop species is needed as an input for more comprehensive analyses of the net water-use efficiency of entire bioenergy production chains in which output:input energy ratios and the water requirements of different energy conversion technologies are also considered (Giampietro and Mayumi 2009, Giampietro et al. 2012).

For each representative crop species, genus, or hybrid, we searched the literature using a list of 15 keywords individually and in combination, including the common name and the scientific name of the species and the terms *photosynthesis*, *stomatal conductance*, *transpiration*, *hydrology*, *water-use efficiency*, *evapotranspiration* (and its abbreviation, *ET*), *water relations*, *biomass production*, *short-rotation coppice*, *bioenergy*, and *production*. The search was conducted until

no new sources were identified. The data were extracted from sources containing information on net photosynthesis, stomatal conductance, instantaneous (leaf-level) water-use efficiency (WUEi), leaf isotopic composition ($\delta^{13}C$), aboveground net primary production (ANPP), understory evapotranspiration (UET), overstory transpiration (OT), stand-level water-use efficiency, and bioenergy water-use efficiency. The data for instantaneous physiological process rates were normalized for diurnal or seasonal variation to maximum the daily rates, whereas ANPP and transpiration were normalized to annual values if they were reported only for the growing season. The bioenergy water-use efficiency was calculated as ANPP ÷ OT using an energy content for lignocellulosic biomass of 16.73 MJ per kilogram (Giampietro et al. 1997) or crop-specific values when they were available. The data on mean annual P (MAP) and mean annual temperature were extracted from each source, and the ratio of MAP to AET calculated as MAP ÷ (UET + OT). For tree species, we attempted to restrict the reports to only short-rotation coppice bioenergy cropping or young age classes, but for many genera, such data were scarce, and the values from older age classes were occasionally included. Similarly, for both grass and tree species, we tried to normalize the management regimes across studies by using data only from moderate-to-low-input systems, but on occasion, data from high-input systems were included. The complete bioenergy water-use efficiency database with calculations and a bibliography can be accessed at *www.ua.ac.be/pleco* and in the supplemental material for the present article, available online at *http://dx.doi.org/10.1525/bio.2013.63.2.6*.

Results of the literature survey

In the following sections, we outline the results of our survey of the literature.

Data availability and quality. During the course of our survey, thousands of references were searched, of which we found a total of 271 studies containing data for the selected trees and 100 for the selected energy grasses (tables 1a–2d). Across tree taxa, there were generally more data available for physiological process rates (photosynthesis, stomatal conductance) and ANPP, a few studies reported some hydrological parameters (e.g., sapflow-based estimates of OT and measured P), but few data were reported on UET, stand-level water-use efficiency, and $\delta^{13}C$ or from operational bioenergy production systems (see the supplemental material). In only two experiments were both ecophysiological data and a complete water balance reported for a bioenergy-cropping system based on at least 1 year of measurements of the full hydrologic cycle (Grip et al. 1989, Hall et al. 1996). The trends were similar for the grasses. Therefore, the data contained in tables 1a–2d had to be summarized across studies; hence the resulting differences in age, genetics, management regimes, physiographic settings, and so on. Of the trees, the best represented taxa were *Populus* (87 studies) and *Salix* (60 studies), whereas most others were poorly represented. The warm-season (C_4) and cool-season (C_3) grass species were more evenly represented, although the data were most abundant for mixed prairie grasses (19 studies). Finally, in all of the literature reviewed, we found no published estimates of the bioenergy water-use efficiency for any of the taxa investigated. A first conclusion from our study, then, is that the data needed to develop water-efficient and climatically robust bioenergy-cropping systems is woefully inadequate, and concerted effort is urgently needed in order to implement representative field studies that will allow for the testing, improvement, and modeling of the productivity potential and water use of a widespread bioenergy industry (see box 1). Such a network of research studies, especially if it is paired with relevant forest products and energy industry partners, would be extremely beneficial (see box 2).

Ecophysiology, productivity, and water use of tree-based bioenergy systems. The rates of physiological processes varied widely across the tree genera examined. The mean net photosynthesis rate ranged from 4.7 micromoles (μmol) per square meter (m^2) per second for *Pinus* to as high as 20.6 μmol per m^2 per second for *Salix* hybrids, with a mean across genera of 10.5 μmol per m^2 per second (table 1a and 1b). *Eucalyptus* had the second highest photosynthesis rate at 16.8 μmol per m^2 per second. The mean stomatal conductance rate ranged from a very low 56 millimoles (mmol) per m^2 per second for *Larix* to a high of 396 mmol per m^2 per second for *Eucalyptus*, with a mean across genera of 230 mmol per m^2 per second. There was a very strong positive correlation between the rates of photosynthesis and stomatal conductance (supplemental table S1, available online at *http://dx.doi.org/10.1525/bio.2013.63.2.6*). WUEi ranged from a low of 0.031 μmol per mmol for *Liquidambar* to a high of 0.125 μmol per mmol in *Larix*, and the mean WUEi across genera was 0.054 μmol per mmol. *Alnus* and *Liriodendron* were also very water efficient in this context, whereas *Platanus*, *Populus* hybrids, and *Robinia* were heavy water users. This is surprising, in that *Robinia* has been considered a drought-tolerant short-rotation coppice species (Grünewald et al. 2009), although it has also been reported to have low WUEi relative to other deciduous species (Raper et al. 1992). The $\delta^{13}C$ values ranged from –24.2 parts per thousand (‰) to –28.8‰, which is a very large range within C_3 plants, but $\delta^{13}C$ was not correlated with the other measures of leaf physiological activity. However, it was marginally ($p = .065$) correlated with the bioenergy water-use efficiency (table S1), and since it is not difficult to measure, it may have value as a monitoring tool and possibly as a selection criterion for increasing water-use efficiency in bioenergy systems (Dillen et al. 2011).

Tree stand productivity varied greatly across taxa and was highly correlated with physiological process rates and stand water use (represented by OT) but was only indirectly correlated with stand-level water-use efficiency and the bioenergy water-use efficiency. Our estimates of ANPP ranged from 0.9 megagrams (Mg) per ha per year in *Liriodendron* to a high of 17.5 Mg per ha per year in *Eucalyptus*, with

Box 1. The POPFULL Experiment: Assessment of the water budget and full greenhouse gas balance of a *Populus–Salix* bioenergy plantation.

Within the framework of the search for renewable energy sources, the production and conversion of biomass from fast-growing woody crops grown under intensive short-rotation coppice regimes plays an important role. The European Research Council POPFULL project (figure 2) is intended to aid in the formulation of conclusive answers to three crucial questions that remain unanswered about short-rotation coppice bioenergy systems: (1) Is the greenhouse gas balance of a short-rotation coppice crop positive or negative? (2) Are the energetic and the financial balances beneficial or deficient? And (3) what is the overall environmental balance?

The POPFULL project consists of an 18-hectare operational plantation of selected fast-growing poplar (*Populus*) and willow (*Salix*) genotypes established in East Flanders (Belgium) in April 2010 (figure 3). The short-rotation coppice plantation is intensively managed during two rotations of 2 years each without irrigation or fertilization. Growth, biomass production, and all pools and fluxes of the carbon and water balances are being monitored throughout the two rotations. Fluxes of greenhouse gases are being assessed using destructive and nondestructive techniques at the leaf, plant, and ecosystem scales. Integration of these fluxes over the entire year and an entire rotation allow an examination of the full greenhouse gas balance. The preliminary results indicate that the greenhouse gas balance was positive for the establishment year (i.e., there was a net emission of greenhouse gases from the plantation to the atmosphere) but was already negative during the second year (i.e., there was a net uptake of greenhouse gases by the plantation), which led to a null balance after 2 years.

With regard to the question of the environmental impact, particular attention is being paid to the water budget of the plantation and to the efficiency with which water is used to produce biomass. Ecosystem-based data are complemented with measurements at lower hierarchical scales so that variations between genotypes and the underlying physiological processes are documented. Evapotranspiration is monitored at the ecosystem scale through energy and water fluxes in combination with changes in the groundwater table, in soil water content at different depths, and in incoming precipitation. Additional data from seasonal field campaigns of

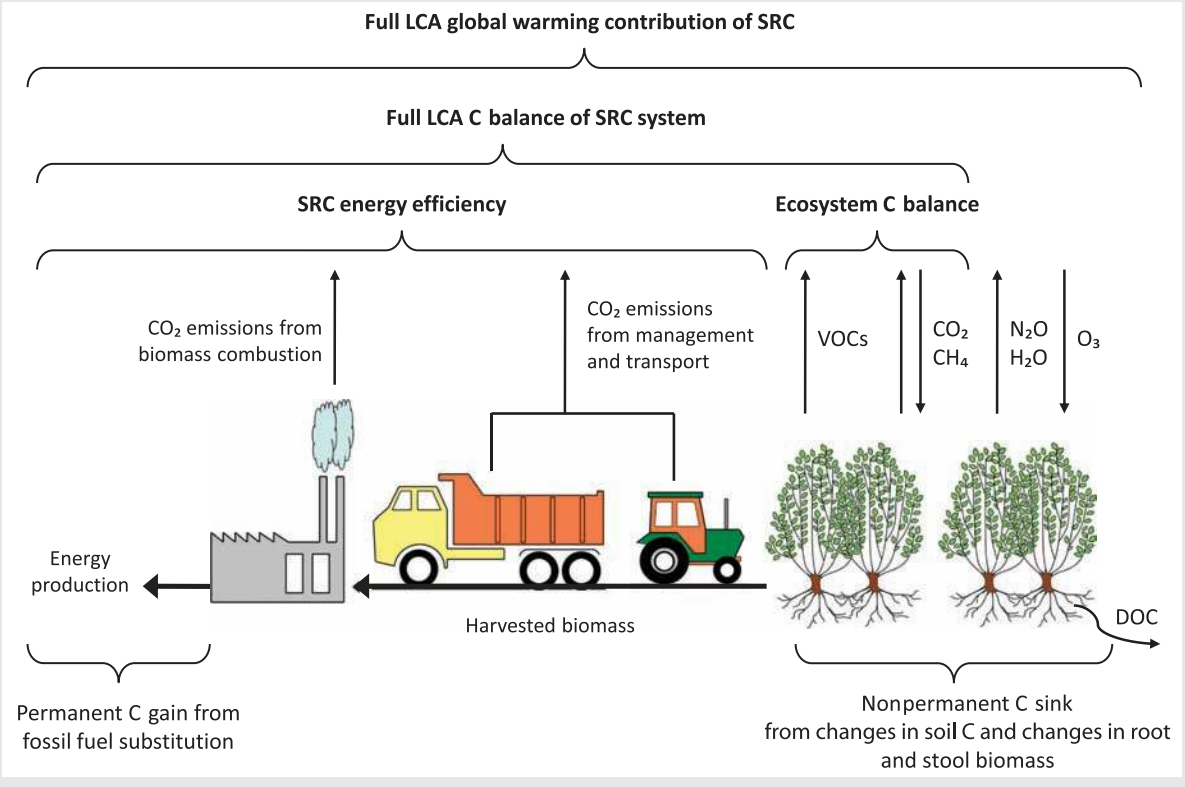

Figure 2. Schematic representation of the full greenhouse gas and energy balance approach of the POPFULL short-rotation coppice (SRC)* Populus *bioenergy experiment of the University of Antwerp. The experiment will last 4 years, over which time two 2-year rotations will be conducted. All greenhouse gas and energy balances are being quantified using continuous eddy covariance and intensive biometric and soil studies; the balances will be used to parameterize a full life cycle analysis. Abbreviations: C, carbon; CH_4, methane; CO_2, carbon dioxide; DOC, dissolved organic carbon; H_2O, water; LCA, life cycle analysis; N_2O, nitrous oxide; O_3, ozone; VOCs, volatile organic compounds. Schematic: Catchlight Energy LLC.

Box 1. Continued.

sapflow measurements are scaled up from the tree to the stand level and are further used to cross-validate data obtained at the plantation scale. To close the entire water budget of the plantation, all fluxes (including drainage) are being assessed, with measurements at different hierarchical levels of organization. As a crucial link between water and carbon fluxes, water-use efficiency is assessed at the leaf level by measuring transpiration and net assimilation, at the plant level using sapflow-derived transpiration and net carbon investment derived from growth increments and at the ecosystem scale using eddy covariance fluxes from a meteorological tower. The isotopic signatures (mainly $\delta^{13}C$ and $\delta^{18}O$) of different pools (e.g., leaf, wood, isolated alpha cellulose, phloem sap) are used as complementary indicators of water-use efficiency over different integration scales. All together, the results will provide a more comprehensive assessment of the physiological and environmental controls of the interrelated carbon and water cycles within the plantation. See *http://webh01.ua.ac.be/popfull* for more details, and a full description of the plantation can be found in Broeckx and colleagues (2012).

Figure 3. Overview of the POPFULL experimental field site in Lochristi (East Flanders, Belgium). The experimental site is a total of 18.4 hectares and comprised 12* Populus *species and hybrids planted in a double-row design with a tree density of 8000 trees per hectare. Full greenhouse gas balance and hydrology are being monitored with a combination of eddy covariance, biometric, ecophysiological, and hydrologic approaches. The inset shows the eddy covariance flux tower in the middle of the second growing season among the 16-month-old* Populus *trees. The colors of the blocks of trees result from differences in phenology (senescence) among genotypes used in the experiment. See Broeckx and colleagues (2012) for more details on the plantation layout. Photographs: Melanie S. Verlinden.

an across-taxa average of 6.7 Mg per ha per year (table 1a and 1b). Data for *Acer* were especially scarce, which is surprising, given the broad ecological amplitude of this genus and its good coppice ability (Abrams 1998). The very low estimates of ANPP for *Acer* and *Liriodendron* may not be representative, because they are based on very few data. The low productivity of *Larix* is a reflection of its high-latitude growth environment, where the mean annual temperature is –8.7°C and the MAP is only 230 millimeters (mm). Such low MAP could explain the very high WUEi (0.125 µmol per mmol) of this species and suggests its potential as a water-efficient bioenergy-crop species at high latitudes. It

Box 2. The Lenoir 1 loblolly pine–switchgrass intercropping sustainability study.

The Lenoir 1 intercropping sustainability study (figures 4 and 5) is a collaborative experiment with industry, university, and government partners, including the Weyerhaeuser company, Catchlight Energy, North Carolina State University, Virginia Tech University, Duke University, Yale University, the University of North Carolina at Greensboro, Roanoke College, and the US Department of Agriculture Forest Service. The rationale behind the proposed project is that gains in ecosystem resource-use efficiencies can be realized in an existing land-use system by combining multiple crops with complementary (e.g., a C_3 tree and a C_4 grass) structure, phenology, and physiology to produce a sustainable supply of wood products and biofuel feedstocks and to enhance environmental quality. The study was initiated through support from Catchlight Energy, a joint venture between the Chevron and Weyerhaeuser companies. Although Catchlight Energy continues to provide financial and operational support, several grants have been received to complement these funds to support the science needed to characterize ecological impacts and sustainability.

The study is located in Lenoir County, North Carolina, and was established in 2008. The previous stand was a 1974 loblolly pine plantation that covered 109 hectares (ha). Preharvest sampling occurred during the summer of 2008, which included baseline soil nutrient data, plant biodiversity, aboveground productivity, soil strength, and foliar nutrient analyses on the crop trees. These baseline data are essential to evaluate the long-term sustainability of the various biomass management regimes. Treatments (figure 4) were installed between December 2008 and June 2009. Similar soil and productivity data have been collected annually (pine and switchgrass) and will continue at least through canopy closure. The study consists of seven treatments replicated four times, for a total of 28 treatment plots that are approximately 0.8 ha in size. The crop trees were planted at 1075 trees per ha. In addition to the treatment plots, a reference stand adjacent to the experiment will remain unharvested at least until 2015. This reference loblolly pine stand was planted in 1974 and is approximately 28 ha in size and is planted in the same soil type as the rest of the study.

Seasonal fluctuations in diurnal leaf-level gas exchange (photosynthesis, stomatal conductance, and instantaneous water-use efficiency) and water potential values are quantified in pines and switchgrass grown alone and in combination. Photosynthetic and hydraulic variables obtained from these diurnal measurements will be used to parameterize a soil–plant–atmosphere model (Williams et al. 1996). This is a mechanistic model that predicts gross primary productivity and canopy water use, which will allow

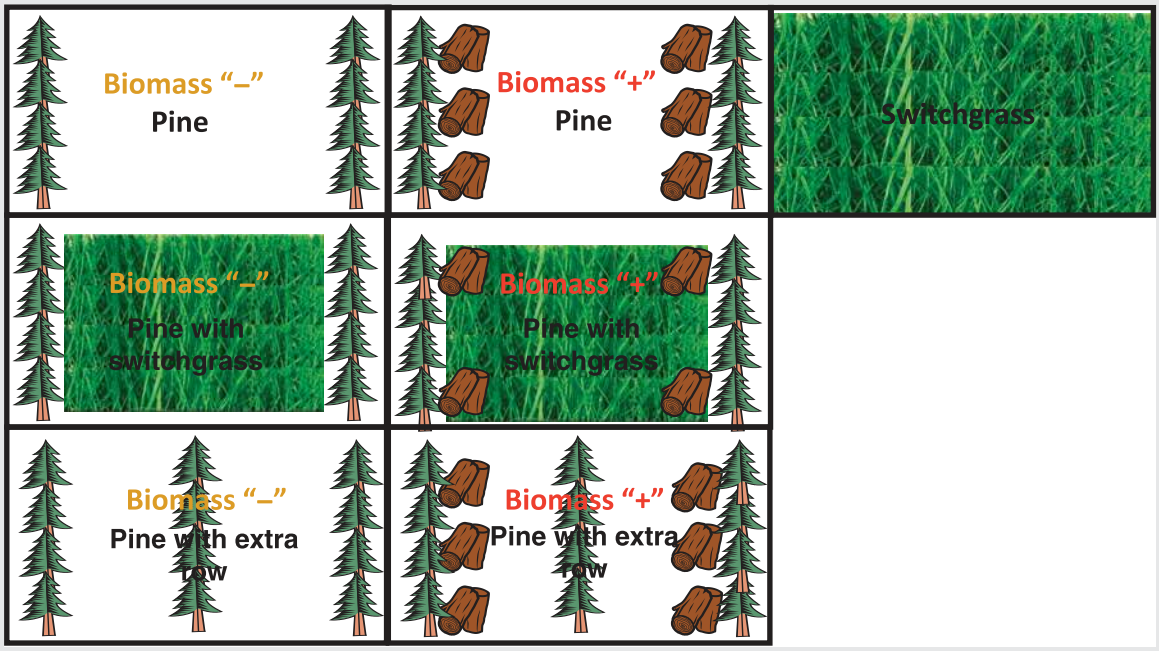

Figure 4. Schematic of the experimental design of the Lenoir 1 pine–switchgrass intercropping sustainability study located along the lower coastal plain in Lenoir County, North Carolina. The seven treatments of this long-term (25-year) study are (1) traditional pine establishment with biomass residuals left in place, (2) traditional pine establishment with biomass residuals removed, (3) intercropped pine–switchgrass with biomass residuals left in place, (4) intercropped pine–switchgrass establishment with biomass residuals removed, (5) pine establishment with an extra row of biomass trees planted in between crop-tree rows with biomass residuals left in place, (6) pine establishment with an extra row of biomass trees planted in between crop-tree rows with biomass residuals removed, and (7) switchgrass only. The biomass residuals consist of coarse woody debris and root systems left from harvesting the previous pine stand.

Box 2. Continued.

us to determine the effect of intercropping on water and carbon uptake. Heat-dissipation sapflow probes were installed in spring 2011, in pine-only and pine–switchgrass intercropped treatments, to continuously monitor tree water use; these values will be scaled to the stand level using inventory data. A water budget of this intercropped system will be constructed using tree and switchgrass evapotranspiration estimates, micrometerological data collected from an on-site weather station, and changes in volumetric soil water content and groundwater. Finally, integrated water-use efficiency will be calculated over the growing season as the total usable plant biomass produced per total amount of water transpired per unit of land area.

Figure 5. Switchgrass intercropped with traditional loblolly pine silviculture at the Lenoir 1 bioenergy sustainability study along the lower coastal plain in Lenoir County, North Carolina, in September 2011. Project-design, implementation and operational support are provided by Catchlight Energy and the Weyerhauser company. An interdisciplinary team of academic, industry, and government scientists supported by federal competitive grants perform the science to determine the productivity, sustainability, and life cycle analysis of the system. The inset shows a tree equipped with sapflow sensors to quantify tree transpiration, which, when it is combined with grass evapotranspiration, hydrology, and micrometeorological data, will provide the site water balance of this novel intercropping system. Photographs: Janine M. Albaugh.

is also interesting that pure species of both *Populus* and *Salix* exhibited higher productivity than did their hybrids, which is contrary to the commonly held view of heterosis in trees (Zobel and Talbert 2003), although the strength of this observation is necessarily limited by the nature of our analysis. Still, there is some evidence that hybrid *Populus* species lose productivity relative to pure parental species after several rotations in short-rotation coppice (Al Afas et al. 2008). Given the potential widespread deployment of *Populus* in bioenergy plantations, this remains an important hypothesis that needs further testing.

ANPP was strongly correlated with photosynthesis and stomatal conductance (table S1), which suggests that these are good (and easily measured) metrics for bioenergy-crop

selection or improvement. A mean ANPP of almost 7.0 Mg per ha per year may seem low relative to the hoped-for rates of bioenergy feedstock production of 18–25 Mg per ha per year (Hoogwijk et al. 2005, Smeets et al. 2007), but it reflects the early stage of stand development targeted in our study and the (realistic and observed) growth limitation by abiotic and biotic environmental stresses of these low-input systems. Since bioenergy is a commodity with a low marginal price that may not support economically or ecologically expensive high-input silvicultural regimes, ANPP rates of 7–10 Mg per ha per year may be practical. Although ANPP was not correlated with WUEi or $\delta^{13}C$, it was very strongly correlated to OT (table S1), which indicates that leaf-level metrics of water-use efficiency and stand-level water use (OT) may be decoupled at some point (although the stomatal conductance was marginally correlated with OT: $p = .067$) and that productivity is crucially dependent on water availability to support OT, as has been demonstrated for other energy crops (Mueller et al. 2005). The average absolute water use by tree-based bioenergy systems (UET + OT) was 618 mm per year, with 425 mm used by the trees and 193 mm used by the understory. These results suggest that widespread bioenergy production will be especially sensitive to future water availability and will potentially compete with other demands for water, a situation that is likely to be exacerbated in many regions because of climate change (figure 1; Berndes 2002, Beringer et al. 2011). Our stand-level estimates of bioenergy water-use efficiency ranged from 10.6 MJ per cubic meter (m^3) for *Larix* to 72.2 MJ per m^3 for *Robinia*, with an across-taxa average of 33.3 MJ per m^3. These estimates are in strong agreement with the estimates of bioenergy water-use efficiency of 14–142 MJ per m^3 reported by Berndes (2002) for agricultural crops; the (unrealistically) high value of that study came from irrigated *Miscanthus*.

Physiology, productivity, and water use of grass-based bioenergy systems. In grasses, the rates of physiological processes were generally higher than those in trees, but productivity was comparable. Across taxa, net photosynthesis averaged 18.4 μmol per m^2 per second and was generally higher in C_4 (20.5 μmol per m^2 per second) than in C_3 (16.4 μmol per m^2 per second) species (table 2a–2d). *Miscanthus* and *Arundo* had notably high photosynthesis rates relative to their C_4 and C_3 cogenera, respectively. The mean stomatal conductance rate was 238 mmol per m^2 per second for the warm-season grasses and 267 mmol per m^2 per second for the cool-season C_3 grasses. The rate of stomatal conductance for high-diversity mixed prairie (455 mmol per m^2 per second) is much higher than that for any other taxa but appears to be correct, since this value was calculated from six independent studies (see the supplemental material). Unlike in trees, the rates of photosynthesis and stomatal conductance were not strongly correlated among the energy grasses, which could be because of our summarizing across physiologically distinct groups. Higher photosynthesis rates combined with lower stomatal conductance rates conferred the well-known higher WUEi to the warm-season grasses: WUEi averaged 0.087 and 0.069 μmol per mmol in C_4 and C_3 grasses, respectively. Finally, consistent with our understanding of the carbon isotope discrimination of photosynthesis, $\delta^{13}C$ averaged –27.1‰ for C_3 grasses, similar to the value for trees, and –13.3‰ in the C_4 grasses. Our ability to draw inferences regarding this parameter is limited, however, by the paucity of data available in the literature.

Productivity was variable within both groups of grasses and not necessarily greater than that of trees. The rates of ANPP ranged from 4.6 to 25.6 Mg per ha per year and were slightly higher for C_4 than for C_3 grasses (13.7 and 12.2 Mg per ha per year, respectively), but both groups had very productive genera. *Miscanthus* (C_4) had a mean productivity of 21.7 Mg per ha per year, whereas *Arundo* (C_3) reached 25.6 Mg per ha per year. As were those of trees, these higher rates of grass productivity were associated with higher inputs (e.g., 80–168 kg of nitrogen per ha per year), which may not be practical for operational bioenergy production systems. The relatively large nitrogen requirement and level of nitrogen export in biomass of *Arundo* and the extreme efficiency of *Panicum* in this regard could be important considerations in designing low-input bioenergy production systems (Kering et al. 2012, Knoll et al. 2012). As was the case in trees, the grass productivity was tightly correlated with photosynthesis but, in contrast to trees, was also strongly correlated to WUEi. Interestingly, both C_4 and C_3 grasses appear to have a common relationship between ANPP and WUEi (ANPP = 217.79 × WUEi – 4.1589, $R^2 = .902$). The determination of WUEi is straightforward using portable photosynthesis systems, which suggests its utility in the selection and improvement of water-efficient, productive bioenergy grass crops. Although grass ANPP was not as strongly correlated with UET as was tree ANPP with OT, biomass production was strongly linked to ecosystem-level water-use efficiency. Averaged across taxa, the grass communities transpired 588 mm per year, with C_4 grasses using 496 mm and C_3 grasses using 657 mm (table 2a–2d). These rates of transpiration are greater than the average for bioenergy trees (425 mm) but are comparable when UET (193 mm) is included for tree-based systems (table 1a and 1b). In contrast to that of trees, grass ANPP was strongly correlated with the bioenergy water-use efficiency (supplemental table S2, available online at *http://dx.doi.org/10.1525/bio.2013.63.2.6*), which could be related to the better water economy of C_4 grasses relative to C_3 plants. Bioenergy trees had a mean bioenergy water-use efficiency of 33.3 MJ per m^3, C_3 grasses had a bioenergy water-use efficiency of 36.5 MJ per m^3, and by contrast, the C_4 grasses had a bioenergy water-use efficiency of 47.1 MJ per m^3. Therefore, in situations in which it was climatically and operationally appropriate, the use of C_4 grass species in bioenergy production could greatly enhance the water-use efficiency of the system, even when differences in biomass production may not be marked.

Bioenergy-crop productivity–water-use-efficiency relationship across taxa. In summary, stand-level bioenergy water-use efficiency was strongly correlated to productivity across all taxa but much more so for grasses than for trees (figure 6). However, ANPP and bioenergy water-use efficiency were significantly correlated in trees only when *Eucalyptus* was removed from the relationship (table S1, figure 6). The slope of the relationship was much higher for grasses, which indicates a significantly greater increase in productivity for a unit increase in the bioenergy water-use efficiency than that in trees. Although *Eucalyptus* had the highest ANPP of any tree genera, it was associated with relatively low level of bioenergy water-use efficiency, which echoes concerns of large water consumption by this genus (Whitehead and Beadle 2004). From an ecophysiological and water conservation perspective, it could be argued that the relationship between ANPP and bioenergy water-use efficiency indicates that grasses should always be the first choice as energy crops—in particular, the C_4 grasses—but climatic, social, and market considerations will also influence the composition and multifunctionality of bioenergy-cropping systems.

Agroclimatic drivers of bioenergy system productivity and water relations. The correlations among agroclimatic variables and their relationship to physiological process rates and ANPP suggest that bioenergy productivity will be more sensitive to changes in water availability than to changes in temperature. In trees, the mean annual temperature and the MAP were highly correlated (table S1) because of the higher water-holding capacity of warm air, which explains why the high-latitude systems received only 230 mm per year P, whereas the more-equatorial systems received more than 1300 mm per year. Such xeric conditions could act as a selective force on northern genera such as *Larix*, which would explain its extremely high WUEi (0.125 µmol per mmol). The ratio of MAP to AET (MAP:AET) was correlated with MAP and the mean annual temperature, which, along with the strong correlation between ANPP and OT, supports the contention of the primary importance of water availability. In addition, OT, which was strongly correlated with ANPP in trees, was also correlated with MAP and (marginally) with the mean annual temperature. Therefore, it appears that trees will be able to tolerate the higher temperatures in the range predicted (figure 1b) as long as sufficient water is available to support OT. In grasses, MAP:AET was marginally correlated with physiological processes (which were correlated with bioenergy water-use efficiency) and MAP, whereas temperature was not, which again speaks to the primary importance of water availability.

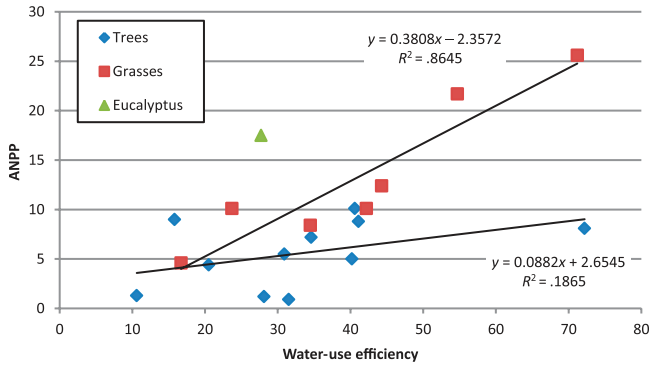

Figure 6. The relationship between aboveground net primary production (ANPP, in megagrams per hectare per year) and bioenergy water-use efficiency (in megajoules per cubic meter) for tree and grass bioenergy-crop species from a literature survey of 371 studies. ANPP is significantly correlated with bioenergy water-use efficiency for C_3 and C_4 grasses, but the two measures are correlated for trees only if* Eucalyptus *is removed from the analysis. Physiologically,* Eucalyptus *appears to be more like a grass in terms of the productivity and stand-level water-use efficiency relationship.

The relationship between bioenergy system productivity and agroclimatic drivers was somewhat different between tree- and grass-based systems. In trees, photosynthesis rates and ANPP were significantly correlated only with MAP:AET, and the genera broke out into two distinct groups (table 1a and 1b). One group had generally higher productivity (5.0–17.5 Mg per ha per year); included *Eucalyptus*, *Populus*, *Robinia*, *Salix*, and *Larix*; and exhibited an MAP:AET ratio close to 1.0. The second group had lower productivity (4.4–9.0 Mg per ha per year); included *Alnus*, *Quercus*, *Platanus*, *Pinus*, and *Liquidambar*; and had an MAP:AET ratio of about 1.7. This indicates that the productive systems were operating at the limit of available water (i.e., using almost all of it) and suggests that future productivity could be vulnerable in regions in which water availability is decreased by climate change, including areas in which these genera (e.g., *Populus*) now predominate (figure 1). This finding also supports the contention that widespread bioenergy production will create additional demand for water that must be carefully managed in view of competing uses (Berndes 2002, Varis 2007, Beringer et al. 2011). However, there appear to be opportunities for increasing bioenergy production of the second group of tree genera, at least with respect to water availability. This could be especially important at higher latitudes, at which the human population is low and a large fraction of annually available water is lost as drainage because of low PET and a short growing season in cold climates. Careful selection of appropriate genotypes (e.g., cold-tolerant *Alnus*, *Larix*) might support a reasonably productive bioenergy industry with minimal hydrologic impact to the function of natural ecosystems and competing human land use.

In grasses, photosynthesis rates and ANPP were not correlated with any of the agroclimatic variables, in contrast to those of trees. However, the stomatal conductance rate was marginally correlated with the MAP:AET ratio (table S2), which averaged 1.1, suggesting that energy grasses operated close to the limit of available water in the studies investigated;

however, the low productivity of mixed prairie resulted in a greater annual surplus of water (MAP:AET of 1.7). At the stand scale, bioenergy water-use efficiency was highly correlated with physiological processes and ANPP and, therefore, indirectly with MAP:AET. As in trees, MAP:AET was correlated with MAP but not with mean annual temperature. Taken together, these findings suggest that grass-based bioenergy systems will be responsive to and limited by future water availability (as opposed to changes in the mean annual temperature), but the data on ecophysiology and ecosystem-scale water cycling are very limited—even more so than for trees. Therefore, targeted research is crucially needed on the ecohydrology of grass-based bioenergy production systems (see box 2).

Considerations for designing bioenergy systems for the future climate. Consistent with a recent modeling study of bioenergy potentials (Beringer et al. 2011), our analysis of future climate based on a comparison of 16 global circulation models (figure 1) strongly suggests a warmer, drier world that will require the engineering of tree- and grass-based bioenergy systems for maximum water-use efficiency if we are to achieve a productive, reliable, and sustainable energy supply while balancing the need for water with other uses. Importantly, our study advances the science by considering the interactive effects of changes in P and temperature, which together determine water availability to support net primary production, with spatially explicit confidence levels. The ratio of MAP to PET (MAP:PET) indicates the recent historical global distribution of relative water availability (figure 1a), which, when combined with the MAP:AET ratio (tables 1a–2d), suggests which areas will be climatically suitable for the various bioenergy-crop types. Projected increases in temperature (figure 1b), which will, in most cases, lead to higher evaporative demand combined with considerable decreases in P in many regions (figure 1c), will contribute to the intensification of drought stress across the globe (figure 1d), with reasonably high confidence over most of the projection area. Many areas in lower and middle latitudes that currently have the highest relative water availability will experience the greatest increase in drought stress. In our analysis, tree productivity and OT were positively correlated, and ANPP was highest in areas with favorable MAP:AET ratios (i.e., those in which the ratio was greater than 1.0). Therefore, tree-based bioenergy systems would best be deployed at middle to high latitudes, where the availability of water is expected to change the least or even to increase. In grasses, ANPP and bioenergy water-use efficiency were also strongly correlated (figure 6, table S2), and in general, the use of C_4 species confers substantial benefits in terms of bioenergy water-use efficiency and tolerance of low water availability, which would maintain productivity even when the MAP:AET ratio were less than 1.0, which will be of increasing importance in the decades to come. Because of seasonal variation in water availability and phenology, there may be advantages to combining C_3 and C_4 crops within a single cropping system (see box 2) to increase the overall system bioenergy water-use efficiency.

Conclusions

In the present study, we extracted data on the physiology, ANPP, and water use of representative bioenergy tree and grass crops from 371 refereed publications. Only two experiments provided a comprehensive treatment of a complete bioenergy water balance. We therefore conclude that the data needed to design water-efficient bioenergy-cropping systems are currently not available and that a widespread network of research sites encompassing the major climatic zones and soils needs to be installed with an eye toward quantifying a site's water balance as a function of climate variation. The data reported here provide a useful reference point of the climatic tolerance, productivity, and water relations of major bioenergy crops, but if terrestrial net primary production is to provide a major fraction of humanity's energy supply, our understanding of its environmental performance and its chemical and physical properties must match that of other energy sectors. More investment in research is needed. We tried to focus on low- to moderate-input systems to simulate production of a low-marginal-value commodity and found that rates of 7–13 Mg per ha per year may be expected, with a bioenergy water-use efficiency of 33–47 MJ per m^3 of transpired water. Rather than hope for the maximum rates of potential productivity, which would require high inputs, it seems reasonable to develop systems of moderate productivity with a higher tolerance to variation in environmental conditions that will provide a more sustainable and reliable energy supply over time. Finally, our analysis of the agroclimatic drivers of productivity and bioenergy water-use efficiency strongly suggests that water to support a large-scale deployment of lignocellulosic bioenergy systems could be severely limited in the future climate. The characterization of relative water availability by the MAP:PET ratio is intuitive and amenable to scaling using available meteorological data, and its incorporation into climate projections is straightforward.

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