WATER AND LIGHT COMPETITION AMONG
MULTIPLE SPECIES

A Dissertation in
Agricultural and Biological Engineering

by

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ABSTRACT

Solar radiation and water are two of the most important resources in agriculture. Therefore, plant competition for these resources has direct implications for understanding and designing agricultural systems. The goal of this research is to improve the understanding of solar radiation and water competition in multi-species agroecosystems. The research was divided twofold: 1) light interception and water uptake models intercomparisons; and 2) greenhouse experiments to improve understanding of water uptake and water stress. After comparing light interception in various simulation models, a new simple light interception method was created, allowing for the simulation of canopies with more than two species of different height and leaf architecture. This simple model yields comparable results to more complex simulation methods and can be easily integrated in agroecosystems models. Water uptake and water stress methods were compared among the APSIM, CropSyst, DSSAT, EPIC, SWAP and WOFOST agroecosystem models. This comparison revealed meaningful differences among the models’ water uptake and stress methods. The major difference between methods derived from the degree to which each model enabled the use of water in the subsoil. CropSyst, DSSAT, EPIC and SWAP developed a “drying front”, as usually observed in field conditions, while APSIM and WOFOST showed a more uniform water depletion with depth in the soil profile.

In the second phase of this research, maize, sunflower, orchardgrass and white clover were used as the model species in greenhouse experiments. Plants were grown in plant root observation chambers called rhizotrons. This experimental approach allowed for the measurement of soil water potential at different soil depths, the root density at
those depths, leaf water potential and transpiration. This study clarified the mechanisms of water uptake in different competing and non-competing plant species under drought conditions. No inter-species competition effect was observed for maize, sunflower, orchardgrass and white clover in transpiration in mixed species rhizotrons. This facilitates the development and implementation of multi-species crop models, since they can treat each species individually focusing on their respective competitive strategies.
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Dedicated to

General José Maria de Toledo Camargo

and

Carmen Gerin Silva Garcia
Chapter 1. Introduction and Objectives

In today’s society, agriculture has to meet conflicting demands. Agricultural production is responsible for meeting increased food requirements from a world growing both in terms of population and in average standard of living. To fulfill these needs with current production systems, however, agriculture must be intensified, which in turn can lead to accelerated land, water, and air degradation (Foley et al., 2011; Vergé et al., 2007).

Thus, a challenge of our time is to develop local, regional and globally integrated production systems that produce high output per unit of input and per unit area while maintaining environmental integrity. Assessing the tradeoffs between socio-economic and environmental attributes requires understanding the implications of two key processes: agricultural intensification and expansion. Agricultural intensification refers to the use of irrigation, fertilizers and other agrochemicals, mechanization, robotics, improved genetics, and frequent harvests to increase overall crop production from land that is currently managed. Agricultural expansion is the conversion of natural or minimally altered ecosystems to managed cropland or pastureland. Both intensification and expansion can have severe side effects on the environment that need to be taken into account in global and local assessments of agricultural production. The effects of agricultural intensification can be seen most strongly in data related to water and nutrients. Nutrient loss through the leaching of fertilizer, legume nitrogen fixation, and manure impacts water quality and generates eutrophication and hypoxic zones (Diaz and Rosenberg, 2008). Agriculture needs to break away from systems that facilitate nutrient leakage and pollution. This can be accomplished by moving away from water and
nutrient intensive systems, which can limit productivity given the current production model, or by redesigning systems to maintain high productivity in a relatively closed nutrient loop. Among the options that are compatible with current systems are the re-introduction of multi-species pastures and forage crops (Picasso et al., 2008). This chapter introduces the importance of multi-species systems research and provides a rational for focusing on plant competition for solar radiation and water. Simulating plant competition for solar radiation and water are the first steps in enhancing the capabilities of pasture system production models for local and regional assessments.

1.1. Importance of mixed pastures in the Northeast US

Grassland or pasture agriculture uses grasses and legumes for livestock consumption, and is a major component of the northeast US dairy farm operations (Barnes and Baylor, 1995; Winsten et al., 2010). Pastures are used as hay, silage or grazing by livestock. In addition to the economic benefits gained from this type of farming, grassland agriculture provides an array of environmental benefits such as soil erosion reduction, water quality, and wildlife protection (Barnes and Baylor, 1995).

Cool season grasses are predominant in the northeast US with common species including orchardgrass (*Dactylis glomerata* L.), perennial ryegrass (*Lolium perenne* L.), tall fescue (*Schedonorus arundinaceus* (Schreb.) Dumort), smooth bromegrass (*Bromus inermis* Leyss.), timothy (*Phleum pratense* L.), and festulolium (*Festulolium braunii*, K.A.) (Baylor and Vough., 1985; Houser et al., 2012). The frost tolerance and good
forage quality of cool season grasses make them suitable for the production systems and climate of the northeast (Kephart et al., 1995).

Legume crops such as alfalfa (*Medicago sativa* L.), white clover (*Trifolium repens* L.), red clover (*Trifolium pretense* L.), and birdsfoot trefoil (*Lotus corniculatus* L.) are also common in the region. Legume crops are able to reduce di-nitrogen through biological fixation, providing for their own N requirements and that of a companion (grass) or other crops in a rotation (Sanderson and Elwinger, 2002), and their high protein content results in outstanding nutritional quality. These features incentivize producers to use grass-legume pasture mixtures to reduce nitrogen fertilizer dependence (Nelson and Moser, 1995). A mixture of orchardgrass and white clover is a popular example of a pasture that combines the drought resistance and productivity of a grass (orchardgrass) with the nitrogen fixation of a legume (white clover) (Christie and McElroy, 1994; Sanderson and Elwinger, 2002).

As early as the 18th century, and perhaps earlier, it was recognized that increasing the number of species in a pasture can result in a higher total biomass production, yield stability, biodiversity and nutrient uptake efficiency (Darwin, 1859; Sanderson et al., 2004). These attributes encourage agro-ecologists to experiment with species mixtures that render more stable feed production throughout the year together with numerous biodiversity benefits (Comas et al., 2011) and other functions that are fitting for the local climate, soil, and landscape (Sanderson et al., 2007). One key component in evaluating mixed pastures is competition for limited resources (which vary seasonally) such as solar radiation, water, and nutrients. Understanding how different plants behave under different resource conditions is crucial in designing these cropping systems.
1.2. Plant competition for resources

Solar radiation and water are one the most important resources affecting multi-species growth. Therefore, plant competition for solar radiation and water have direct implications in understanding pasture systems and designing more sustainable agricultural systems (Kephart et al., 1995). In the water resource side, extensive studies of water stress in pastures have focused on subjects such as yield (Skinner, 2008), carbon assimilation and partitioning (Hall et al., 1988), and allocation to root as well as root distribution with depth (Bennett and Doss, 1960; Skinner and Comas, 2010).

Despite much progress in understanding the role of the rooting system in plant productivity (Palta and Watt, 2009), our understanding of underground competition is far less developed than that for aboveground competition. This includes competition between roots of the same plant, roots of the same species in different plants (i.e., monocultures), and rooting systems of different species sharing the same soil volume (e.g., legume-grass pastures). Belowground processes are as complex, or perhaps more complex, than aboveground processes that are easier to visualize and measure. The resulting disparity in knowledge about roots and shoots is problematic given the role of roots as the interface between plants and water, nutrients, and soil biota.

The combination of measurement difficulty and system complexity has limited the representation of root structure and functions in agroecosystem models. In general, when developing simulation models each component of the system should be understood and modeled at a comparable level of detail, and for agroecosystem models soil-root
processes can be viewed as the weak link in the chain. Understanding root competition and the development of algorithms to simulate the complex biophysical interaction in the soil-plant-atmosphere system clearly require more research, as well as packaging this knowledge in algorithms suitable for simulation models. Improving our capabilities in this area has far-reaching implications for simulating conventional and novel crop and pasture systems and their interactions with the environment.

1.3. Crop Simulation Modeling

Simulation models are becoming more and more prevalent as tools to assess environmental impacts and design sustainable cropping systems in agroecosystems (van Ittersum and Donatelli, 2003). Computational simulations can complement field experiments, interpolating and extrapolating from measurements and exploring alternative scenarios. Simulation models have become an intricate part of agricultural research; they are used in a wide range of subjects from characterizing root architecture (Lynch et al., 1997), to simulating dairy farms (Rotz et al., 2009), entire watersheds (Duffy, 2010), and global biomass potential (Bondeau et al., 2007). These models are designed to study the effects of climate, soil, and management on productivity and the environment.

There are several crop simulation models available including CropSyst, DSSAT, APSIM, SWAP and EPIC (Dam, 2000; Jones et al., 2003; Keating et al., 2003; Sharpley and Williams, 1990; Stöckle et al., 2003). CropSyst is the model selected to introduce the improvements suggested in this research, however the improvements are model independent. CropSyst is a process-based cropping systems simulation model that
belongs to a large family of models able to simulate relatively complex crop rotations. CropSyst has been applied to a variety of annual crops (Pala et al., 1996), perennial crops (Confalonieri and Bechini, 2004), and in several regions of the world (Donatelli et al., 1997).

These agroecosystem models have primarily been designed for monoculture crops and rotations of annuals, and several annual crops have been successfully verified in CropSyst (Stöckle et al., 2003). Simulations for perennial crops are still challenging (Teixeira et al., 2009), and multi-species competition among perennial or annual plants has received little attention. Understanding and modeling such competition is critical for proper simulation of agricultural systems that include mixed pastures for grazing or haying.

1.4. **Goal and specific objectives of this research**

The goal of this research is to improve the understanding of solar radiation and water competition in multi-species agroecosystems systems. To this purpose, this study will investigate the fundamental biophysical mechanisms explaining solar radiation interception and water acquisition in mixed, herbaceous plant communities. The experimental design for water competition includes both contrasting annual species (maize (*Zea mays* L.) and sunflower (*Helianthus annus* L.)) that will serve as model plants, and two perennial forage species (orchardgrass (*Dactylis glomerata* L.) and white clover (*Trifolium repens* L.)) that are representative of forage mixtures in the northeastern United States and beyond. The specific objectives of this research are:
• Dissect existing pasture models on each modeling component, compare different approaches, and discuss required improvements (Chapter 2);
• Evaluate and improve current solar radiation interception methods (Chapter 3);
• Evaluate current water uptake and water stress methods of current models (Chapter 4)
• Quantify intra and inter species water competition in the two model plants maize and sunflower (Chapter 5).
• Quantify intra and inter species water competition between orchardgrass and white clover (Chapter 6).

1.5. Chapter outlines

This section provides an overview of the dissertation chapters. Chapter 2 reviews current pasture growth models, and summarizes the main functionalities with emphasis on the representation of root water competition. Based on the strengths and weaknesses of these existing models, components that are suitable for direct inclusion in the CropSyst/Cycles framework will be extracted and knowledge gaps enumerated.

Chapter 3 and 4 evaluate current simulation methods of solar radiation and water uptake/stress, respectively. Knowing the current capabilities and differences between methods are important when developing new multi-species models.

Chapter 5 evaluates water competition between the two model plants, maize and sunflower, in rhizotrons. Experimental data is used to evaluate the fundamental water uptake framework based on Campbell (1985). This provides a test of the experimental
design and rhizotron infrastructure in a relatively simple system. In chapter 6 this basic approach is used with the perennial grass-legume mixture of orchardgrass and white clover. The data for annual and perennial species presented in these chapters will be used to improve CropSyst’s water uptake and competition algorithms. Results from this research will improve the simulation multi-species and its competition for resources, which could improve profitability and help producers adapt to changing market and climate conditions and to enhance stewardship of the land.
Chapter 2. Multi-species simulation models review

2.1. Introduction

In plant communities, competition can arise when the combined demand for critical growth factors such as nutrients, water, or light of all individuals exceeds the capacity of the environment to supply one or more of these resources (Clements et al., 1929). In agroecosystems, competition is managed to optimize grain, forage, or other economic outputs. In annual grain crops such as maize, wheat and sunflower, competition studies have typically two main goals: to quantify the effect of weeds on crop performance (Zimdahl, 2004), and to optimize economic output per unit area by managing plant density, fertility, and other factors. In fact, part of the genetic improvement in corn grain yield over the past decades has been based on the ability of plants to withstand high population densities (Duvick, 2005).

Competition is more dynamic in perennial multi-species pastures. The dynamic soil and climatic conditions determine resource acquisition through the interaction between plant phenology and environmental conditions. For example, different pasture species can attain better growth in different weather conditions during the growing season (Scarisbrick and Ivins, 1970). However, the biophysical mechanisms underlying competition are the same for mono- or multi-species systems (Kemanian and Marcos, 2011).

The competition mechanisms among plant communities for shared resources have been incorporated in several simulation models. These models differ in their approaches to address the concepts and practical perspectives of plant competition. The variety of
plant competition modeling approaches makes difficult in inter comparisons of the existing models. More specifically, models have various degrees of input requirements, rigidity in mechanisms structures, and modularity (Deen et al., 2003).

Researchers have compared from specific processes nested in models such as light interception (Keating and Carberry, 1993), water uptake (Jara and Stöckle, 1999; van den Berg et al., 2002), nutrient uptake (Kropff and Laar, 1993) to full model implementations (Asseng et al., 2013; Bassu et al., 2014). In some comparisons, the capabilities of models such as the number of competing species that can be handled or the processes addressed through competition are listed (Caldwell, 1995; Deen et al., 2003; Malézieux et al., 2009; Taubert et al., 2012). However, these comparisons have not yielded a clear blueprint of the processes that can be successfully modeled nor have produced a clear cut list of important research subjects in the area of modeling competition in multispecies communities.

My conceptual framework for modeling competition in multispecies models has two pillars, one pertaining to the model science and the other to software designing. First, competition must emerge from the fundamental mechanisms of plant resources acquisition and growth for each species incorporated in the model; it should not be forced through parameters that determine that one species will outcompete another independently of the environment. Second, the software design should follow an object-oriented design in which one species is an object with a given set of attributes, and a multispecies community is simply a community of objects. While object oriented programming has been conventional wisdom in the software development community for decades, many plant-based simulation models have a mixture of coding styles that do not
benefit from the power and efficiency of object oriented programming (Affholder et al., 2012). In facts, codes can be hard to follow and share (Papajorgji and Shatar, 2004). I surmise that progress in modeling plant competition will benefit from both clarity in the science behind the model that introduces competition as an emergent property of a community with individual with a given set of properties, and from a coding style that uses the full power of object-oriented programming. The modularization associated with object-oriented design will facilitate a systematic scaling up of systems, from plants to fields and from field to landscapes and global scales.

My goal in this chapter is to review and compare the competing mechanisms of multi-species models. The objectives are to 1) clarify differences in competition methods specifically for light and water, 2) identify potential improvements, and 3) provide a multi-species modeling framework for competition.

2.2. Crop-weed competition modeling

Crop-weed relationships were the primary focus of initial efforts to model resource competition in agricultural systems (Kropff, 1988; Kropff and Spitters, 1992). The models resulting from these efforts over the last thirty years evaluate the impact of weeds in reducing yields of cash crops by accounting for weed density, radiation interception, water and nutrient use, and economic outcomes. These models include SETSIM (Orwick et al., 1978), SOYWEED (Wilkerson et al., 1990), ALMANAC (Kiniry et al., 1992), INTERCOM (Kropff and Laar, 1993), NTRM-MSC (Ball and Shaffer, 1993) and CropSys (Caldwell and Hansen, 1993), among others (Beyschlag et al., 1990; Graf and Hill, 1992; Grant, 1994; Weaver et al., 1994).
Comparisons of the capabilities of some of these models identified create two types of challenges: it is still difficult to simulate the growth of individual species within a community, and so is to compare competition processes between models due to lack of modularity of the model structures. Additional problems might arise when models are “validated” with the same data used to develop them, thus reducing their broader applicability (Deen et al., 2003).

2.3. Grassland and pasture models

While in crop-weed modeling it is clear which species are considered “beneficial”, in pasture modeling each species has growth characteristics and roles in the community, which creates more complex interactions (Malézieux et al., 2009; Sanderson et al., 2007). Grassland and pastures models have core components for plant growth, soil processes and the response of plants to cutting and grazing. In each model, these components and the way in which resource competition is handled are developed to different degrees. Progress has been made in this area in the past three decades, but still there is no clear blueprint of the challenges that the research community needs to overcome and their relative importance in order to improve the simulation of competition for resources and growth in multispecies models.

In Table 2.1 I present an inventory of existing models and highlight some of their characteristics. For most models, the starting point is the simulation of growth of a canopy that has a set of characteristics, namely a leaf area index ($L$, ratio of half of the leaf area to the ground area, $m^2$ leaves $m^2$ ground), a canopy architecture usually condensed into the extinction coefficient (ratio of projected shadow of the canopy on a
leveled surface to the actual half-area of leaves). This canopy captures radiation, and depending on plant and environmental conditions, uptakes CO₂ through photosynthesis. Several grassland models follow Johnson et al. (1983) to simulate light interception, photosynthesis, and growth limiting factors (Table 2.1). Other models simulate growth based on radiation use efficiency (e.g. APSIM) or both radiation use efficiency and transpiration use efficiency (CropSyst). When the models have a subdaily time step, the interception of radiation by each species in a community has to be computed within the time step and it depends on the leaf angle distribution, distribution of leaf area with height, and the absolute leaf area. This computation is feasible but requires significant amount of inputs as described below. Daily time step models require simplified assumptions to apportion radiation among species within a community. This is critical because the demand for water is determined largely by radiation interception; competition for light is therefore intimately linked with the competition for water.

The competition for water at the root level is less developed in simulation models. Existing models evolved from single species models having legacy simplifications that may preclude direct application in competition models. The models evolving from the Washington State University soil physics use variations of the approach presented in Campbell (1985). These are the models CropSyst and GAPS. In these models, flux of liquid water is calculated as a function of a gradient in water potential and a resistance to the water flow. The plant resistance plays a major role in determining water flux. Other models bypass potentials and resistances and use empirical or lumped approaches that depend mostly on soil water content (e.g. APSIM, EPIC, and the DSSAT models).
When including the competition modules in large scale simulation models, other components of the model become relevant. Many models have simplified water balances that make their applicability rather limited. For example the Hurley Pasture Model drains all water in excess of field capacity during infiltration events. Thus, nutrient leaching would be overestimated with such approach which makes the model less useful to model nutrient-water interactions. Other models are more balanced and should be the basis for further development (e.g. APSIM or CropSyst).

In summary, while many models seem to simulate competition, their capabilities are limited in the competition algorithm themselves, due to simplicity or lack of relevant feedbacks, or due to limitations in other aspects of the modeling system such the nutrient or water balance. Thus, there is an evident lack of harmonization among modeling approaches. In this chapter, I focus on the competition for light and water. I compare briefly existing approaches in preparation for chapters that deal with science of modeling competition for these to resources. I highlight, nonetheless, that my aim is a modeling system that can handle multi-species pastures and that therefore model development should be compatible with a full modeling system.
Table 2.1. Light and water characteristics of mono- and multi-species pasture and grassland models. Not all the models listed here are available for use; and their description was taken from the literature.

<table>
<thead>
<tr>
<th>Model</th>
<th>Leaf area growth</th>
<th>Max. coexisting species</th>
<th>Water stress</th>
<th>Soil Evaporation</th>
<th>Plant Transpiration</th>
<th>Water infiltration/ redistribution</th>
<th>Runoff</th>
<th>Light interception</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Agroecosystem models</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>APSIM / EcoMOD / AgPasture</td>
<td>Function of temperature</td>
<td>unlimited</td>
<td>0</td>
<td>P-M</td>
<td>P-M</td>
<td>1) Cascading</td>
<td>Modified Curve Number</td>
<td>Exponential</td>
</tr>
<tr>
<td>CropSyst</td>
<td>SLA; biomass</td>
<td>one</td>
<td>Ψ</td>
<td>P-M, P-T</td>
<td>Ψ and R</td>
<td>1) Cascading</td>
<td>Curve Number or numerical</td>
<td>Exponential</td>
</tr>
<tr>
<td>EPIC</td>
<td>Thermal time follows present L curve</td>
<td>unlimited</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>Water redistributes up to Ψ at k_sat</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>STICS</td>
<td>n/a</td>
<td>one</td>
<td>n/a</td>
<td>Potential ET</td>
<td>Potential ET</td>
<td></td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td><strong>Pasture and rangeland models</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grassplan/GrassGro</td>
<td>SLA; biomass</td>
<td>four</td>
<td>θ</td>
<td>31,32</td>
<td>31</td>
<td>Cascading</td>
<td>Curve Number</td>
<td>Exponential</td>
</tr>
<tr>
<td>Hurley Pasture Model (HPM)</td>
<td>n/a</td>
<td>one</td>
<td>Ψ</td>
<td>Assumed zero</td>
<td>P-M</td>
<td>Soil recharged until field capacity. Excess water drains.</td>
<td>Ψ</td>
<td>Exponential</td>
</tr>
<tr>
<td>Pasture Simulation Model (PaSim)</td>
<td>SLA; biomass</td>
<td>five</td>
<td>Ψ</td>
<td>P-M</td>
<td>Ψ and R</td>
<td>Richards equation or Capacitance model</td>
<td>n/a</td>
<td>Equally available to all photosynthetic tissues</td>
</tr>
<tr>
<td>PROGRASS</td>
<td>SLA; biomass</td>
<td>two</td>
<td>θ</td>
<td>3</td>
<td>3</td>
<td>Excess after infiltration, ET and drainage.</td>
<td>M</td>
<td></td>
</tr>
<tr>
<td>SGS Pasture Model / DairyMod</td>
<td>SLA; biomass</td>
<td>five</td>
<td>0</td>
<td>P-M</td>
<td>P-M</td>
<td></td>
<td>n/a</td>
<td></td>
</tr>
<tr>
<td>SPUR</td>
<td>Function of biomass</td>
<td>seven</td>
<td>Ψ</td>
<td>n/a</td>
<td>n/a</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Other models</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GAPS</td>
<td>1) Function of biomass</td>
<td>n/a</td>
<td>Ψ</td>
<td>P-M, P-T, Linacre Pan</td>
<td>Ψ and R</td>
<td>n/a</td>
<td>n/a</td>
<td>L based and exponential</td>
</tr>
</tbody>
</table>

**Abbreviations:** θ = water concentration (m$^2$ m$^{-3}$); Ψ = water potential (J kg$^{-1}$); ET = evapotranspiration (kg water m$^{-2}$ s$^{-1}$); k = light extinction coefficient, LAI = leaf area index (m$^2$ one sided of leaf m$^2$ ground); P-M = Penman-Monteith (Allen et al., 1998; Monteith, 1965); P-T = Priestly and Taylor; R = resistance to water flow, L = leaf area index (m$^2$ leaf m$^{-2}$ ground); SLA = specific leaf area (m$^2$ leaf kg$^{-1}$ leaf); k_sat = saturated hydraulic conductivity (kg m$^{-2}$ s$^{-1}$).

2.4. Competition for light

Light interception of plant canopies is typically simulated following variations of Beer-Lambert light extinction law in physics, which is in turn an application of the binomial probability theory. A light beam can be intercepted by a leaf element, or not, with a probability equivalent to the ratio of the projected shadow of the leaf element on a horizontal surface, divided the subtending area. When a population of randomly distributed leaf elements is considered, and the area of the leaf element is much smaller than that of the subtending ground, then the probability of a beam to travel through the canopy without being intercepted by a leaf element approaches a Poisson distribution. This is true for a light beam with a specific zenith angle, and should not be confused with the daily cumulative light interception of plant canopies. As seen below, daily accumulation of radiation has, fortuitously, a similar dependence than the interception of a directional light beam. The first to recognize this relationship were Monsi and Saeki (1953) who introduced the dependence of downward radiation flux to $L$ as follows:

$$\Phi = \Phi_o \times e^{-k \times L}$$  \hspace{1cm} (2.1)

where, $\Phi$ is the attenuated radiation flux density ($\text{W m}^{-2}$), $\Phi_o$ is the unattenuated radiation flux density ($\text{W m}^{-2}$), and $k$ is the extinction coefficient for the canopy ($\text{m}^{-2} \text{ground m}^{-2} \text{canopy}$).

Throughout this chapter I assume that this exponential relationship applies to daily radiation interception as used in most models; $k$ is a daily integrated attenuation or extinction coefficient.

For multi-species models, both $L$ and $k$ are composites of the canopies of the different species. Assuming that these leaves are randomly distributed through the thickness of the
canopy from top to bottom the radiation intercepted by different species depends on \( L \) and \( k \) (Kiniry et al., 1992; Spitters and Aerts, 1983):

\[
f = 1 - e^{\sum_{i=1}^{n} -k_i L_i}
\]

(2.2)

where, \( f \) is the total fractional radiation interception of the multispecies canopy, \( n \) is the number of species, \( k_i \) is the light extinction coefficient of the \( i^{th} \) species, and \( L_i \) is the leaf area index of the \( i^{th} \) species (m\(^2\) leaf m\(^{-2}\) ground). Therefore, the interception by each individual species \( (f_i) \) is (Carberry et al., 1996):

\[
f_i = f \frac{k_i L_i}{\sum_{i=1}^{n} (k_i L_i)}.
\]

(2.3)

Thornley and Johnson (2000) use a similar approach (eq. 2.3) but include scattering of radiation in the canopy.

When the leaf area of species is distributed over different heights, i.e. one species is taller than the other, different assumptions are needed. Wallace (1997) proposed to treat species as fully dominant, i.e. they overtop other species with all the leaf area, or fully suppressed. Using the superscripts \( d \) for dominant and \( s \) for suppressed, Wallace (1997) suggested that \( f_i \) for each species of a canopy composed of two species with different height \( (h_i, m) \) must fall between these two extremes:
The coefficient $\zeta$ is a weighing factor that moves the species between the dominant or suppressed extremes depending on their relative height.

The light competition models described here represent most methods used in grassland/pasture models. Other light interception methodologies exist in multi-species (Kropff and Laar, 1993) but may require unrealistic inputs for most applications. Division of canopy into layers is possible but it requires tracking the distribution of leaves in different canopy strata. Such approach can use models as the one presented by (Sinoquet et al., 2000), but is difficult to envision a generalized use of this method as it will be loaded with assumptions regarding leaves distribution within the canopy with multiple species.

Wallace (1997) method is a clever simplification and works well for two species (i.e. dominant and suppressed) but it is clearly inadequate for more species and to the best of my knowledge a solution has not been presented. Clearly, this is an area that needs

\[
f_1^d = 1 - e^{-k_1 \times L_1} \quad (2.4)
\]

\[
f_2^s = (e^{-k_1 \times L_1}) \times (1 - e^{-k_2 \times L_2}) \quad (2.5)
\]

\[
f_2^d = 1 - e^{-k_2 \times L_2} \quad (2.6)
\]

\[
f_1^s = (e^{-k_2 \times L_2}) \times (1 - e^{-k_1 \times L_1}) \quad (2.7)
\]

\[
f_1 = f_1^s + \zeta \times (f_1^d - f_1^s) \quad (2.8)
\]

\[
f_2 = f_2^s + (1 - \zeta) \times (f_2^d - f_2^s) \quad (2.9)
\]

\[
\zeta = \frac{h_1}{(h_1 + h_2)} \quad (2.10)
\]
more research. Chapter 3 presents my solution to the problem of modeling light interception in canopies with more than two species and with varying canopy height.

2.5. Competition for water

Models of water uptake can be divided in two types: those that use water content as that determinant of the water supply and those that use an electrical circuit analog with water potential being the driving potential and the soil and plant being resistances to water flow to represent the water movement in the soil-plant-atmosphere continuum (SPAC) (Campbell, 1985; Campbell, 1991; Cowan, 1965; van den Honert, 1948). Both methods require empiric data and some assumptions, yet the water potential based method is more fundamental. Water content and water potential are used to represent the state of water in the soil. Trade-off exists between water content and potential. Water content is easier to measure but it is not a driving force of water movement. Conversely, water potential, an intensive soil property, is difficult to measure and varies little over the narrow range of water potential of biological importance to plants, but it is the driving force of liquid water movement in the SPAC. The water content and the water potential approaches reflect in part these tradeoffs.

The major components in the analog electrical system representation are soil, root, xylem, and leaf water potentials and resistances. There are methods to calculate each of the potentials and resistance, the best summary of which can be found in Campbell (1985). Soil resistance is a function of root radius, root length, soil depth, water content and saturated conductivity; root resistance is a function of root radial resistivity and root length. The soil resistance is challenging to compute as it depends on the water
potential at the soil-root interface, which is not known. However, this resistance is relevant only in relatively dry soils or coarse textures (Bristow et al., 1984). The plant resistance (root, leaf and xylem) are the most important resistances to water flow in the systems. They are considered fixed for expediency, but data and theory have shown that they vary substantially. I expand on this subject in Chapters 5 and 6.

A conceptual framework based on the electric analog is presented in Figure 2.1 for multispecies communities. In this framework, species compete for soil water and their competitiveness depends on species characteristics such as root density and depth of root exploration.
Figure 2.1 Schematic of the soil plant atmosphere continuum (SPAC) for multi-species communities. Transpiration (T), plant resistances (R) and water potentials (ψ) are represented in an electrical analog. Water movement in the soil is not represented, but is implicit as water can move between soil nodes.

A summary of the studies conducted on water transport in plants has been presented by (Hopmans and Bristow, 2002). Water uptake is driven by transpiration demand. Water is removed from different soil layers based functions that take into account the soil water content or potential and root density in each layer. There are significant variations among models on how to handle these complex interactions. In multi-species simulations, uptake can be obtained by resolving the water balance of each soil node based on the demand from a representative root segment of each species and flux among nodes. This is numerically possible but usually overly-complex without much
advantage in the accuracy of the simulation. Models usually simplify this step by varying the soil water content (Johnson et al., 2008; Zhai et al., 2004) or maintaining the soil water potential constant (Rossiter and Riha, 1999) within a time-step. During species development, water can become limiting in the soil, resulting in transpiration reduction and consequently reducing biomass production. The reduction in transpiration emerges from the sharp decrease in soil water capacitance ($\partial \theta / \partial \Psi$, volumetric water content per unit of water potential) as the soil dries, and due to the response of stomata to the low water potential of soil or leaf. It is well known now that there is also an increase in plant resistance as the plant water potential lowers (Sperry et al., 1998), but the effect is to reduce transpiration as the soil water potential drops or the atmospheric demand increases beyond the capacity of the plant to support a given flux (Campbell, 1985).

In models based on water content instead of water potential driven flux, water stress is typically simulated using threshold values in soil water content (Figure 2.2). The first threshold (e.g., onset of stomatal closure) signals the start of transpiration reduction until it reaches a second threshold (e.g., permanent wilting point) when transpiration stops (Table 2.1). Since water content by soil layer varies, this requires using weighing functions to allow for compensation among layers. Many models (e.g. EPIC) will simply move downward from the top layers down to check if plant water can be satisfied; water is extracted first from the top layers as in imposed property of the system, not because of the existing allocation of roots. This approach provides satisfactory results but is rigid and lacks the mechanism to represent differences in root distribution. The ratio between actual and potential transpiration can be used to reduce photosynthesis.
2.6. Discussion

Improvements in water competition in models can occur in several areas. Multi-species modeling efforts should go beyond specific binary species (e.g. crop – weed), where one model is developed or modified to simulate a single crop and weed to answer a specific question. Modeling design should focus in creating frameworks for the user to add its own species characteristics in a simple and clean format.

To simulate multi-species systems such as mixed pastures, models should be able to accommodate several species. Of the models reviewed, only APSIM, DairyMod, EPIC, PaSim and SPUR support more than two species, yet they have limitations. In multi-species simulations, it is important to account the competitive edge each species have in the above and belowground environments. In the canopy, none of these models accommodate variations in LAI with height. This impacts water competition since it mediates the partitioning of the transpiration demand by the environment among species. In the belowground, water uptake must be distributed to roots of different species, and that will depend on root density and water demand from each roots system (i.e. each
species). Root density is important to determine from where water is removed in the soil column and in Campbell (1985) approach it is explicitly considered. Yet, other factors no accounted for in that model seem to be important because it has been observed that pastures (chicory) with roots in both dry topsoil and relatively wet subsoil colonized by roots show water stress (Skinner, 2008). No model represents explicitly this behavior.

Methods to account for water stress in multi-species still needs to be improved. The use of water potential is more fundamental than water content because of assumptions needed to characterize the soil in the water content method. The water content approach does not offer a way to model isohydric or anisohydric behavior (Tardieu and Simonneau, 1998). The electrical analog using water potentials, water flow, and plant resistances in the SPAC between soil, root, xylem, and leaf in an electrical circuit is a useful representation to simulate water stress. However, the problem with this approach is that these resistances are assumed constant, an assumption that proved incorrect (Franks et al., 2007). Sperry et al. (1998) simulated variable resistances dependent on water potentials in different locations in the SPAC which is important but still under explored in agroecosystems models. Similarly, different water uptake behaviors between species have been investigated experimentally (Tardieu and Simonneau, 1998), but mechanisms are not implemented in simulation models and the implications not fully explored.

The interplay of competition for light and water also has implications for the competition for nutrients. For example, during early succession, annual plants obtain resources from the soil and outcompete perennial plants that are slow to develop. However, as their rooting systems and crown colonize the soil space, and nutrients
accumulate in their storage organs, perennials can slowly outcompete annuals, if anthropogenic or natural disturbances do not regress the succession to earlier stages. However, this competition for nutrient interacts with phenology and the ability of plants to capture resources, determining the structure and dynamics of the community through time. Simulating this dynamics, is in my opinion, a task that has not been accomplished for multi-species pastures.

2.7. Conclusions

Processes that explain the competition for light and water have been only partially incorporated in agroecosystem models. I identified several processes that require attention to simulate realistically multispecies pastures. These processes are competition for light in canopies in which individual species vary in height, and the effect of root distribution and plant hydraulic properties on water uptake. These processes are interactive given that radiation capture affects transpiration. Even though several models exist, few are up-to-date and able to represent important characteristics such as mixed species and water use, which is important particularly under stressful conditions. These are research subjects that need additional experimental and modeling efforts, and the following chapters attend these needs.
Chapter 3. Modeling light interception in multi-species canopies

Abstract

Simulating light interception by single plant species within multi-species canopies is critical to modelling growth and transpiration. While there is solid theory and empirical knowledge on light interception by plant canopies, the methods used in process-based agroecosystem models to simulate competition for light do not account simultaneously for variations in canopy architecture, leaf area, and height among more than two species. Our objective is to present a new method to simulate light interception in multi-species canopies and to compare it with existing methods. The new method (Cycles) uses a daily time step and accounts for unlimited species with different heights. It assumes that depending on the relative canopy height, the species light interception is between that of a fully dominant and a fully suppressed species. Leaves from different species are assumed to be randomly mixed in the canopy layer. The methods compared with Cycles were: a sub-daily time step model (Campbell), a daily time step model with unlimited species (APSIM), and a daily time step model for two species with different heights (Wallace). The daily methods provided a good balance between complexity of calculations and accuracy of results when compared to the sub-daily method. When compared for two species, the Cycles and Wallace methods yielded similar results. The Cycles method successfully combined the best attributes of the APSIM and Wallace methods: an unlimited number of species with different heights. The simulations show that representing competition becomes important in species with the same light extinction
coefficient and leaf area index \((L)\), but different heights, when the total canopy \(L\) is larger than 2 m\(^2\) m\(^{-2}\). The Cycles method allows simulating in a relatively simple fashion the light interception of different species in the canopy. This method can be easily integrated in agroecosystems models to simulate inter-specific competition in multi-species canopies.

Key words: Light interception, modeling competition, multi-species canopies modelling, canopy architecture.

### 3.1. Introduction

The amount of light intercepted by an individual plant species within a multi-species or multi-phenotype canopy determines in part its competitive ability. Multi-species canopies are present in most natural and managed systems. When modeling agroecosystems, simulating competition for light is critical in order to model growth, transpiration and other vegetation processes, since the amount of light intercepted by plants controls photosynthesis and transpiration. By controlling photosynthesis and transpiration, competition also affects the demand for nutrients and water, creating a feedback with competition at the root level. Therefore, it is important for agroecosystem models to have a module to simulate light interception by different species or phenotypes growing together. (Hereafter, and for expediency, I refer to this type of canopy as multi-species canopy even though the concept also applies to mono-specific canopies with individual members whose phenotypes differ.)
Following Vos et al. (2010), the approaches to model light interception by plants can be divided in two: the process-based and the functional-structural approaches. Process-based approaches typically focus on the community level (a canopy) while the functional-structural approaches focus on the individual plants, and even plant segments (stems, leaves), that compose that community. Functional-structural modeling follows a “bottom up” path to modeling and has potential to link gene expression with plant architecture traits that can empower plant breeding (Chelle and Andrieu, 1998; Drouet, 2003; Godin and Sinoquet, 2005; Leyser, 2009). In this study I focus on process-based approaches. These approaches are suitable to simulate average properties of different species or genotypes growing together in plant communities, and are amenable for inclusion in comprehensive agroecosystem models that by design have to simplify the representation of each component of the system.

While there is solid theory and empirical knowledge about how to simulate light interception by plant canopies (Campbell and van Evert, 1994; Goudriaan, 1977; Ross et al., 1972), the simulation of competition for light by plant canopies at the field level has received comparatively less attention. Currently, no process-based method can simulate light interception of more than two species with different heights in a robust and simple fashion.

In multi-species canopies, the allocation of intercepted light among the different species in the community is challenging because it depends on both plant dimensions and plant architecture. The factors that contribute to the variation in light interception of different species within a canopy are the leaf area index \( L, m^2_{\text{leaf}} \), plant height
(h, m), leaf angle distribution, leaf light transmissivity and absorptivity, and the angular distribution of the incoming light, which depends on the solar zenith angle (ψ) and atmospheric and surface properties (Campbell and Norman, 1998). In theory, these factors can be accounted for to calculate accurately the light interception by individual components of a canopy. In practice, however, there are properties that are difficult to model such as atmospheric scattering of incoming and reflected light and the variation in leaf density and leaf angle distribution with h. Thus, it is convenient to use simplified models that capture the important attributes that explain the outcome of competition at the right level of complexity for the objective, as customarily done with other biophysical processes (Hammer et al., 2004).

Models of light interception by multi-specific canopies must minimally account for the variation in architecture, leaf area, and height among species. None of the existing modules for competition that are included in agroecosystem models (Keating and Carberry, 1993; Sinoquet et al., 2000; Wallace, 1997) account for all factors simultaneously. In detailed models of light interception in mono-specific canopies, the variation in light interception throughout the day is calculated at a sub-daily or sub-hourly time step for a canopy discretized in layers of small ΔL (e.g. Goudriaan, 1977). Compared with simpler, daily time step models that use a lumped “big-leaf” approach to compute light interception, the detailed models are computationally slower with relatively small gains in accuracy (Stöckle, 1992), and therefore agroecosystems models tend to use the simpler but robust big-leaf approach to simulate single species canopies (Stöckle et al., 2003; Villalobos et al., 1996). It has not been explored, however, if a daily time step suffices to describe light interception by different species within a canopy.
Light interception models typically use an exponential decay to describe light attenuation throughout the canopy’s depth, with the attenuation increasing in proportion to the cumulative $L$ and the light extinction coefficient $k$. This exponential model has been shown to work for instantaneous light interception calculations and conforms to theory with minimal simplifications (a useful synthesis in Campbell and Norman, 1998). The same exponential model has been used for daily calculation of light interception by the canopy and shown to be empirically adequate for a mono-specific canopy (e.g. Kemanian et al., 2004). This result is somewhat fortuitous, as a daily, seasonally constant $k$ is not to be expected for a canopy with an invariant leaf angle distribution throughout the season; in other words, a constant $k$ requires specific assumptions regarding changes in leaf angle distribution as $L$ changes (this is clearly illustrated in Fig. 15.1 in Campbell and Norman (1998)). Hence, while it is plausible to assume that a daily time step model can be used to allocate the light intercepted by a canopy among the many species that compose it, neither this possibility nor the variation among existing models have been explored systematically.

Accordingly, the goal of this study is to develop a method to account for light competition in multi-species canopies that is fitting for agroecosystem models. The specific objectives are to: 1) introduce and test through simulations a new daily time step light interception model for multi-species canopies (Cycles) that can accommodate more than two species that differ in canopy height; 2) compare Cycles with current methods that simulate light interception in multi-species canopies in daily and sub-hourly time-steps. Two big-leaf daily time steps methods described in the literature for multispecies canopies were compared. The sub-hourly time step method follows Campbell (1990) and
Campbell and Norman (1998). The models and the specific comparisons are described below.

3.2. Model Descriptions

3.2.1. Sub-hourly light interception

The model and simplifications described in Campbell and Norman (1998) were used to implement instantaneous calculations of light interception at different sun zenith angles (ψ) and integrated to a cumulative daily estimate (Campbell method). The specific equations are not repeated here except when needed for discussion or comparison. The main assumptions for our purpose are that leaves are randomly distributed horizontally and vertically within the top and bottom of the canopy, that the leaf angle distribution does not vary with height, and that it remains constant as L changes. The leaf angle distribution is represented by the ratio \( \chi \) of the horizontal to vertical axis of an ellipsoid (Campbell, 1990), where \( \chi = 0 \) represents a completely vertical canopy, \( \chi = 1 \) represents a spherical leaf angle distribution (and thus slightly vertical), and \( \chi > 1.6 \) (mean leaf angle \( \sim 45^\circ \)) represents leaf angles increasingly horizontal. This one-parameter model has been shown to represent canopy light interception well when compared with other models with more parameters (Wang et al., 2007).

Light interception is calculated as follows. The canopy intercepts both beam and diffuse light (fractionally expressed as \( f_b \) and \( 1 - f_b \), respectively). Each of these two components is intercepted with a corresponding \( k \) for beam and diffuse light (\( k_b \) and \( k_d \)).
The $k$ varies with $\chi$ and $\psi$ for beam light, and with $\chi$ and $L$ for diffuse light. In a canopy with $n$ species, the total fractional canopy light interception ($F_T$) at a given $\psi$ is:

$$F_T = 1 - f_b e^{-\sum_{i=1}^{n} k_{b,i}L_i} - (1 - f_b) e^{-\sum_{i=1}^{n} k_{d,i}L_i} \quad (3.1)$$

The subscript $i$ represents each species. The fraction of the total light transmitted through the canopy ($\tau_T$) is the complementary quantity $\tau_T = 1 - F_T$. For a given $\psi$ and $f_b$, and using the total $L$ ($L_T = \sum_{i=1}^{n} L_i$), an effective $k$ for the canopy ($k_e$) can be calculated:

$$k_e = -\frac{\ln \tau_T}{L_T}. \quad (3.2)$$

An analogous $k_e$ for each species ($k_{e,i}$) can be calculated by assuming that the species is alone in the canopy. Thus, the fractional light intercepted of each species ($F_i$) can be apportioned based on $F_T$ as follows:

$$F_i = F_T \frac{\omega_i k_{e,i}L_i}{k_{e,i}L_T}. \quad (3.3)$$

The weighting factor $\omega = 1$ if all species are of equal $h$, and $L_i$ is distributed uniformly with $h_i$, but can be changed empirically to accommodate differences in $h$ or $L$ distribution without resorting to a layered canopy calculation. When integrated throughout the daytime, these equations yield estimates of daily $F_i$ ($F_{i,d}$) and daily $F_T$ ($F_{T,d}$), allowing comparisons with daily time-step models. The subscript $d$ represents each day.

3.2.2. Daily radiation interception: APSIM method and Wallace method

The methods to compute daily light interception selected for this analysis are from the APSIM agroecosystem model (Keating and Carberry, 1993) and from Wallace (1997). The APSIM method allows simulating a canopy with any number of species but
it assumes that $h$ is the same for all species and that $L$ is distributed uniformly throughout $h$. Thus, if each species has a light extinction coefficient ($k$) applicable to a daily time step calculation (with $k$ assumed to be constant), the total fractional light interception ($F_T$) and that of each species ($F_i$) is:

\[
F_{T,d} = 1 - e^{\sum_{i=1}^{n} -k_i L_{i,d}} 
\]

\[
F_{i,d} = F_{T,d} \frac{k_i L_{i,d}}{\sum_{i=1}^{n} k_i L_{i,d}}. 
\]

Eq. 3.5 is a daily time step version of Eq. 3.3 with the weighting factor $\omega_i = 1$.

The Wallace (1997) method handles only two species, but $h$ is taken into account. It is based on determining $F_{i,d}$ of each species as if it were a totally dominant species ($F_{i,d}^d$) or a totally suppressed species ($F_{i,d}^s$) with respect to the other species. For species $i = 1$ the equations are:

\[
F_{1,d}^d = 1 - e^{-k_1 L_{1,d}} 
\]

\[
F_{1,d}^s = (e^{-k_1 L_{1,d}})(1 - e^{-k_2 L_{2,d}}). 
\]

Since $F_{i,d}$ must be between the fully dominant or fully suppressed extremes, Wallace (1997) devised a simple method that uses a weighting factor ($\zeta$) that depends on $h$ to determine the level of dominance of a species and $F_{i,d}$. For species $i = 1$ the equations are:

\[
F_{1,d} = F_{1,d}^s + \zeta_d (F_{1,d}^d - F_{1,d}^s) 
\]

\[
F_{2,d} = F_{2,d}^s + (1 - \zeta_d)(F_{2,d}^d - F_{2,d}^s) 
\]
The method works well for two species, but it is not amenable for more than two species.

3.2.3. A new method for multi-species with different height (Cycles method)

A new method is presented here for daily time step calculations. This method is intended for the agroecosystem model Cycles, an evolution of the C-Farm model (Kemanian and Stöckle, 2010), but can be implemented in any agroecosystem model. To preserve the convention used with APSIM, I will call this new method the Cycles method. It uses the Wallace (1997) concept of fully dominant or fully suppressed species and the weighting factor $\omega$ introduced in Eq. 3.3. For a given species $i = 1$, the following applies:

$$
\zeta_d = \frac{h_{1,d}}{h_{1,d} + h_{2,d}}.
$$

The equations are easily expanded to all species in the canopy. The actual $F_i$ will depend on the degree of the dominant or suppressed condition of a given species. That condition can be stipulated based on $h$ by modifying the weighting factor $\omega$ in Eq. 3.14 (similar to Eq. 3.3) as follows. If Eq. 3.14 (or Eq. 3.3) is combined with Eq. 3.6 or Eq.3.7, a value of $\omega_i$ for the dominant ($\omega_i^d$) or suppressed ($\omega_i^s$) condition can be obtained:
The $\omega_i$ for a given species must be between these two extremes. In the Cycles method I proposed to calculate it as follows. I assumed that if $h$ is equal to the average $h$ of all species in the canopy, then $\omega_i = 1$ (i.e., the case of the APSIM method). For all other cases, $\omega_i$ is bounded in the “suppressed” side by $\omega_i^s$ and in the “dominant” side by $\omega_i^d$.

Any solution to $\omega_i$ must ensure that $\sum(\omega_{i,d}k_iL_{i,d}/\sum_{i=1}^{n} k_i L_{i,d}) = 1$. The simplest solution is a linear interpolation between the suppressed condition ($\omega_i^s$) and the even $h$ condition, when $\omega = 1$, and between $\omega = 1$ and the dominant condition ($\omega_i^d$):

$$\omega_{i,d} = \begin{cases} 
\omega_{i,d}^s + m_{i,d}(1 - \omega_{i,d}^s), & m_{i,d} < 1 \\
1, & m_{i,d} = 1 \\
1 + \left(\frac{m_{i,d} - 1}{n - 1}\right)(\omega_{i,d}^p - 1), & m_{i,d} > 1
\end{cases}$$

(3.17)

$$m_{i,d} = \frac{nh_{i,d}}{\sum_{i=1}^{n} h_{i,d}}$$

where $m$ is a species canopy dominance factor based on $h$ and $n$ is the total number of species. The derivative of Eq. 3.17 is discontinuous when $m_{i,d} = 1$ (i.e. $\omega$ has an “elbow”),
except in particular conditions. The $F_{i,d}$ can now be calculated with Eq. 3.14. The code used to implement this method and the figures in this article is presented in the Appendix.

3.3. Methods Evaluation and Intercomparison

3.3.1. Comparison of sub-daily and daily light interception methods

I compared the sub-daily calculation integrated over the daytime using a sun zenith angle angular step of $5^\circ$ ($\Delta\psi = 5^\circ$) with the daily Cycles method for a canopy with two species. I made calculations for both clear sky and overcast conditions and for a maximum solar zenith angle ($\psi$) that varied from $0^\circ$ to $65^\circ$ to represent different latitudes and seasons. When the results were integrated over a full day, changes in the outcome were minor and I show only results for clear sky conditions and solar zenith angle $\psi = 0^\circ$. An atmospheric transmittance of 0.75 was assumed to represent clear skies. The two species in the canopy have contrasting leaf geometries. Based on the ellipsoidal model the geometries were assumed to be $\chi_1 = 0.5$ (erectophile canopy, mean angle inclination $\sim 70^\circ$) and $\chi_2 = 2$ (planophile canopy, mean angle inclination $\sim 40^\circ$) for species 1 and 2 respectively, because they were comparable with $k$ of 0.4 and 0.6 which are approximately the extremes of $k$ (solar) reported for plant canopies (Kemanian et al., 2004; Yunusa et al., 1993).

The results of the comparison, shown in Figure 3.1, indicate that when the canopies of the two species have each 50% of $L_T$ ($L_i = 0.5L_T$), the two methods yield remarkably similar outcomes. Similar conclusions were presented by Fuchs et al. (1976) for mono-specific canopies, stating that the average light interception over a whole day calculated with a detailed model is approximated well with an exponential model of daily
time step. The same concept seems to apply to a canopy mixture when $L$ is distributed uniformly throughout the canopy $h$. It is interesting to note that including the daily dynamics of the sun path does not change the results significantly, even for days in late fall, winter, or early spring, when the sun does not reach low zenith angles (maximum sun elevation is low); the main reason is that most of the light load is within the hours around solar noon.

The most remarkable difference among the methods is at $L_T < 2$. Under such conditions the disadvantage of more vertical canopies at capturing light is less marked in the daily method. In other words, a simple method may overestimate light interception of the more erectophile species in a mixture. This would be the only situation in which a detailed sub-daily model or an adjustment of $k$ based on the sub-daily results would be helpful, but even in that case, I surmise that this adjustment would be irrelevant compared with the uncertainty from variations of other attributes in field conditions such as clumps of species rather than homogenous mixtures, or a stratified distribution of $L$ for a given species (Faurie et al., 1996). Thus, the daily calculation in Cycles provides a good trade-off between complexity of calculations and accuracy of results for canopies that have leaves distributed uniformly throughout $h$. 
3.3.2. Comparison of the Cycles method and Wallace method

Three scenarios were created with two species with equal $h$ (since $h$ is the same for all species, the Cycles method is the same than the APSIM method). The scenarios differed in the $k$ and the fraction of $L_T$ of each species. The scenarios are shown in Figure 3.2: Panel A shows a comparison when $L_T$ is allocated equally to each species (50/50), and panels B and C show a comparison when $L_T$ is allocated disproportionately to the more erectophile or more planophile species (80/20 and 20/80, respectively).

For $L_T < 3$ the methods yield almost identical results. As $L_T$ increases, the Cycles method gives more advantage to the species with higher $k$ than the Wallace method does. If I were to interpret $k$ as a “correction” that changes $L$ to an effective canopy of
horizontal leaf elements that are randomly distributed, then the Wallace method has the intrinsic assumption that as $L_T$ increases, the leaves of the erectophile species are distributed preferentially towards the top of the canopy compared with the planophile species. In other words, in the Wallace method the distribution of leaves with $h$ as $L$ increases is implicitly assumed to vary rather than being uniform. This property of the Wallace method expresses both when $L_T$ is equally distributed among the two species (Figure 3.2 A) and when it is not (Figure 3.2 B and C). It is important to understand that while at low $L_T$ these two render similar results, at higher $L_T$ differences exist and should be considered in interpreting model outcomes. Overall, there seems to be no advantage of the Wallace method over the Cycles (or APSIM) method when $h$ is the same for two species.
Figure 3.2. Comparison of light interception between the Cycles method and the Wallace method for two species that have the same height, different canopy architecture (erectophile $k = 0.4$ and planophile $k = 0.6$) and share equal (Panel A) or unequal (Panels B and C) proportions of the total leaf area index.
3.3.3. *Cycles method for two and three species with different heights*

To illustrate the impact of variation in $h$ between species using the Cycles method I created six scenarios with two species with the same $k$ (0.5) or different $k$ (0.4 or 0.6), same or different $L_T$ fraction (50/50, 20/80 or 80/20), and $h$ (0.5 or 1 m) in each species (Figure 3.3). As expected, the higher $L_T$ and therefore the higher the competition level, the higher the proportion of the light that is intercepted by the species with higher $k$ or $h$. Competition becomes significant in species with the same $k$ and $L$, but different $h$, when $L_T \approx 2$ (Figure 3.3A). For instance, a short but planophile species ($k = 0.6, h = 0.5$) can have the same light interception than a taller but erectophile species ($k = 0.4, h = 1$) (Figure 3.3C). In addition, changes in $L_T$ allocation ($L\%$) contribute to differences in light interception between species. For example, a species with $k = 0.6$, $L\% = 80$ and $h = 1$ has about a seven-fold higher light interception than a species with $k = 0.4$, $L\% = 20$ and $h = 0.5$ (Figure 3.3F).
Figure 3.3. Cycles method comparison for two species (sp1 and sp2) with different heights \((h)\) and leaf area index allocation \((L\%)\).

To illustrate the differences between a method that considers \(h\) (Cycles) and one that does not do so (APSIM), I created a three species canopy scenario. In Figure 3.4 I plot the light interception for three species in the canopy with the same \(k\), \(L\) fraction, and different \(h_i\) for the Cycles method; APSIM method used the same \(h\) for all species. At \(L_T = 3\), APSIM light interception was 38\% higher, 8\% higher and 27\% lower than the Cycles method for the species with \(h_1 = 1\), \(h_2 = 2\) and \(h_3 = 4\), respectively. The difference in light interception between methods accentuates as \(L_T\) increases because the upper portion of the canopy intercepts most of the light (Figure 3.4, inset). Thus, the magnitude of the error introduced when not accounting for differences in \(h\) among species increases as \(L_T\) increases.
Figure 3.4. Comparison of the light interception in a three-species canopy calculated with the Cycles method and the APSIM method for species with the same height \( h \), a third of the total leaf area allocated to each species, and a common extinction coefficient \( k = 0.6 \).

Thus, the Cycles light interception method seems to reproduce well the competitive trade-offs between two species in terms of leaf area density, species height, and leaf angle distribution. This method allows the modeling of the competitive behavior of plant species with tall and planophile canopies like sunflower \((Helianthus annuus\ L.)\) and weeds like velvetleaf \((Abutilon theophrasti\ Medic.)\); an example with a synthetic wheat – pea \((Triticum aestivum – Pisum sativum)\) mixture is discussed below.

### 3.4. Discussion

The Cycles method has significant advantages over the other evaluated methods, since it accounts for differences in \( h \), \( k \), and \( L \) for an unlimited number of species. However, it carries the same limitations as detailed models regarding the representation of the optical properties of canopies. Chiefly, leaves in canopies are assumed to be randomly
distributed. This assumption rarely holds, at least in row crops, except when the canopy fully covers the ground. Plants, and therefore their leaves, are clumped to the planting row rather than being randomly distributed. In addition the leaves are clumped to a plant axis (crown or stem). These two factors tend to reduce light interception, but compensation may occur as leaves colonize aerial spaces as to minimize mutual shading. Once the canopy covers the inter-row space, the assumption of random distribution is satisfactory, but before that condition, which occurs usually for $L_T < 3$, or in widely spaced rows, corrections might be needed (Timlin et al., 2014).

There is limited data to compare modeled and measured light interception in multispecies canopies. Lantinga et al. (1999) measured light interception in a grass/clover mixture and some results are reproduced in Table 3.1 along with calculations using the Cycles method. The comparison is not strictly independent, for the $k$ values presented by these authors were derived from measurements. However, the comparison indicates that the Cycles method reproduces well the attenuation of light and its allocation to species with different $k$ when the distribution of leaves along the canopy height does not differ significantly among species.
Table 3.1. Comparison of Lantinga et al. 1999 and the Cycles method photosynthetically active light (PAR) interception of two ryegrass (*Lolium perenne* L.) - clover (*Trifolium repens* L.) mixtures. The total leaf area index for both mixtures was 5.8 m$^2$ m$^{-2}$ and was distributed between ryegrass and clover as 36%/64% for mixture 1, and 32%/68% for mixture 2.

<table>
<thead>
<tr>
<th></th>
<th>Mixture 1</th>
<th>Mixture 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Perennial ryegrass</td>
<td></td>
</tr>
<tr>
<td>Extinction coefficient for PAR</td>
<td>0.5</td>
<td>1.00</td>
</tr>
<tr>
<td>Leaf area index</td>
<td>2.1</td>
<td>3.7</td>
</tr>
<tr>
<td>PAR interception from Lantinga et al. 1999</td>
<td>0.19</td>
<td>0.81</td>
</tr>
<tr>
<td>PAR interception with Cycles</td>
<td>0.22</td>
<td>0.77</td>
</tr>
</tbody>
</table>

As opposed to the simplified approach of Cycles, functional-structural models describe canopies in three dimensions and account for the geometry of different organs (Vos et al., 2010). These models permit a better description of the light micro-environment within a canopy which can be critical to model the conditions experienced not only by the leaves but by insects and microorganisms throughout the day.

Nonetheless, this advantage can be less relevant on a daily time step. To gain a sense of the degree with which a simplified model can represent the light interception by each species in canopy compared with a functional-structural model on a daily basis, I used Cycles to simulate the results obtained with a functional-structural plant model of a pea-wheat mixture (Barillot et al., 2014). These authors reported the total light interception of these two species as their $L$ and $h$ varied with time. Using their data, I used an optimization algorithm to find a unique $k$ for each species that would minimize the error between the reported and Cycles-calculated light interception. The estimated $k$ for pea and wheat were 0.54 and 0.51 respectively. Interestingly, and despite its simplicity, Cycles was able to replicate most of the variation of the light interception of each species and the total interception for the mixture (Figure 3.5). This suggest that the Cycles
method can account for a large fraction of the variability caused by $L$ and $h$ on a daily basis, provided that the $k$ of each species are known and that the properties of the canopy do not depart severely from the method assumptions: random distribution of the leaves vertically and horizontally.

Figure 3.5. Light interception with Cycles with data presented by Barillot et al. (2014) for a pea and wheat canopy mixture in which height and leaf area index of each species varied with the time progression.

Departures from these assumptions may require adjustments to the method. For instance, the canopy can be easily layered to accommodate a non-uniform distribution of leaves with $h$. However, other situations may require simulating hedgerows (Campbell and van Evert, 1994) or ultimately scaling down to functional-structural models. For
example it is plausible that in mixtures of weeds and crops the weeds occupy the inter-row space so that crop and weed leaves are not uniformly mixed. The same consideration applies to intercropping systems. In multi-species pastures, each species can be in patches so that the mixture resembles a mosaic of mono-specific patches. An extreme case is that of woodlands with trees and grasses which are considered discontinuous canopies (McMurtrie and Wolf, 1983). A similar argument can be made for mature forests because given the size of the tree crowns, the leaves are grouped by species rather than intermixed in the canopy, at least in the upper part of the canopy. The method presented here does not apply to such conditions, which require modeling each component separately as a mono-specific canopy with a variable degree of mutual shading depending on plant architecture, solar zenith angle, and atmospheric turbidity.

### 3.5. Conclusion

Calculations of light interception by individual species in multi-species canopies produce similar results if calculations are made with a detailed sub-daily time step method that represents the leaf angle distribution of a canopy, or at daily time step with big-leaf models that use an effective daily $k$ to represent canopy architecture.

The Cycles method presented here to simulate light interception in a multi-species canopy has the advantages of earlier process-based methods (Wallace and APSIM) and incorporates the ability to simulate any number of species with different heights. Together with a model for root water and nutrient uptake, this method allows for the
simulation of competition in multi-species canopies in comprehensive agroecosystem simulation models.
Chapter 4. Do crop models differ in their simulation of water uptake? A comparison of APSIM, CropSyst, DSSAT, EPIC, SWAP and WOFOST

ABSTRACT

Root water uptake is an essential component of crop models since it affects plant growth and, through its effect on the soil water balance, multiple soil and nutrient cycling processes. Several water uptake methods exist; however, differences among them have not been evaluated. I compared the water uptake methods implemented in six crop models: APSIM, CropSyst, DSSAT, EPIC, SWAP and WOFOST. These methods range from simple empiric approaches (WOFOST) to mechanistic approaches based on the water potential gradient and root distribution in the soil-plant system (CropSyst). I compared the six models’ water uptake algorithms in scenarios with different evaporative demand, soil texture, and water distribution with depth in the soil profile. The main difference among methods derived from the degree to which each model enabled the use of water in the subsoil (below ~0.5 m). In a rooted, 1-m deep silt loam soil in which the root density decreased geometrically with depth, and which was subjected to an evaporative demand of 5 mm d\(^{-1}\) for 60 days, APSIM, EPIC, DSSAT and SWAP transpired about 83% of the total plant available water while SWAP and CropSyst transpired 70% and 60% of it, respectively. When methods were compared with initially dry bottom layers, cumulative transpiration became similar for all methods, while the opposite initial condition exacerbated differences. All methods, except CropSyst, increased transpiration as the evaporative demand rose to relatively high rates (10 mm d\(^{-1}\)) because they lack a feedback mechanism that reduces transpiration when the demand
exceeds the plant’s ability to conduct water. CropSyst, DSSAT, EPIC and SWAP developed a “drying front”, as usually observed in field conditions, while APSIM and WOFOST showed a more uniform water depletion with depth in the soil profile. In conclusion, the models differ meaningfully in their simulation of water uptake, and careful consideration of these differences is needed to properly use and interpret the outcome of model simulations.

**Highlights**
- Simulation of water uptake differed among crop models
- The differences derive from the degree to which each method uses subsoil water
- CropSyst, DSSAT, EPIC and SWAP developed a drying front; APSIM and WOFOST did not
- Only CropSyst simulated water stress under high transpiration in moist soils

**Key words:** crop modeling, transpiration, water uptake, water use, water stress, agriculture

**4.1. Introduction**

Root water uptake affects plant growth and development and, indirectly through its control over soil moisture, multiple soil and landscape processes such as nutrient cycling and transport. For this reason, it is critically important in agroecosystems model to get the water uptake “right”. Simulation models quantitatively encapsulate the putative controls of soil, plant and the atmosphere on water uptake. Nonetheless, no single agreed-
upon model to simulate water uptake exists in the academic community, and different approaches are used in comprehensive models as described in several reviews (Ahuja et al., 2008; Cardon and Letey, 1992; de Willigen et al., 2012; Green et al., 2006; Hopmans and Bristow, 2002; Mathur and Rao, 1999). Few studies have evaluated systematically the effects of the differences among models on the progression of the drying front and cumulative water uptake (van den Berg et al., 2002). This lack of comparative studies casts uncertainty on the interpretation of outputs from different models when simulating distinct climate or management scenarios.

There is renewed interest in exploring differences among models, as exemplified by the Agricultural Model Improvement and Intercomparison Project (AgMIP, Rosenzweig et al., 2013). Model intercomparison studies typically compare the overall results of several crop growth models in relation to experimental data and focus on a limited set of measured variables (Doussan et al., 2006; Jara and Stöckle, 1999). Understanding the differences among simulation models through this approach is challenging because modeling systems are made up of many interconnected modules that affect the overall results (Asseng et al., 2013; Bassu et al., 2014). To understand differences in simulation approaches for a particular process, it seems more effective to extract the relevant algorithms and compare them directly while keeping other system attributes constant. This allows isolating the model properties or scenarios that explain the differences among models.

I have applied this approach to compare the water uptake methods used in six prominent crop models. The models selected for this comparison were: 1) Agricultural Production Systems Simulator (APSIM) (Keating et al., 2003), 2) CropSyst (Stöckle et
al., 2003), 3) Decision Support System for Agrotechnology Transfer (DSSAT) (Boote et al., 2008; Jones et al., 2003), 4) Erosion Productivity Impact Calculator (EPIC) (Williams, 1990; Williams et al., 2014), 5) Soil, Water, Atmosphere Plant (SWAP) model (Dam, 2000; Feddes et al., 1978) and 6) World Food Studies (WOFOST) model (Supit et al., 1994). These models were selected because they represent a wide range of variation in the representation of water uptake, from relatively simple methods based on soil water content and considering roots only as present or absent (WOFOST), to methods based on the gradient of water potential and conductances to water flow in the soil-plant system (CropSyst). To compare the methods, the water uptake algorithms were extracted from the models’ code or manuals and re-coded in Python (Python Software Foundation).

I compared the models across scenarios that differed with respect to fundamental controls on plant water uptake: soil texture, evaporative demand, and water distribution in the soil profile. Water distribution scenarios differed with respect to initial plant available water (PAW), initial water distribution through the soil profile, and arrangement of the soil profile in layers of uniform thickness or of geometrically increasing thickness with depth. Soils were dried without recharge. I used differences in the patterns of water use and in the derived shape of the drying front progression to understand the fundamental differences among water uptake methods.

To facilitate the presentation, the results and discussion section answer a series of questions: (1) Does soil texture affect the differences in water uptake among methods? (2) Do methods vary in their response to increasing transpiration demand? (3) How do the methods respond to different initial soil moisture and its distribution in the soil profile? (4) Does the soil layering method (uniform or geometrically increasing layer
thickness with depth) affect the results within and among methods? Before proceeding with the evaluation of methods and these questions, a brief description of the main properties of each method is presented.

4.2. Description of Water Uptake Methods

The methods reviewed in this study use algorithms that operate at the macroscopic scale: water uptake is simply a sink term in the water balance of a soil layer. The level of detail or the simplifications made to represent this sink term vary among models and can be classified in two types. In one type, water uptake is a function of the difference in water potentials \( \psi \) (J kg\(^{-1}\)) and the conductances \( C \) (kg s m\(^{-4}\)) between adjacent components in the soil-plant system. In this type, accurately representing water flow (kg s\(^{-1}\) m\(^{-2}\)) depends on appropriate calculation of gradients and conductances. The other type represents the system functionally through the water content \( \theta \) (m\(^3\) m\(^{-3}\)), the root depth \( z_r \) (m), and root density \( \rho_r \) (m m\(^{-3}\)) or root fraction \( f_r \) (unitless) of the system. In this type, there is no calculation of a gradient but an empirical relationship between \( \theta \) and the ability of the plant to uptake water which is modulated with varying degree in each model by the \( \rho_r \). Of the methods used for this study CropSyst and SWAP belong to the first type and the other methods belong generally to the second type. Both types require some empirical data for model parameterization. Table 4.1 describes the variables used in all algorithms and Table 4.2 summarizes the thresholds that drive each water uptake method. The equations used to compute water uptake for each method follow. As I shall see, these methods produce different emergent properties.
<table>
<thead>
<tr>
<th>Variable</th>
<th>Model</th>
<th>Explanation</th>
<th>unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>( c_2 )</td>
<td>D</td>
<td>Constant</td>
<td>--</td>
</tr>
<tr>
<td>( c_{pit} )</td>
<td>C</td>
<td>Total plant water conductance</td>
<td>kg s m(^{-4})</td>
</tr>
<tr>
<td>( ET_o )</td>
<td>All models</td>
<td>Daily evapotranspiration demand</td>
<td>mm d(^{-1})</td>
</tr>
<tr>
<td>( f_i )</td>
<td>All models</td>
<td>Radiation interception fraction</td>
<td>--</td>
</tr>
<tr>
<td>( f_e )</td>
<td>C, S</td>
<td>Root fraction</td>
<td>--</td>
</tr>
<tr>
<td>( f_{rt} )</td>
<td>--</td>
<td>Fraction of thermal time progression</td>
<td>--</td>
</tr>
<tr>
<td>( i )</td>
<td>All models</td>
<td>Julian calendar day</td>
<td>d</td>
</tr>
<tr>
<td>( j )</td>
<td>All models</td>
<td>Soil layer</td>
<td>--</td>
</tr>
<tr>
<td>( kl )</td>
<td>A</td>
<td>Soil-root water availability parameter</td>
<td>--</td>
</tr>
<tr>
<td>( p )</td>
<td>W</td>
<td>Soil water depletion factor</td>
<td>--</td>
</tr>
<tr>
<td>( R_{LI} )</td>
<td>--</td>
<td>Rate of change of fractional light interception</td>
<td>--</td>
</tr>
<tr>
<td>( R_{rd} )</td>
<td>--</td>
<td>Rate of change of fractional root depth</td>
<td>--</td>
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<tr>
<td>( s_1, s_2 )</td>
<td>E</td>
<td>Water stress logistic curve parameters</td>
<td>--</td>
</tr>
<tr>
<td>( T )</td>
<td>All models</td>
<td>Daily transpiration demand</td>
<td>mm d(^{-1})</td>
</tr>
<tr>
<td>( T_a )</td>
<td>All models</td>
<td>Actual transpiration</td>
<td>mm d(^{-1})</td>
</tr>
<tr>
<td>( T_p )</td>
<td>All models</td>
<td>Potential transpiration</td>
<td>mm d(^{-1})</td>
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<tr>
<td>( T_h )</td>
<td>F</td>
<td>High transpiration demand</td>
<td>mm d(^{-1})</td>
</tr>
<tr>
<td>( T_l )</td>
<td>S</td>
<td>Low transpiration demand</td>
<td>mm d(^{-1})</td>
</tr>
<tr>
<td>( T_x )</td>
<td>C</td>
<td>Maximum water uptake in canopy</td>
<td>mm d(^{-1})</td>
</tr>
<tr>
<td>( U )</td>
<td>All models</td>
<td>Total water uptake</td>
<td>mm d(^{-1})</td>
</tr>
<tr>
<td>( U_x )</td>
<td>D</td>
<td>Maximum water uptake</td>
<td>mm d(^{-1})</td>
</tr>
<tr>
<td>( u_k )</td>
<td>E</td>
<td>Previous layer water uptake sum</td>
<td>mm</td>
</tr>
<tr>
<td>( U_{rl} )</td>
<td>D</td>
<td>Water uptake per unit of root length</td>
<td>m(^3) m(^{-1}) d(^{-1})</td>
</tr>
<tr>
<td>( U_{dx} )</td>
<td>D</td>
<td>Maximum water uptake per unit of root length</td>
<td>cm(^3) cm(^{-1})</td>
</tr>
<tr>
<td>( WA )</td>
<td>A, E</td>
<td>Water available</td>
<td>mm</td>
</tr>
<tr>
<td>( WT )</td>
<td>E</td>
<td>Soil limitation of water uptake of each layer</td>
<td>--</td>
</tr>
<tr>
<td>( WS )</td>
<td>A</td>
<td>Water supply</td>
<td>mm d(^{-1})</td>
</tr>
<tr>
<td>( z )</td>
<td>All models</td>
<td>Cumulative soil depth</td>
<td>m</td>
</tr>
<tr>
<td>( z_r )</td>
<td>All models</td>
<td>Root zone depth</td>
<td>m</td>
</tr>
<tr>
<td>( \gamma )</td>
<td>E</td>
<td>Exponent of parameter of soil limitation of water uptake</td>
<td>--</td>
</tr>
<tr>
<td>( \Delta z )</td>
<td>A, E</td>
<td>Soil layer thickness</td>
<td>m</td>
</tr>
<tr>
<td>( \zeta_s )</td>
<td>E, S</td>
<td>Stress factor</td>
<td>--</td>
</tr>
<tr>
<td>( \eta )</td>
<td>E</td>
<td>Compensation factor</td>
<td>--</td>
</tr>
<tr>
<td>( \theta )</td>
<td>A, D, E, W</td>
<td>Water content</td>
<td>m(^3) m(^{-3})</td>
</tr>
<tr>
<td>( \theta_c )</td>
<td>W</td>
<td>Critical water content</td>
<td>m(^3) m(^{-3})</td>
</tr>
<tr>
<td>( \theta_{fc} )</td>
<td>E, W</td>
<td>Water content at field capacity</td>
<td>m(^3) m(^{-3})</td>
</tr>
<tr>
<td>( \theta_{mp} )</td>
<td>A, D, E, W</td>
<td>Water content at permanent wilting point</td>
<td>m(^3) m(^{-3})</td>
</tr>
<tr>
<td>( \Lambda )</td>
<td>E</td>
<td>Water uptake distribution</td>
<td>--</td>
</tr>
</tbody>
</table>
Table 4.2 Root, soil and water stress thresholds driving each water uptake method.

<table>
<thead>
<tr>
<th>Model</th>
<th>Plant properties</th>
<th>Soil properties</th>
<th>Combined plant-soil properties</th>
<th>Soil water status</th>
</tr>
</thead>
<tbody>
<tr>
<td>APSIM</td>
<td>$f_i$</td>
<td>$\theta_{pwp}$, $\theta_{ic}$</td>
<td>$kl$</td>
<td>$\theta$</td>
</tr>
<tr>
<td>CropSyst</td>
<td>$f_i$, $\Psi_L$, $\Psi_{Lsc}$, $\Psi_{Lpwp}$, $C_{pl}$, $T_x$</td>
<td>$\psi_{Spwp}$, $\psi_{Sc}$</td>
<td>--</td>
<td>$\psi_S$</td>
</tr>
<tr>
<td>DSSAT</td>
<td>$f_i$, $\rho_r$, $U_{dx}$</td>
<td>$\theta_{pwp}$, $\theta_{ic}$</td>
<td>$s_1$, $s_2$, $\eta$, $\Lambda$</td>
<td>$\theta$</td>
</tr>
<tr>
<td>EPIC</td>
<td>$f_i$</td>
<td>$\theta_{pwp}$, $\theta_{ic}$</td>
<td>$\zeta_s$</td>
<td>$\psi_S$</td>
</tr>
<tr>
<td>SWAP</td>
<td>$f_i$, $f_r$</td>
<td>$\psi_{Spwp}$, $\psi_{Sc}$, $\psi_{Sat}$</td>
<td>$\zeta_s$</td>
<td>$\psi_S$</td>
</tr>
<tr>
<td>WOFOST</td>
<td>$f_i$</td>
<td>$\theta_{pwp}$, $\theta_{ic}$</td>
<td>$\theta_t$</td>
<td>$\theta$</td>
</tr>
</tbody>
</table>

2.1. Description of water uptake methods

**APSIM**

In APSIM, water uptake ($U$, mm d$^{-1}$) is determined from daily transpiration demand ($T$, mm d$^{-1}$), soil water available ($WA$, mm d$^{-1}$), and water supply ($WS$, mm d$^{-1}$) for each $i^{th}$ day and soil layer $j^{th}$ as:

$$T_i = f_i ET_{o,i}$$  \hspace{1cm} (4.1)
\[ WA_{i,j} = (\theta_{i,j} - \theta_{pwp,j})z_j \rho_w \]

\[ WS_{i,j} = WA_{i,j} kl_j \]

\[ U_{i,j} = \begin{cases} 
0, & T_i = 0 \\
T_i \frac{WS_{i,j}}{\sum_{j=1}^{n} WS_{i,j}}, & T_i < \sum_{j=1}^{n} WS_{i,j} \\
WS_{i,j}, & T_i > \sum_{j=1}^{n} WS_{i,j} 
\end{cases} \]

\[ U_i = \sum_{j=1}^{j=n} U_{i,j} \]

where \( f \) is the intercepted solar radiation fraction, \( ET_o \) is the daily reference evapotranspiration (mm d\(^{-1}\)), \( \theta_{pwp} \) is the water content at permanent wilting point (m\(^3\) m\(^{-3}\)), \( z \) is the soil layer depth (m), \( \rho_w \) is the water density (kg m\(^{-3}\)) and \( kl \) is the rate of water extraction, an empirical soil-root factor for the fraction of available water that can be supplied to the plant in each soil layer with roots. Conceptually, once a soil layer is colonized, it will supply water at a decaying rate, which represents a maximum supply determined by root density and the resistance to water flow (Monteith, 1986; Passioura, 1983) and the change in soil water capacitance \( (d \theta/d\psi) \) as \( \theta \) decreases. The challenge is to determine the right \( kl \) progression with depth for a given crop and soil, and to represent
variations in $kl$ due to dynamic stresses. To the best of our knowledge, $kl$ is not affected by abiotic or biotic stresses in APSIM.

**CropSyst**

The CropSyst water uptake method is a simplification of the water uptake algorithm described by Campbell (1985). Water flux in the soil-plant system depends on the difference in water potential between the soil ($\psi_s$, J kg$^{-1}$) and the leaf ($\psi_L$, J kg$^{-1}$), and a total soil-root-shoot conductance which is dominated by the plant ($C_{plt}$, kg s m$^{-4}$). The plant conductance is calculated by inverting the transpiration equation using a maximum expected transpiration ($T_x$, kg H$_2$O m$^{-2}$ d$^{-1}$), the soil water potential at field capacity ($\psi_{Sfc}$, J kg$^{-1}$) and the leaf water potential at the onset of stomatal closure ($\psi_{Lsc}$, J kg$^{-1}$):

$$ C_{plt} = \frac{-T_x}{\psi_{Sfc} - \psi_{Lsc}} $$

(4.6)

To compute transpiration, both $\psi_s$ and $\psi_L$ need to be computed. The average soil water potential ($\overline{\psi}_s$, J kg$^{-1}$) is calculated based on a representative root length fraction for each soil layer ($f_{r, j}$):

$$ \overline{\psi}_s = \sum_{j=1}^{n} f_{r,j} \psi_{s,i,j} $$

(4.7)

The root fraction can be conceived as a representative root “activity” of each layer. In practice it can be adjusted dynamically depending on the actual root density and $\psi_s$.

Parameterization with CropSyst shows that and approximately linear decrease in $f_r$ works best in soils with no limitations to root exploration (Jara and Stöckle, 1999), even if the
actual \( f_r \) is strongly exponential with most of the roots in the soil surface. This reflects plant control of root conductance, likely through aquaporins (Moshelion et al., 2014; Tyerman et al., 1999) and root hair growth (Mackay and Barber, 1985). For simplicity, it has been assumed in this study that \( f_r \) is that calculated based on \( \rho_r \) and \( \Delta z \) (i.e. the root fraction).

The \( \psi_L \) is calculated using \( T, C_{plt} \) and \( \bar{\psi}_S \). If \( \psi_L \) is lower than \( \psi_{Lsc} \), \( \psi_L \) is recalculated (Eq. 4.8) to represent stomata closure and the corresponding reduction in \( T \) (Eq. 4.9). If \( \psi_L \) falls below that of permanent wilting point (\( \psi_{Lpwp} \)), then \( U_a = 0 \):

\[
\psi_{L_i} = \max \left\{ \min \left( \bar{\psi}_{S_i} \right), \frac{T_i}{C_{plt}}, \frac{C_{plt}\bar{\psi}_{S_i}(\psi_{Lsc} - \psi_{Lpwp}) + \psi_{Lpwp}T_i}{C_{plt}(\psi_{Lsc} - \psi_{Lpwp}) + T_i}, \psi_{Lpwp} \right\} \tag{4.8}
\]

Finally, \( U_i \) and \( U_j \) are calculated using \( \psi_s \) and \( \psi_L \), \( C_{plt} \) and \( T_i \):

\[
U_i = \begin{cases} 
T_i, & \psi_{L_i} > \psi_{Lsc} \\
T_i \frac{\psi_{L_i} - \psi_{Lpwp}}{\psi_{Lsc} - \psi_{Lpwp}}, & \psi_{L_i} < \psi_{Lsc} \\
0, & \psi_{L_i} \leq \psi_{Lpwp} 
\end{cases} \tag{4.9}
\]

\[
U_{i,j} = C_{plt}(\psi_{S_{i,j}} - \psi_L) \frac{U_i}{T_i} \tag{4.10}
\]

Choudhury and Idso (1985) presents a non-linear response of stomatal conductance to \( \psi_L \), but a linearized version as used in CropSyst (Jara and Stöckle, 1999) works as well and makes computations simpler. For this research \( T_x = 10 \text{ mm d}^{-1}, \psi_{Lsc} = -1,100 \text{ J kg}^{-1} \) and \( \psi_{Lpwp} = -2,000 \text{ J kg}^{-1} \). This set of equations has an implicit feedback mechanism that
reduces \( T \) if the demand is higher than \( T_x \) even in moist soils. Because it is assumed that \( C_{\text{plt}} \) remains constant, a high demand causes \( \psi_L \) to fall below \( \psi_{LSC} \), reducing \( T \) (Eq. 4.9).

**DSSAT**

In DSSAT, root water uptake is calculated in two steps. First, water uptake per unit of root length is computed in each soil layer (\( U_{rl,i}, \text{ m}^3 \text{ m}^{-1} \text{ d}^{-1} \)) as an exponential function that depends on: (i) eight parameters provided in the algorithm and determined empirically (Eq. 4.11 and 4.11), (ii) the root length density (\( \rho_{rl}, \text{ m} \text{ m}^{-3} \)), and (iii) the \( \theta \) for each soil layer:

\[
U_{rl,i} = \begin{cases} 
\min \left( 0.0013 \frac{e^{(\min(c_2 j, \theta_{i,j} - \theta_{pwp,j}) \times 40)}}{7.01 - \ln \left( \rho_{rl,i}/10^4 \right)}, U_{rl,x} \right), & \theta_{pwp,j} > \theta_{pwp,j} \\
0, & \theta_{i,j} \leq \theta_{pwp,j}
\end{cases}
\]

with the maximum water uptake per unit of root length \( U_{rl,x} = 0.03 \text{ cm}^3 \text{ water cm}^{-1} \text{ root} \).

Second, the maximum potential water uptake for the profile (\( U_x, \text{ mm d}^{-1} \)) is obtained by multiplying \( U_{rl} \) times \( \rho_{rl} \) for each layer and summing over the soil profile:

\[
U_{x,i} = \sum_{j=1}^{n} U_{rl,i} z_j \rho_{rl,i,j}
\]

The actual plant water uptake is the minimum between \( T \) and \( U_x \):

\[
U_i = \min(T_i, U_{x,i})
\]

If \( T < U_x \) then \( U_i \) is adjusted by the ratio \( T/U_x \).
These equations state that the moister the soil and the higher the $\rho_{rl}$ the higher the uptake per unit root length. It can be shown that the $U_{rl}$ decreases when the ratio $\theta/\theta_{pwp}$ falls below about 1.3 or 1.5. For example, for a soil with $\theta_{pwp} = 0.1 \text{ m}^3 \text{ m}^{-3}$, the reduction becomes noticeable at $\theta = 0.15 \text{ m}^3 \text{ m}^{-3}$; if $\theta_{fc} = 0.3 \text{ m}^3 \text{ m}^{-3}$ (a loam soil) this means that stress is triggered by PAW $\sim 25\%$. The proposed response to $\rho_{rl}$ is counterintuitive, for the equation indicates that the uptake per unit length increases as $\rho_{rl}$ increases, a curious proposition. Regardless, this effect is minor in most conditions: to reduce $U_{rl}$ by 50\%, the root density needs to be reduced by a factor of 500. Thus, these equations essentially reduce the water uptake when $\theta$ is in the vicinity of 25\% of PAW, with some adjustments by $\rho_{rl}$. As seen below, this is the typical threshold of most empirical models.

**EPIC**

The EPIC water uptake method has a fully functional form and requires no input of root morphological parameters. It simply assumes that water is used preferentially from the top layers, and the potential water depletion rate decreases exponentially downward. However, an allowance is made for the user to determine how much the lower layers can compensate for the water that is not obtained from drier upper layers. The formulation uses a water uptake exponential distribution parameter ($A = 10$), $T$, $\theta$, $z$, soil layer thickness ($\Delta z$, m), the water uptake from previous soil layers ($u_k$, mm d$^{-1}$), a compensation factor ($\eta$) and an a stress factor ($\zeta$):
where $\theta_{fc}$ is the water content at field capacity (m$^3$ m$^{-3}$), $s_1$ and $s_2$ are parameters of a logistic curve (9 and 0.005, respectively), and $w$ represents the soil limitation of water uptake of each layer. The limitation by water stress slowly decreases the ability of the soil to fulfill the demand when the soil approaches $\theta_{pwp}$. While the shape is user-defined, earlier versions of EPIC used 25% PAW as a typical threshold. This limitation is unrelated to the evaporative demand. The $\eta$ used in this study was 0.5 (J.R. Williams, personal communication). Thus, once the top layer cannot supply all the water potentially demanded from that layer, the deficit can progressively be taken from lower layers. This can almost compensate for the deficit, but never completely, unless $\eta=1$. In EPIC, abiotic stresses can limit uptake in each soil layer (e.g. temperature or pH); for simplicity I assumed that the soil does not impose any stress other than water stress.

**SWAP**

The SWAP water uptake method is based on $T$, $f_c$ and an empirical stress factor relationship $\zeta$: 

\[
U_{l,j} = \min \left( \frac{T_l}{1 - e^{-A}} \left( 1 - e^{-\Delta z_j} \right) - \eta \sum_{k=1}^{j-1} u_k - \left( 1 - \eta \right) U_{l,j-1}, \left( \theta_{l,j} - \theta_{pwp} \right) \frac{\Delta z_j}{\rho_w} \right) \zeta_{e,l,j} \tag{4.14}
\]

\[
\zeta_{e,l,j} = 1 - \frac{w_{l,j}}{w_{l,j} + e^{s_1 - s_2 w_{l,j}}} \tag{4.15}
\]

\[
w_{l,j} = \max(5, 10^{\gamma_{l,j}}) \tag{4.16}
\]

\[
\gamma_{l,j} = 3.18 - 1.66 \times \log \left( \frac{\theta_{l,j} - \theta_{pwp,j}}{\theta_{fc_i} - \theta_{pwp,j}} \right)
\]
The stress factor $\zeta_s$ is calculated based on a soil water potential near saturation ($\psi_{Sat} = -10 \text{ J kg}^{-1}$) and a lower water potential threshold that depends on the transpiration demand. When the demand is low ($T_l = 1 \text{ mm d}^{-1}$) then the threshold ($\psi_{Sl}$) is $\psi_{Sl} = -500 \text{ J kg}^{-1}$, and when it is high ($T_h = 5 \text{ mm d}^{-1}$) then the threshold is $\psi_{Sh} = -400 \text{ J kg}^{-1}$ (Diamantopoulou et al., 2011).

$$U_{i,j} = \zeta_{s_{i,j}} f_{r_{i,j}} T_{i}$$

(4.17)

$$\zeta_{s_{i,j}} = \begin{cases} 
\frac{\psi_{si,j} - \psi_{spwp}}{\psi_{spwp} - \psi_{spwp}}, & \psi_{spwp} < \psi_{si,j} < \psi_{sat} \\
1, & \psi_{sat} \leq \psi_{si,j} \leq \psi_{fc} \\
\frac{\psi_{si,j} - \psi_{sat}}{\psi_{fc} - \psi_{sat}}, & \psi_{fc} < \psi_{si,j} < \psi_{sat} \\
0, & \psi_{si,j} \leq \psi_{spwp} \\
0, & \psi_{si,j} \geq \psi_{sat} 
\end{cases}$$

(4.18)

$$\psi_{si} = \begin{cases} 
\psi_{sl}, & T_i < T_l \\
\psi_{sh}, & T_i > T_h \\
\psi_{sh} + \frac{T_h - T_i}{T_h - T_l} (\psi_{sl} - \psi_{sh}), & T_i \leq T_l \leq T_h 
\end{cases}$$

(4.19)

where $\psi_{spwp}$ is the soil water potential at permanent wilting point. In this model, the water supply from each layer depends on $f_r$ and $\psi_s$, which bears some resemblance to CropSyst. Unlike the latter no plant resistance to water flow is included in the water flow path, but must be empirically included in $f_r$. As explained below, this feature has been considered in later iterations of this model (de Jong van Lier et al. (2008), but the term plant conductance or resistance has not been explicitly included.
WOFOST

The WOFOST water uptake method, the simplest of all methods, calculates water uptake as a function of the rooting depth and the water available in that rooting depth with disregard to the soil water distribution with depth. Water uptake depends linearly on the integrated $\theta$ and threshold water content ($\theta_t$, m$^3$m$^{-3}$):

$$ U_i = \min \left(T_i, T_i \frac{\theta_i - \theta_{pwp}}{\theta_t - \theta_{pwp}} \right) $$

(4.20)

$$ \theta_t = (1 - p_i)(\theta_{fc} - \theta_{pwp}) + \theta_{pwp} $$

(4.21)

where $p$ is the soil water depletion factor calculated as 0.56, 0.43, 0.34 for $T = 5, 7.5, 10$ mm d$^{-1}$ respectively, and drought category 4 as suggested for grain crops as explained in (Supit et al., 1994). In this model, the higher the demand, the higher the $\theta_t$ at which transpiration is limited by $\theta$.

In summary, the methods described differ in the number of parameters they require. The APSIM method has a number of parameters proportional to the number of soil layers, although if $k_l$ is assumed constant for some layers or varies in a simple pattern the number of parameters can be just one or two (Table 4.3). CropSyst has the lowest number of required input parameters ($\psi_{LSC}$, $\psi_{Lpwp}$, and $T_x$) but requires an estimate of $f_r$. DSSAT, EPIC and WOFOST have eight required parameters: DSSAT to calculate $c_2$, $U_{nl}$ and $U_{rh}$; EPIC to calculate $A$, $\zeta$ and $\gamma$, and WOFOST to state the drought category and to calculate $p$. SWAP requires four parameters ($\psi_{SHR}$, $\psi_{SHW}$, $T_i$, $T_h$). Thus, simple methods such
as WOFOST do not necessarily require fewer parameters than more mechanistic methods.

Table 4.3. Parameters (parms) in the compared water uptake methods. The integer \( j \) is the number of soil layers.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameters</th>
<th>Equation</th>
<th>No. of parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>APSIM</td>
<td>( k \times j )</td>
<td>Eq. 4.3</td>
<td>( j )</td>
</tr>
<tr>
<td>CropSyst</td>
<td>( \psi_{LSG}, \psi_{Lpwp}, T_x )</td>
<td>Eq. 4.5, 4.8</td>
<td>3</td>
</tr>
<tr>
<td>DSSAT</td>
<td>( c_2 ) (4 parms), ( U_{HI} ) (3 parms), ( U_{RI} )</td>
<td>Eq. 4.10, 4.11</td>
<td>8</td>
</tr>
<tr>
<td>EPIC</td>
<td>( \eta, \Lambda, \zeta(s_1, s_2), \gamma ) (4 parms)</td>
<td>Eq. 4.14, 4.15, 4.16</td>
<td>8</td>
</tr>
<tr>
<td>SWAP</td>
<td>( \psi_{Stb}, \psi_{Shb}, T_h )</td>
<td>Eq. 4.18</td>
<td>4</td>
</tr>
<tr>
<td>WOFOST</td>
<td>Drought category, ( p ) (7 parms)</td>
<td>Eq. 4.22</td>
<td>8</td>
</tr>
</tbody>
</table>

**4.3. Comparison of water uptake methods**

I compared the water uptake methods using two complementary approaches, one with a dynamic canopy and root system establishment and one with a static canopy and root system. For the dynamic approach, I created scenarios in which a virtual crop was allowed to develop a canopy starting from zero light interception and, simultaneously, develop a root system. Both the canopy cover (\( f \)) and the root depth (\( z_r \)) and root density (\( \rho_{rd} \)) progression were affixed and independent of the water uptake method under consideration. To facilitate the comparison, water stress (i.e., when water uptake was less than the transpiration demand) did not affect canopy or root growth. For the static approach, I compared the methods using an established root system and canopy, or in other words, assuming that the comparison starts with a canopy intercepting all of the incoming light and with the root system fully established.

The scenarios consider variations in soil texture (four textures, Table 4.4), soil layering (layers of uniform or geometrically increasing thickness with depth, Table 4.5), transpiration demand, and initial \( \theta \). The length of the simulation was 100 and 60 days for
the dynamic and static simulation scenarios, respectively. The soil was 1-m deep, divided in 10 layers with uniform texture, and the rooting system had a maximum depth of 1 m. Pedotransfer functions using soil texture were used to calculate bulk density, $\theta_{fc}$, $\psi_{fc}$, $\theta_{pwp}$, $\psi_{pwp}$, saturated $\theta$ and $\psi$, and the air entry $\psi_S$ (Table 4.3) (Campbell, 1985; Saxton and Rawls, 2006). To feed the pedotransfer functions, organic matter was assumed to be 50% of that at saturation as defined by Hassink and Whitmore (1997).

Table 4.4. Soil texture, water content and plant available water (PAW) for the scenarios evaluated. The PAW is the difference between field capacity ($\theta_{fc}$) and wilting point ($\theta_{pwp}$) water content expressed in mm of water.

<table>
<thead>
<tr>
<th>Soil</th>
<th>Clay content</th>
<th>Sand content</th>
<th>$\theta_{fc}$</th>
<th>$\theta_{pwp}$</th>
<th>PAW</th>
</tr>
</thead>
<tbody>
<tr>
<td>Silt loam</td>
<td>5</td>
<td>20</td>
<td>0.28</td>
<td>0.05</td>
<td>230</td>
</tr>
<tr>
<td>Silty clay</td>
<td>45</td>
<td>10</td>
<td>0.40</td>
<td>0.27</td>
<td>130</td>
</tr>
<tr>
<td>Sandy clay</td>
<td>40</td>
<td>53</td>
<td>0.35</td>
<td>0.25</td>
<td>100</td>
</tr>
<tr>
<td>Loamy sand</td>
<td>7</td>
<td>81</td>
<td>0.13</td>
<td>0.06</td>
<td>70</td>
</tr>
</tbody>
</table>

For the dynamic approach, the variables $f$, $z_r$ and $\rho_{rt}$ changed continuously. I assumed a constant daily $ET_0$ of 5 mm d$^{-1}$ with no soil water evaporation. The rate of change of fractional light interception ($R_{LI}$) and that of root depth ($R_{rd}$) were calculated for each day using a method analogous to that in Olson et al. (2012):

$$R_{rd} = \frac{15e^{6-15f_{tt}}}{(1 + e^{6-15f_{tt}})^2}$$  \hspace{1cm} (4.22)

$$R_{LI} = \frac{20e^{6-20f_{tt}} - 15e^{15f_{tt}-16}}{(1 + e^{6-20f_{tt}} + e^{15f_{tt}-16})^2}$$  \hspace{1cm} (4.23)

where $f_{tt}$ is the fractional thermal time progression and was assumed to increase by 0.01 per day. The equation for $R_{LI}$ is the derivative of a double exponential that represents a
sharp increase in \( f_i \) early in the season, stabilizes at a maximum value (=1) and decreases when the cumulative fractional thermal time approaches 1 (senescence). The \( z_r \) and \( f_i \) were determined each day accumulating their respective rates of change. In addition, it was assumed that \( z_r = 0.2 \) m at leaf emergence. Figure 4.1 shows a graphical representation of \( f_i \) and \( z_r \) progression.

![Graphical representation of \( f_i \) and \( z_r \) progression.](image)

**Figure 4.1 Root depth and fractional solar radiation interception progression.**

To convert \( z_r \) to \( \rho_{rl} \) and APSIM’s \( kl \), I used a standard \( \rho_{rl-std} \) and \( kl_{std} \) for a root system fully established, by assuming that when fully rooted, the top layer of 0.1 m had an average \( \rho_{rl-std} \) of 50,000 m m\(^{-3}\) as reported for maize (Zea mays L.) in Jara and Stöckle (1999), and that it decays by a third every 0.1 m (Table 4.4). For soil layers where the rooting front did not reach the layer lower bound, \( \rho_{rl} \) and \( kl \) were adjusted proportionally to the progression depth in that layer. APSIM’s \( kl \) decreased linearly from 0.085 to 0.055 (Hammer et al., 2009; Meinke et al., 1993).

For the static approach, and to compare soil textural and transpiration demand effects, I created six scenarios that combine four soil textures (Table 4.3) and three \( T \)
demands (5, 7.5 and 10 mm d\(^{-1}\)). The soil was initialized with \( \theta = \theta_{fc} \) throughout the soil profile. The transpiration demand was set to values representing average, high, and very high transpiration depending on the scenario of interest. I used 5 mm d\(^{-1}\) as the average because this is the reference \( ET_o \) (Allen et al., 1998) for a day with 25 °C maximum and 10 °C minimum temperature, 25 MJ m\(^{-2}\) solar radiation, 1.25 kPa of vapor pressure, and 2.5 m s\(^{-1}\) wind speed in summer in mid latitudes. Higher radiation, drier air, or higher wind speed can increase the evaporative demand. During the simulations the soil was allowed to dry due to transpiration assuming no evaporation from the soil surface and no recharge.
Table 4.5 Layer thickness distribution, root density and fraction, and APSIM’s $kl$ used in simulations for a soil with constant or geometric variation of layer thickness. The total root length is ca. 15 km m$^{-2}$.

<table>
<thead>
<tr>
<th>Soil layer</th>
<th>Layer thickness m</th>
<th>Root density m$^{-3}$</th>
<th>Root fraction --</th>
<th>$kl$ --</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Constant</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.1</td>
<td>50,000</td>
<td>0.336</td>
<td>0.085</td>
</tr>
<tr>
<td>2</td>
<td>0.1</td>
<td>33,500</td>
<td>0.225</td>
<td>0.081</td>
</tr>
<tr>
<td>3</td>
<td>0.1</td>
<td>22,445</td>
<td>0.151</td>
<td>0.077</td>
</tr>
<tr>
<td>4</td>
<td>0.1</td>
<td>15,038</td>
<td>0.101</td>
<td>0.073</td>
</tr>
<tr>
<td>5</td>
<td>0.1</td>
<td>10,076</td>
<td>0.068</td>
<td>0.069</td>
</tr>
<tr>
<td>6</td>
<td>0.1</td>
<td>6,751</td>
<td>0.045</td>
<td>0.066</td>
</tr>
<tr>
<td>7</td>
<td>0.1</td>
<td>4,523</td>
<td>0.030</td>
<td>0.062</td>
</tr>
<tr>
<td>8</td>
<td>0.1</td>
<td>3,030</td>
<td>0.020</td>
<td>0.058</td>
</tr>
<tr>
<td>9</td>
<td>0.1</td>
<td>2,030</td>
<td>0.014</td>
<td>0.054</td>
</tr>
<tr>
<td>10</td>
<td>0.1</td>
<td>1,360</td>
<td>0.009</td>
<td>0.050</td>
</tr>
<tr>
<td><strong>Geometric</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.009</td>
<td>60,156</td>
<td>0.036</td>
<td>0.087</td>
</tr>
<tr>
<td>2</td>
<td>0.013</td>
<td>57,531</td>
<td>0.051</td>
<td>0.086</td>
</tr>
<tr>
<td>3</td>
<td>0.020</td>
<td>53,811</td>
<td>0.072</td>
<td>0.086</td>
</tr>
<tr>
<td>4</td>
<td>0.030</td>
<td>48,682</td>
<td>0.098</td>
<td>0.085</td>
</tr>
<tr>
<td>5</td>
<td>0.045</td>
<td>41,900</td>
<td>0.126</td>
<td>0.083</td>
</tr>
<tr>
<td>6</td>
<td>0.067</td>
<td>33,477</td>
<td>0.151</td>
<td>0.081</td>
</tr>
<tr>
<td>7</td>
<td>0.101</td>
<td>23,938</td>
<td>0.162</td>
<td>0.078</td>
</tr>
<tr>
<td>8</td>
<td>0.151</td>
<td>14,515</td>
<td>0.147</td>
<td>0.073</td>
</tr>
<tr>
<td>9</td>
<td>0.226</td>
<td>6,898</td>
<td>0.105</td>
<td>0.066</td>
</tr>
<tr>
<td>10</td>
<td>0.339</td>
<td>2,291</td>
<td>0.052</td>
<td>0.055</td>
</tr>
</tbody>
</table>

To analyze the impact of the initial $\theta$ in both magnitude and distribution throughout the profile, I compared seven new scenarios: (1) 100% PAW uniform, (2) 50% PAW uniform, (3) 100% PAW in top half and 50% PAW in bottom half, (4) 50% PAW in top half and 100% PAW in bottom half, (5) alternating 100% and 50% PAW, (6) 100 to 10% PAW gradually decreasing from top to bottom, and (7) 10% to 100% PAW gradually increasing from top to bottom of the soil profile. The $T$ demand was 5 mm d$^{-1}$ and the soil of silt loam texture. WOFOST was not evaluated in these scenarios since it does not account for soil layering.
In summary, eight parameters, the ratio of actual to potential transpiration \((T_a/T_p)\), cumulative \(T_a\), and \(\theta\) and \(\psi\) in the soil profile, variable \(T_p\), variable soil texture, variable PAW, and variable soil layering, were used to evaluate differences in the water uptake methods (Table 4.5). These eight parameters are critical inputs to other modules in the corresponding simulation models, including crop growth.

Table 4.6. Parameters used to evaluate the dynamic and static simulation approaches.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Dynamic</th>
<th>Static</th>
</tr>
</thead>
<tbody>
<tr>
<td>(T_a/T_p)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Cumulative (T_a)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>(\theta) in soil profile</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>(\psi) in soil profile</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Variable (T_p)</td>
<td>--</td>
<td>x</td>
</tr>
<tr>
<td>Variable soil texture</td>
<td>--</td>
<td>x</td>
</tr>
<tr>
<td>Variable plant available water</td>
<td>--</td>
<td>x</td>
</tr>
<tr>
<td>Variable soil layering</td>
<td>--</td>
<td>x</td>
</tr>
</tbody>
</table>

\(T_a\): actual transpiration; \(T_p\): potential transpiration; \(\theta\): soil water content; \(\psi\): soil water potential.

### 4.4. Results and discussion

#### 4.4.1. Dynamic simulation of water uptake

Since the dynamic simulation was initialized with the soil at \(\theta_{fc}\), cumulative \(T\) increased steadily and without limitation while the canopy was expanding (Figure 4.1); by day 40 the roots reached the bottom of soil profile. Once the total extraction amounted to 60 - 100 mm, the methods differed in the degree with which a drying soil limited water uptake (Figure 4.2). Three methods, CropSyst, WOFOST and especially SWAP, reduce transpiration relatively early in comparison with the other methods. APSIM and DSSAT
had an intermediate onset of water stress, approximately 10 days or nearly 50 mm after SWAP. EPIC used most of the available water before transpiration was limited. Once a drying soil limited transpiration, the $T_a/T_p$ ratio decayed with a concave shape in all methods except EPIC (Figure 4.2).

Figure 4.2. Cumulative actual transpiration ($T_a$, mm d$^{-1}$) and $T_a$ divided by potential transpiration ($T_p$, mm d$^{-1}$) for the APSIM, CropSyst, DSSAT, EPIC, SWAP and WOFOST water uptake methods.

Water uptake differed in the dynamic simulation due to substantive variation in the explicit or implicit mechanisms of water uptake embedded in each algorithm, and in some cases due to the parameterization. These differences produce striking divergence in the shape of the water extraction front with time. The $\theta$ (Figure 4.3) and $\psi$ (Figure 4.4) across the soil profile differed between the water uptake methods with two major groupings. CropSyst, EPIC and SWAP, and to a lesser extent DSSAT, developed a
drying front; APSIM and WOFOST had a more uniform water uptake across the profile.
This development of a drying front is expected in a method like CropSyst, because of the
way in which root density affects the root conductance: when the water potential is
uniform, more water will be taken from the layer with more root length. Similar
considerations apply to SWAP. In a method like EPIC, the drying front reflects the
concept of the functional algorithm that takes up water from top to bottom with an
implicit and fixed consideration of root geometry. In DSSAT the water use also has a
semblance of a drying front (Figure 4.4), albeit less marked than that in CropSyst or
SWAP. This is because the wetter the soil and the higher the root density, the higher the
water uptake from that layer, thus replicating through different means a similar water use
pattern than that of CropSyst, SWAP, or EPIC. In CropSyst and SWAP, the sharpness of
the drying front can be easily manipulated by changing the distribution with depth of \( f_r \).
In DSSAT similarly, it can be modified by changing the root density. In EPIC, it can be
manipulated by changing the parameter \( \Lambda \) (a lower value makes the drying front less
prominent).

In the case of APSIM, a drying front can be represented if \( k/l \) is progressively
reduced with depth. That is not, however, what emerges from published studies (Hammer
et al., 2009; Meinke et al., 1993; Robertson et al., 1993). Nonetheless, a drying front can
also be generated by a slower progression of the rooting front caused either by the
genotype or by restrictive soil layers.

The WOFOST method, though extremely simple, seems to represent the
cumulative water use reasonably well; the pattern of cumulative water use cannot be
easily distinguished from other methods (Figure 4.2). The distribution of the water use
with depth is, however, clearly unrealistic, being this observation more evident when looking at the water potential profile (Figure 4.4). The distribution of water affects many processes in the soil from water infiltration and redistribution through the profile to heat transfer and nutrient cycling. Therefore, this method can only be applicable, with reservations, to relatively simple water balances.

Figure 4.3. Water content in the soil profile in three different days for the APSIM, CropSyst, DSSAT, EPIC, SWAP and WOFOST water uptake methods.
4.4.2. Static simulations of water uptake

Does soil texture affect the differences in water uptake among methods?

The answer is yes. Clearly, the higher the soil PAW due to increasing silt or clay, the longer the plant canopies can transpire at a rate set by the atmospheric demand. When the soils have low storage, all methods show a sharp decrease in transpiration and are difficult to distinguish from each other (Fig 5, loamy sand soil). In the silt loam soil, the results can be grouped as follows: CropSyst and SWAP exhibited more conservative water use, and DSSAT, EPIC, APSIM and WOFOST exhibited less conservative water use.
use. This is, however, somewhat dependent on the parameterization: a more linear $f_r$
distribution with depth will approach CropSyst and SWAP to the other methods. At the end of the simulation, the group of less conserving methods used about 83\% of the total PAW (i.e., 191 mm) regardless of the transpiration demand. In the other group, CropSyst transpired about 60\% and SWAP transpired 70\% of total PAW (Figure 4.6).

**Do methods vary in their response to increasing transpiration demand?**

Methods differed sharply in their response to an increased demand. Most methods except CropSyst increased transpiration as the demand increased. In CropSyst, increasing the transpiration demand causes a low $\psi_L$, which in turn causes stomatal closure and, therefore, reduction in transpiration (Campbell, 1985; Jara and Stöckle, 1999). Thus, this algorithm has a built-in feedback system to show stress under high transpiration demand, even if the soil is relatively moist. Other methods tend to simply supply more water as the demand increases for there is no mechanistic feedback to reduce transpiration. In SWAP the threshold $\psi_s$ that triggers a reduction in transpiration does increase the higher the evaporative demand, thus incorporating an interaction of soil water status and evaporative demand.

In the silt loam and loamy sand soils, the EPIC method had the highest water uptake, using most of the water available in a layer and then moving to the next layer until depleting most of the water in the soil profile. This study did not include the water uptake reduction factors for different soil layers that are implemented in the EPIC model since they cannot be separated from the model (for example, the effect of suboptimal soil
temperature). Including these factors would reduce and never increase the overall water uptake, perhaps bringing the cumulative water uptake in line with the other methods.

The APSIM method was the first method to start reducing $T$ in the loamy sand soil even though it continued transpiring until consuming 93% of PAW. Interestingly, the DSSAT water uptake method behaved similarly to CropSyst and SWAP in loamy sand, sandy clay, and silty clay soils, but it became less conservative in the silt loam soil when PAW is larger. This similar behavior between CropSyst and DSSAT was also observed by Jara and Stöckle (1999) when they compared daily water uptake methods with measurements of sap flow and $\theta$ for maize. The water uptake in DSSAT is related to $\theta_{pwp}$, but neither to the pore space between $\theta_{pwp}$ and $\theta_{fc}$ nor directly to $\psi_s$ as in other methods. As a result, the methods are likely to perform differently across scenarios and will not produce a consistent ranking of water uptake.
Figure 4.5. Simulated transpiration ($T_a$, mm d$^{-1}$) divided by potential transpiration ($T_p$, mm d$^{-1}$) for six water uptake methods and six scenarios with different soil texture and transpiration demand.
Figure 4.6. Cumulative actual transpiration ($T_a$, mm) for six water uptake methods and six scenarios with different soil and potential transpiration ($T_p$, mm$^{-1}$).

To evaluate water depletion through the soil profile, $\theta$ (Figure 4.7) and $\psi$ (Figure 4.8) were plotted for 15, 30 and 45 days in a silt loam soil with a $T_d$ demand of 5 mm d$^{-1}$. CropSyst, DSSAT, EPIC and SWAP generated $\theta$ and $\psi_S$ curves that were similar to typical measured soil water depletion profiles (Cabelguenne and Debaeke, 1998; Campbell and Norman, 1998; Jara and Stöckle, 1999). CropSyst and SWAP had similar and slower rates of water depletion in the soil profile than the other methods, while DSSAT and EPIC were faster. CropSyst was the only method to allow the soil to go beyond the putative $\psi_{Spwp}$ in the top layers, resembling observations by Cabelguenne and
Debaeke (1998). This feature is hard to detect in simulations that include soil evaporation for this process can easily drive $\theta$ well below $\theta_{pwp}$.

APSIM’s almost-uniform water depletion across the soil profile reflects $k'$’s linear distribution. Fitting $k'$ with experimental data would change the shape of APSIM’s $\theta$ and $\psi$ in the soil profile, but when using $k'$ as prescribed in Hammer et al. (2009) the water extraction in this 1-m soil is rather uniform. The WOFOST method shows a uniform $\theta$ throughout the profile since it does not account for soil layering, treating the soil as a single large 1-m thick layer. As expressed before, it is somewhat surprising that such a simple method provides realistic cumulative $T$ estimates despite the direct summation through the soil profile to calculate the $\theta$. 
Figure 4.7. Water content profile at three different simulation days in a silt loam soil with 5 mm day$^{-1}$ transpiration demand using six water uptake methods.
Figure 4.8. Water potential profile at three different simulation days in a silt loam soil with 5 mm day\textsuperscript{-1} transpiration demand using six water uptake methods.

How do the methods respond to different initial soil moisture and its distribution in the soil profile?

Varying the amount and distribution with depth of available water revealed with more clarity the different mechanisms that are, wittingly or not, embedded in each method. Fixing the transpiration demand to 5 mm d\textsuperscript{-1}, the less conservative methods (APSIM, DSSAT and EPIC) removed more water from lower soil layers than CropSyst and SWAP (Figure 4.9 and Figure 4.10). The water uptake of all methods was similar in scenario 6 where PAW decreases downward from 100\% to 10\%; however if the PAW...
distribution is inverted going up with depth from 10% to 100%, APSIM, DSSAT and EPIC transpired cumulatively and on average for the three methods 104 mm while CropSyst and SWAP transpired 69 mm. While these behaviors can be manipulated through parameterization, the differences reflect intrinsic differences among methods.

Changing the initial PAW of soil layers from 100% to 50% (from scenario 1 to 2 in Figure 4.9) reduced total cumulative $T$ from 144 mm to 83 mm for CropSyst and SWAP (43% reduction), and from 190 mm to 95 mm for APSIM, DSSAT and EPIC (50% reduction). Thus, the less conservative methods follow exactly the average reduction in PAW of the soil, with lesser influence in water uptake of the soil water distribution. Similar results occurred when using a sandy clay soil texture.

Thus the methods differed more the drier the upper soil layers, and render similar results when the lower layers were dry (Figure 4.10 SC6). This is an important result. Based on these simulations, and for example, during the progression of a dry spell, the water use simulated by these models will produce different water uptake (and growth and nutrient uptake) of crops, and also differences in landscape level hydrology. How do different species react to a soil that has dry upper layers and moist subsoil? Observations in the field indicate that dry upper soil layers limit overall water uptake, even when the moist subsoil is colonized with roots (Skinner, 2008). This behavior is closer to that simulated by CropSyst and SWAP.
Figure 4.9. Simulated transpiration ($T_a$, mm d$^{-1}$) divided by potential transpiration ($T_p$, mm d$^{-1}$) for a silt loam soil with varying initial soil moisture distribution with depth. Soil layers have equal thickness. The initial moisture patterns are based on different plant available water (PAW). Five water uptake methods, APSIM, CropSyst, DSSAT, EPIC and SWAP, were compared in this simulation.
Figure 4.10. Cumulative transpiration ($T_a$, mm) simulated for a silt loam soil with varying initial soil moisture distribution with depth. Soil layers have equal thickness. The initial moisture patterns are based on different plant available water (PAW). Five water uptake methods, APSIM, CropSyst, DSSAT, EPIC, and SWAP were compared in these simulations.

**Does the layering method change the results within and among methods?**

Changing the layers from uniform thickness to a geometrically distributed thickness, and weighting properly the root density (or any depth-dependent property), only caused differences in water uptake in DSSAT (only the silt loam soil) and EPIC, with the latter being more sensitive to soil layering. The other methods were remarkably robust, yielding similar results regardless of the layering scheme or soil texture (Figure 4.11). That result was difficult to predict in the case of DSSAT and reflects the threshold response to moisture (Eq. 4.10). Below a given moisture threshold, the uptake per unit
root length ($U_r$) decreases, thus creating “steps” in the simulated $T_a/T_p$ once that moisture threshold is reached. The somewhat discontinuous change in the rate of water use (Figure 4.5) reflects sharp transitions between limited and unlimited water use in a layer that, interestingly, are smoothed out and difficult to detect if only considering the cumulative transpiration.

In the case of EPIC, the compensation among layers, while qualitatively logical, shows limitations. This method seeks to make up the water deficit in the top layers from the layers below. But if the top layers are relatively thin, the limitation emerges quickly, and the ability to compensate is limited by a fixed factor ($\eta$) that bounds the volume that can be compensated. If $\eta$ varied with depth, for example, $\eta = 1$ for top layers and $\eta = 0.5$ for the bottom layers, this effect might be ameliorated, but at a cost of increasing the number of parameters and without a clear guidance about what parameterization is reasonable. Thus, when using EPIC, the method must be calibrated and used with a relatively stable soil layering criterion.
Figure 4.11. Simulated transpiration ($T_a$, mm d$^{-1}$) divided by potential transpiration ($T_p$, mm d$^{-1}$) for sandy clay and silt loam soil textures with equally and geometrically distributed soil layers thickness. Five water uptake methods, APSIM, CropSyst, DSSAT, EPIC and SWAP, were included in this comparison. Initial plant available water (PAW) was 100%.

4.5. General discussion

The methods presented have in common the goal of representing a reduction in water uptake as the soil dries. The methods, however, vary widely in the approach to accomplish that goal. The more process-based methods (CropSyst and to some extent SWAP) rely on the water potential gradient as the driver for liquid water flow in the soil-plant system. Because the soil capacitance decreases drastically as the soil dries, the water uptake become limited by both the supply and by a gradual reduction of the stomatal conductance. This result is not fortuitous: as suggested by Campbell and Norman (1998), the plant hydraulic conductance is adapted to match the evaporative demand to the soil supply. In these methods, the reduction in water uptake as the soil dries is an emergent and not an imposed property of the system. Even if the $\psi_L$ is allowed
to decrease beyond $\psi_{Lwp}$, water uptake will be limited by the reduction in soil water capacitance.

The approach in APSIM is commendable for its simplicity, but requires knowledge of a combined plant-soil property: the $k_l$ constant per layer. This problem is analogous to defining the correct $f_r$ for CropSyst: as stated before, this variable, more than representing $f_r$, represents the effective root activity.

In methods such as DSSAT, EPIC, and WOFOST, in which the surrogate “driving force” for liquid water flow is the soil water concentration $\theta$, the threshold that starts limiting water uptake is imposed through equations that translate empirical knowledge. The results are reasonable because there is a theoretical basis to expect decreasing water uptake as soil moisture reaches 25 to 35% PAW (e.g. Campbell and Norman, 1998) and because the threshold is higher when the transpiration demand is higher. Nonetheless, the response to a drying soil emerges naturally in APSIM, CropSyst and SWAP, and the response to high transpiration demand is also accommodated as an emergent and not an imposed property.

There is an interaction of water uptake method and water distribution in the soil profile. One of the main differences between conservative and less conservative water uptake methods is the use of water from lower layers of the soil profile. These differences are important and may lead to over-estimation of water uptake in less conservative methods, or conversely, an underestimation of water uptake in the more conservative methods. These risks are highest when the top soil layer is dry and the bottom layer is moist. Eitzinger et al. (2004) compared the DSSAT, SWAP, and WOFOST water uptake methods with experimental data and reported an overall tendency of the methods to over-
estimate water uptake in silty loam, sandy loam, and silt clay loam soils, which is consistent with the DSSAT and WOFOST results presented here and different from the SWAP results. This may be due to a different parameterization of the SWAP method.

Simulating water uptake and therefore the soil moisture profile accurately is critical to represent properly the feedbacks among temperature, water use, and carbon and nutrient cycling not only in agricultural systems but in all terrestrial ecosystems. Soil moisture controls microbial activity (Manzoni and Katul, 2014) and therefore nutrient cycling. A drier soil, particularly, a drier topsoil where most of the soil organic carbon resides, can reduce soil respiration and conversely, underestimate soil organic carbon losses. For example, overestimating $\theta$ can accelerate decomposition of organic matter and denitrification (Davidson et al., 2000). Thermal properties also change with $\theta$, thus controlling the temperature of the soil profile (Campbell, 1985). The soil temperature not only controls microbial respiration but also determines the rate of root activity (Boone et al., 1998).

All water uptake methods but EPIC and DSSAT provided stable simulations when the soil layer thickness was held constant (0.1 m) or varied geometrically with depth. The robust response of APSIM, CropSyst, SWAP and WOFOST is encouraging since soil databases provide information usually on a horizon by horizon basis. This information is translated into model input files in which the soil layers are split based on needs or practical considerations. Most users expect that methods are relatively insensitive to this layering, as long as the integrated properties are conserved. With EPIC in particular, it seems clear that users need to calibrate and use the model with a stable soil layering.
To consider mechanisms that compensate for the reduced water uptake from dry layers with increased water uptake from wet layers, de Jong van Lier et al. (2008) modified the SWAP water uptake method. They used Gardner (1958) matric flux potential as a driving force for the flux and included the resistance to water flow from the bulk soil to the edge of the root. This approach is also suggested in Campbell (1985) using directly $d\psi/dz$ as the driving force; the matrix flux potential is recommended to handle infiltration.

However, de Jong van Lier et al. (2008) neglected the plant conductance to water flow, which leads to overestimation of water uptake (Faria et al., 2010). This was corrected with the introduction of an empirical correction factor of 0.05 that multiplies the flow estimated with their method, and implicitly assuming then than the soil has a conductance ~20 times higher than the root. In doing so, the authors are unwittingly acknowledging the control of the root conductance over the water flow.

Comparatively, the method described by Campbell (1985) and used in CropSyst makes this assumption the core of the model, as the plant conductance is orders of magnitude lower than that of the soil in most conditions (Campbell, 1985). Jarvis (2011) also modified SWAP to include water redistribution, which produced a more uniform water content across the soil profile. This resulted in drying profiles similar to those generated with APSIM (Figure 4.3 and Figure 4.7), though the latter model does so with fewer parameters. SWAP is therefore a simplified version of Campbell’s (1985) method, and is better used assuming that $f$ can be adjusted empirically; the inclusion of the root conductance simply leads to Campbell’s (1985) method.

CropSyst and SWAP are relatively sensitive to the soil moisture distribution with depth, while the other methods are built so that compensation among layers operates
through averaging of the soil moisture in the profile (WOFOST), explicit compensation (EPIC), or implicit (emergent) compensation (DSSAT). The APSIM method allows for a relatively simple and straightforward calibration if a soil profile is allowed to dry without recharge so as to calculate the progression of the rooting front and the water extraction rate (Meinke et al., 1993). In practice, obtaining such parameters can be challenging.

I expect that over time the method to simulate water uptake will converge towards the water potential and conductance to flow framework as proposed by van den Honert (1948), refined by Campbell (1985), and with adaptations used in CropSyst and in other modeling exercises (Tardieu and Simonneau, 1998). This approach requires further work, particularly in terms of the variation of the plant conductance (e.g., Sperry et al., 1998).

As I have described, the response of stomatal conductance to $\psi_L$ lumps what in reality is the response to $\psi_L$ (or associated metabolic response) and $C_{pl}$. In other words: the method may predict total water uptake and water uptake per layer correctly, but may not necessarily simulate $\psi_L$ or $C_{pl}$ accurately. This is relevant only if these quantities need to be known with accuracy, which depends on the objectives of the modeling exercise. In the other methods, any improvement may come from more empiric adjustments that with skill may render useful simulations of water uptake, but that do not emerge from a fundamental application of the principles governing liquid water flow in the soil-plant system.

Given the differences among methods to simulate water uptake, it is reasonable to expect that these differences could be found for nearly every module in these comprehensive agroecosystem models, and these differences need to be understood. Kumudini et al. (2014) already documented major differences among methods to
simulate phenology in maize. This calls for caution when interpreting the results of model intercomparisons. While multi-model averaging seem to produce robust estimates of the observed grain yield for wheat (*Triticum aestivum* L.) (Asseng et al., 2013) and maize (Bassu et al. 2014) at a given location, when projecting new scenarios it is relevant to consider in the interpretation the different mechanisms and trajectories by which each model arrived to a given estimated yield, particularly when projecting these yield to climate or management scenarios that operate well beyond the calibration domain.

### 4.6. Conclusions

Existing methods to simulate water uptake in the models APSIM, CropSyst, EPIC, DSSAT, SWAP and WOFOST are different, but through parameterization may render similar results. The emergent or imposed properties of these methods varied among models, namely the onset of water stress under a constant transpiration demand, the distribution of the water uptake with depth, the response of water uptake to different distribution of soil moisture with depth, and their response to high transpiration demand. While CropSyst, EPIC, DSSAT and SWAP seemed to develop similar drying fronts, the temporal pattern of water use in EPIC differed from all other methods, showing a convex instead of a concave progression of the $T_s/T_p$ ratio as the soil dries. Only EPIC and DSSAT were strongly affected by changes in the thickness of soil layers with depth.

The systematic method comparison showed that while most methods allow representing similar patterns of cumulative water use, the patterns of soil drying and water use with depth vary among models. It is expected that these differences translate to different timings of water stress development in simulated crops, as well as to a number
of cascading effects on other components of the simulation (e.g. soil respiration and landscape level hydrology).

It seems that methods such as those used in CropSyst (Campbell, 1974; Campbell, 1985) have the properties required in a simulation model while maintaining simplicity. Other models that use more empiric approaches can produce similar patterns of water uptake, but at the cost of more input parameters and with the risk of misrepresenting water uptake in situations beyond the calibration domain. In that regard, APSIM might be the simplest method to calibrate while using a minimum of parameters.

The interpretation of the results of multi-model intercomparisons can be enriched by considering explicitly the differences among models, particularly when the simulations use environmental forcing outside the range use to develop or parameterize the models.
Chapter 5. Competition mechanisms for water uptake in drought conditions using maize and sunflower as model plants

5.1. Introduction

Water is typically a limiting resource in the soil, potentially leading to competition between plants sharing a finite soil volume. Water competition can arise between the same species (i.e., intra-specific) and different species (i.e., inter-specific) coexisting in a plant community. Quantification of water competition and water stress between species is challenging, yet understanding the underlying drivers of competition is essential to quantify and predict the hydrological balance of multi-species plant communities.

Many relationships have been proposed regarding water competition and water stress (Jones, 1988), however, there is no consensus of what the mechanisms and relationships are between soil, plant, and atmospheric impacts on water use (Moshelion et al., 2014). Furthermore, plant species differ in the relationship between water flux and leaf water potential. The most contrasting behaviors in this regard are the isohydric and anisohydric behavior (McDowell et al., 2008; Moshelion et al., 2014; Tardieu and Simonneau, 1998). An isohydric plant maintains a quasi-constant leaf water potential ($\psi_L$, J kg$^{-1}$) by regulating stomata opening during the day regardless of the soil water potential ($\psi_s$, J kg$^{-1}$), reducing both water loss and water uptake as soil dries, until the point that the plant is close to wilting. Conversely, in anisohydric plants the stomata remain open, so that $\psi_L$ follows the same descending shape as $\psi_s$ around the plant’s roots in a drying soil.
Maize (*Zea mays* L.) and sunflower (*Helianthus annuus* L.) are well known for their isohydric and anisohydric behaviors, respectively, and are often used as model plants to study plant water uptake (Asch et al., 2009; Tardieu and Simonneau, 1998; Turner et al., 1985).

Root water uptake and plant water stress have also been extensively studied using simulation models with different degrees of complexity and uncertainty (see Chapters 2 and 4, and Ahuja et al., 2008). However, water uptake and water stress experiments have not been designed to understand competition for water using an explicit modeling framework.

The goal of this study was to verify if a model algorithm based on electrical analog of water potentials, conductances and resistances that is commonly used to simulate water uptake (Campbell, 1985) correctly represents the patterns of water uptake in contrasting species when they are growing isolated or in competition. Preliminary field work growing maize and sunflower growing in the same drying soil volume showed that maize developed acute water stress symptoms and complete stomatal closure while sunflower continued transpiring. To understand these behaviors and to understand competition for water independent of competition for light, maize and sunflower were grown in controlled conditions in the greenhouse. The specific objectives were: (1) To verify the proposition of Campbell’s (1985) model that plants operate as if $\psi_s$ is some weighting of $\psi_s$ and root density per layer; (2) to the test that the resistance to water flow can be considered relatively constant, as assumed in Campbell (1985); and (3) to test if such model can reproduce the patterns of water use of these two species when growing isolated or in competition.
5.2. Materials and methods

5.2.1. Water uptake framework

The conceptual framework for this experimental and modeling study of water flux in the soil plant system was the electrical conductance-resistance analog originally proposed by van den Honert (1948), and followed by others (Bristow et al., 1984; Campbell, 1985; Cowan, 1965). Campbell’s (1985) notation was used to represent the systems as follows:

\[ T = \frac{\psi_s - \psi_L}{R_T} \]  

(5.1)

where \( T \) is the plant transpiration (kg m\(^{-2}\) s\(^{-1}\)), \( \psi_s \) is the soil water potential (J kg\(^{-1}\)), \( \psi_L \) is the leaf water potential, and \( R_T \) is plant and soil total resistance (m\(^4\) kg\(^{-1}\) s\(^{-1}\)).

5.2.2. Set up

The experimental approach was used to measure soil water potential \( \psi_s \) at different soil depths, the root density \( (\rho_r) \) at those depths, \( \psi_L \), and \( T \). Plants were grown in plant root observation chambers called rhizotrons, also known as Sachs boxes (James et al., 1985). The rhizotron design used in this study consists of a wooden box structure with a removable plywood sheet on one side that provides access to the soil-root systems of the plants and permits sampling at the end of the experiment (see Appendix). The rhizotron dimensions were 1.18 m in height, 0.6 m in width, and 0.019 m in thickness, with 0.012 m\(^3\) total soil volume. The soil used in the rhizotrons was a sandy loam top soil. The rhizotrons were filled with topsoil and manure (3/4 sandy loam from purchased soil, 1/4 cow manure on a mass basis) and irrigated to field capacity (see Appendix for
soil texture details). The rhizotron’s sides were covered with aluminum foil to minimize thermal exchange between the environment and the soil and roots. These rhizotrons were installed in a greenhouse with controlled environmental conditions on the Penn State University, University Park campus (40°47’N, 77°51’W). The greenhouse has controlled temperature, humidity, and supplemental light sources; air intakes and fans prevent carbon dioxide levels from dropping below atmospheric concentration due to plant photosynthesis and also mix the air in the greenhouse. The temperatures ranged from 16 °C to 35 °C, relative humidity ranged from 25% to 87%, and the maximum solar radiation was 625 W m² (Figure 5.1).
Figure 5.1. Weather data for the three blocks for the days of the year bracketing “water stress” (i.e., when irrigation was suspended). The variables are solar radiation in MJ m$^{-2}$ d$^{-1}$ (Solar rad), maximum (−) and minimum (—) temperature in °C (Temp), maximum (−) and minimum (—) relative humidity (RH), and maximum vapor pressure deficit in kPa (Max VPD).

The experiment had five treatments and three replicates. Each replicate had a single rhizotron that hosted one plant or two plants, depending on the treatment. Maize and sunflower were selected for this evaluation because of their well-defined isohydric and anisohydric behavior, distinct rooting systems and similar optimal temperature for growth. The treatments were: maize or sunflower growing alone (one plant per rhizotron), maize and sunflower in competition with plants of the same species (two plants per rhizotron), and maize and sunflower in competition with each other (two plants per rhizotron) (Figure 5.2). Treatments were randomly assigned to each of the 15 available rhizotrons. To accommodate the sampling the treatments were divided in three temporal blocks with respect to time: 1) maize, sunflower, maize/sunflower, sunflower/sunflower, maize/maize, maize/maize; 2) sunflower, sunflower, sunflower/sunflower, maize sunflower, maize/maize; and 3) sunflower/sunflower, maize/sunflower, maize sunflower, maize/maize; and 3) sunflower/sunflower, maize/sunflower, maize, maize (Table 5.1).

Figure 5.2. Set of five rhizotrons showing the five treatments for maize (M) and sunflower (S)
Table 5.1. Characteristics of the water stress developing period for each temporal block.

<table>
<thead>
<tr>
<th>Block</th>
<th>Rhizotron</th>
<th>Treatment $^1$</th>
<th>Growth without stress (days)</th>
<th>Growth with stress (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>9, 10, 12, 13, 14, 15</td>
<td>M, S, MS, SS, MM, MM</td>
<td>34</td>
<td>13</td>
</tr>
<tr>
<td>2</td>
<td>2, 4, 7, 8, 11</td>
<td>S, S, SS, MS, MM</td>
<td>43</td>
<td>11</td>
</tr>
<tr>
<td>3</td>
<td>1, 3, 5, 6</td>
<td>SS, MS, M, M</td>
<td>23</td>
<td>11</td>
</tr>
</tbody>
</table>

$^1$M – maize, S – sunflower, MM – two maize, SS – two sunflower, MS – maize and sunflower in rhizotron.

To introduce the effect of water competition, plants were allowed to advance progressively towards water deficit in the competing and non-competing treatments, keeping light and nutrient conditions at the same level. For that purpose, irrigation was stopped until the final sampling, which was executed when plants started showing mild signs of water stress such as leaf rolling in the early afternoon (Table 5.1). During the course of this phase, soil evaporation was minimized by covering the soil surface with polystyrene foam. The total water loss, assumed to be only $T$, was monitored by weighing the rhizotrons daily.

5.2.3. Measurements

For each rhizotron, daily $T$ was measured based on the soil water loss and leaf area measurements during the period without irrigation. Leaf area was estimated by multiplying length by width and a pre-determined correction factor of 0.70. To calculate daily $T$, it was assumed that there was no change in leaf area during this period. In the last day of sampling, leaf water potential $\psi_L$ was measured on excised leaves using a pressure pump (Model 615 Pressure Chamber Instrument, PMS Instrument Company, Albany, OR) (Begg and Turner, 1970). These $\psi_L$ measurements give estimates of water potentials in different parts of the soil-plant system, including soil, root, xylem and leaf (Table 5.2).
Leaf water potential of transpiring leaves was measured at noon in freely transpiring leaves, while xylem water potential ($\psi_x$) was measured also at noon but in leaves covered with aluminum foil to prevent transpiration. At dawn, when leaf and soil water potentials equilibrate (at least in theory), the water potential measured in an aluminum foil covered leaf is an estimate of and integrated soil water potential ($\psi_{s,\text{leaf}}$). A second estimate of soil water potential is measured by sampling the soil at different widths and depths and weighing each measurement using root density ($\psi_{s,\text{soil-root}}$). For this purpose, the soil was sampled in a grid at depths of 0.045 m, 0.101 m, 0.228 m, 0.51 m, 0.769 m and 1.09 m, and widths of 0.1 m, 0.209 m, 0.304 m, 0.406 m and 0.507 m. Root density $\rho_r$ was calculated by dividing the root intersection count for each soil depth by the rhizotron’s area (i.e., 0.0102 m$^2$). The $\rho_r$ used the same widths as soil sampling and depths of 0.03 m, 0.045 m, 0.068 m, 0.101 m, 0.152 m, 0.228 m, 0.342 m, 0.513 m, 0.769 m and 1.153 m. Plant total conductance ($g_T$, kg s m$^{-4}$) was calculated using equation (5.1). Treatments were analyzed statistically through analysis of variance (ANOVA) for the response variables $T$, $\psi_s$, $\psi_x$, $\psi_L$, $\rho_r$, $A_{\text{leaf}}$, and $g_T$ using SAS® Statistical Software (SAS Institute Inc., 2014).

Table 5.2. Water potential measurements’ location, time and equipment.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Symbol</th>
<th>Measurement location</th>
<th>Foil coverage</th>
<th>Time of measurement</th>
<th>Equipment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf water potential</td>
<td>$\psi_L$</td>
<td>leaf</td>
<td>no</td>
<td>noon</td>
<td>pressure pump</td>
</tr>
<tr>
<td>Xylem water potential</td>
<td>$\psi_x$</td>
<td>leaf</td>
<td>yes</td>
<td>noon</td>
<td>pressure pump</td>
</tr>
<tr>
<td>Soil water potential using leaf</td>
<td>$\psi_{s,\text{leaf}}$</td>
<td>leaf</td>
<td>yes</td>
<td>dawn</td>
<td>pressure pump</td>
</tr>
<tr>
<td>Soil water potential using soil and root</td>
<td>$\psi_{s,\text{soil-root}}$</td>
<td>soil</td>
<td>--</td>
<td>--</td>
<td>dewpoint potentiometer</td>
</tr>
</tbody>
</table>
5.3. Results and Discussion

5.3.1. Transpiration, water potential, conductance, root density and leaf area

The overall experimental procedure satisfactorily represented single and multi-species competition settings for $T$, $\psi$, $\rho_r$, $A_{leaf}$ and $g_T$. The ANOVA showed a treatment effect for all evaluated variables and a shoot weight covariate effect for $\psi_s$, $\psi_L$, $\rho_r$, and $A_{leaf}$ (Table 5.3). To test if $T$ in mixtures is similar to that of each species growing in isolation, I calculated the expected total $T$ in mixtures by multiplying the transpiration per unit area from pure rhizotrons times the leaf of plants in the mixtures. By adding the values for each species, I obtained a new estimate of transpiration for the box. Comparing that estimate with that measured, I concluded that indeed that plants in mixtures transpired almost exactly as plants in pure rhizotrons.
Table 5.3. Analysis of variance (ANOVA) and treatment means for transpiration, soil, xylem, and leaf water potential, root density, leaf area, plant water conductance, and conductance per root length.

<table>
<thead>
<tr>
<th>ANOVA</th>
<th>$T$</th>
<th>$\psi_{s, soil \cdot root}$</th>
<th>$\psi_{s, leaf}$</th>
<th>$\psi_x$</th>
<th>$\psi_L$</th>
<th>$\rho_r$</th>
<th>$A_{leaf}$</th>
<th>$g_T$</th>
<th>$g_{T, root len}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Block</td>
<td>&lt;.0001</td>
<td>0.2989</td>
<td>0.9953</td>
<td>0.008</td>
<td>0.0638</td>
<td>0.0004</td>
<td>0.006</td>
<td>0.2175</td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>&lt;.0001</td>
<td>0.1933</td>
<td>0.024</td>
<td>0.0455</td>
<td>0.0002</td>
<td>0.0878</td>
<td>0.0007</td>
<td>0.0008</td>
<td>0.0055</td>
</tr>
<tr>
<td>Covariate</td>
<td>2</td>
<td>0.0192</td>
<td>0.0818</td>
<td>0.018</td>
<td>0.015</td>
<td></td>
<td>0.036</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>2.24</td>
<td>2.12</td>
<td>2.32</td>
<td>-772</td>
<td>-1054</td>
<td>0.6842</td>
<td>0.074</td>
<td>0.000466</td>
<td>0.000013</td>
</tr>
<tr>
<td>RMSE</td>
<td>0.111</td>
<td>4.6</td>
<td>4.73</td>
<td>132</td>
<td>87.6</td>
<td>0.1515</td>
<td>0.011</td>
<td>0.000104</td>
<td>3.11x10^-6</td>
</tr>
<tr>
<td>n</td>
<td>24</td>
<td>24</td>
<td>24</td>
<td>24</td>
<td>24</td>
<td>24</td>
<td>24</td>
<td>24</td>
<td>24</td>
</tr>
</tbody>
</table>

Treatment means

<table>
<thead>
<tr>
<th>units</th>
<th>$J_{kg^{-1}}$</th>
<th>$J_{kg^{l^{-1}}}$</th>
<th>$J_{kg^{-1}}$</th>
<th>$J_{kg^{l^{-1}}}$</th>
<th>$x10^2 m^{-3}$</th>
<th>$x10^{-2} m^2$</th>
<th>$x10^9 kg s^{-4}$</th>
<th>$x10^6 kg s^{-5}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>M</td>
<td>1.50 ± 0.06</td>
<td>-195 ± 8</td>
<td>-381 ± 8</td>
<td>-611 ± 81</td>
<td>83.3 ± 9</td>
<td>9.62 ± 0.7</td>
<td>96.7 ± 4</td>
<td>9.54 ± 2</td>
</tr>
<tr>
<td>MM</td>
<td>1.54 ± 0.03</td>
<td>-512 ± 4</td>
<td>-344 ± 5</td>
<td>-653 ± 63</td>
<td>80.8 ± 7</td>
<td>8.17 ± 0.5</td>
<td>138 ± 2</td>
<td>8.94 ± 2</td>
</tr>
<tr>
<td>MMS</td>
<td>1.62 ± 0.04</td>
<td>-360 ± 7</td>
<td>-358 ± 8</td>
<td>-760 ± 87</td>
<td>56.7 ± 10</td>
<td>7.56 ± 0.7</td>
<td>146 ± 4</td>
<td>11.1 ± 2</td>
</tr>
<tr>
<td>S</td>
<td>3.24 ± 0.05</td>
<td>-640 ± 8</td>
<td>-713 ± 8</td>
<td>-891 ± 91</td>
<td>60.7 ± 10</td>
<td>5.3 ± 0.7</td>
<td>263 ± 4</td>
<td>12.6 ± 2</td>
</tr>
<tr>
<td>SS</td>
<td>3.14 ± 0.03</td>
<td>-413 ± 4</td>
<td>-736 ± 4</td>
<td>-883 ± 62</td>
<td>57.9 ± 7</td>
<td>6.55 ± 0.5</td>
<td>381 ± 2</td>
<td>16.6 ± 2</td>
</tr>
<tr>
<td>SMS</td>
<td>3.27 ± 0.04</td>
<td>-360 ± 7</td>
<td>-759 ± 8</td>
<td>-850 ± 78</td>
<td>51.9 ± 9</td>
<td>6.04 ± 0.6</td>
<td>463 ± 4</td>
<td>18.4 ± 2</td>
</tr>
</tbody>
</table>

M: maize; MM: maize/maize; MMS: maize in a maize/sunflower treatment; S: sunflower; SS: sunflower/sunflower; SMS: sunflower in a maize sunflower treatment; $T$: treatment transpiration per leaf area; $\psi_{s, soil \cdot root}$: soil water potential measured through soil weighted by root density; $\psi_{s, leaf}$: soil water potential measured through leaf; $\psi_x$: xylem water potential; $\psi_L$: leaf water potential; $\rho_r$: root density; $A_{leaf}$: leaf area; $g_T$: total plant conductance; $g_{T, root len}$: total plant conductance by root length; RMSE: root mean square error.

*: analysis performed with values square rooted and readjusted back for treatment means results.

1: shoot weight.

2: $\psi_{s, soil \cdot root}$
Sunflower $T$ was twice of that of maize. Within the same species, there was no significant $T$ difference among any of the treatments: one species per rhizotron, two plants of the same species per rhizotron, and mixed species. This behavior results in an average $T$ in a mixture rhizotron with values that are intermediate between the $T$ for each individual species. It strongly suggest that a sunflower plant will outcompete a maize plant if sharing the same soil with limited water supply because of the sunflower’s comparatively higher use of water. This strategy of anisohydric plants is being evaluated as a genetic improvement for drought tolerance as it is at least partially determined by the induction of aquaporins that increase the root permeability (lower resistance) to water flow (Moshelion et al., 2014; Sade et al., 2009). This in theory can “force” isohydric plants to be less conservative when the soil is drying.

The lack of differences in $T$ between individual plants of the same species in both pure and mixture rhizotrons shows that the results of competition will simply reflect the idiosyncrasy of each species or genotype, with apparently no adjustment due to the presence of neighboring roots of another species. In other words, both species maintained the same survival strategy regardless of whether they were alone in the soil or competing with the same species (i.e., intra-specific). This finding facilitates the development of multi-species simulation models since each species can be treated as a collection of individuals with the same hydraulic behavior, regardless of how many different species growing simultaneously in the same soil are being simulated.

The hydraulics of maize and sunflower are markedly different. Maize had 25% lower soil water potential than sunflower when measured through soil (i.e., $\psi_{s, \text{soil-root}}$) and 51% lower soil water potential when measured through leaf (i.e., $\psi_{s, \text{leaf}}$). The lower $\psi_s$
leaf in sunflower (-736 J kg\(^{-1}\)) when compared to \(\psi_{s, soil-root}\) (-471 J kg\(^{-1}\)) is attributed to possible \(T\) during the night period, which would not allow the plant to equilibrate with the soil. Both of the soil water potential measurements \(\psi_{s, soil-root}\) and \(\psi_{s, leaf}\) shows that maize had a wetter soil than sunflower showing its water conserving strategy typical of isohydric behavior. Furthermore, maize had 27\% higher \(\psi_x\) and 21\% higher \(\psi_L\) than sunflower, also signaling reduced water consumption.

The total \(\psi\) gradient from the soil-root to the leaf can be subdivided into root and shoot components to provide an understanding of the amount of water resistance in each part of the plant. The ratio of resistances between the soil-root and the xylem \((\alpha_{sr-x})\), and then from the xylem to leaf \((\alpha_{x-L})\) (these complementary quantities) can be calculated as:

\[
\alpha_{sr-x} = \frac{\psi_S - \psi_X}{\psi_S - \psi_L}
\]

\[
\alpha_{x-L} = \frac{\psi_X - \psi_L}{\psi_S - \psi_L}
\]

The \(\alpha_{sr-x}\) is 0.56 for maize and 0.58 for sunflower, while the \(\alpha_{x-L}\) is 0.44 for maize and 0.42 for sunflower. Thus, around 60\% of the resistance is in the root-soil system.

Similar figures are used in Campbell’s (1985) water uptake method where total plant resistance is apportioned 66\% to soil-root and 33\% to leaf. Further exploring resistance to water flow, if \(R_T\) is calculated using mean values for \(T\) and \(\psi\), \(R_T\) equals 3.9×10\(^6\) for maize and 2.4×10\(^6\) m\(^4\) kg\(^{-1}\) s\(^{-1}\), which is of the same magnitude of \(R_T\) of 5×10\(^6\) m\(^4\) kg\(^{-1}\) s\(^{-1}\) as reported by Campbell (1985). Similarly, \(g_T\) calculated from measured values in each
treatment yielded a 66% lower value for maize when compared with sunflower, once more showing its conservative nature.

Finally, $\rho_r$ and $A_{leaf}$ in maize were 29% and 42% higher than in sunflower respectively. A higher $\rho_r$ indicated a greater extent of root water exploration, but that does not necessarily imply better access to water as the soil resistance to water flow is low. The best indicator of the conservative strategy of maize is as mentioned above the lower conductance to water flow.

5.3.2. Root density and soil water potential across rhizotron’s profile

Two maize plants per rhizotron had larger root density per layer than one maize plant per rhizotron (Figure 5.3). Sunflower had lower root density than maize, with similar rooting density between one and two plants per rhizotron. Roots, in general, were uniformly populated in the rhizotron regardless of the species, which is not what typically occurs in the field. This was a limitation of the experimental unit (i.e., growing crops in a two dimensional rhizotron), as fast growing maize and sunflower species quickly colonized the rhizotron and did not develop a root gradient with soil depth.
Due to the uniform root density of both species within the rhizotron, $\psi_s$ followed the same uniform pattern across the profile (Figure 5.4). Drier $\psi_s$ in the top layer is likely due to soil evaporation, since the capacitance at low water potentials decreases, small water losses cause a large change in the soil water potential. Anisohydric (i.e., sunflower) and isohydric (i.e., maize) species also distinguished themselves in terms of $\psi_s$ being in general lower for sunflower than maize, collaborating observations previously reported by Franks et al. (2007).
5.3.3. Isohydric vs anisohydric behavior

To evaluate the two stomatal behaviors at different soil water contents, a linear regression of $\psi_L$ was performed using the block, species, and the interaction of $\psi_s,soil-root$ and species (Table 5.4). Results for maize showed a relatively weak relationship, indicating isohydric behavior of maintaining constant $\psi_L$ slope as soil gets drier. On the other hand, the correlation for sunflower was significant and positive, showing its anisohydric behavior. These results confirm that the experimental system was successful in generating and then measuring the expected stomatal behavior of both species. The

Figure 5.4. Soil water potential means in each soil profile depth for maize and sunflower.
isohydric behavior of maize maintained a somewhat constant $\psi_L$ around -800 J kg$^{-1}$, and this constant $\psi_L$ was observed especially when $\psi_s$ was in the range from 0 to -1,000 J kg$^{-1}$ (Figure 5.5). Conversely, sunflower proportionally decreased its $\psi_L$ with decreasing $\psi_s$.

Table 5.4. Linear model of leaf vs soil water potential (J kg$^{-1}$) for maize and sunflower.

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>Standard error</th>
<th>t value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maize intercept</td>
<td>-772</td>
<td>68</td>
<td>1.6</td>
<td>NS</td>
</tr>
<tr>
<td>Sunflower intercept</td>
<td>-881</td>
<td>54</td>
<td>-16.28</td>
<td>NS</td>
</tr>
<tr>
<td>maize slope</td>
<td>0.176</td>
<td>0.099</td>
<td>1.77</td>
<td>S</td>
</tr>
<tr>
<td>sunflower slope</td>
<td>0.388</td>
<td>0.10</td>
<td>3.75</td>
<td>S</td>
</tr>
</tbody>
</table>

$\psi_s$: soil water potential (J kg$^{-1}$).

Figure 5.5. Leaf water potential regression with soil water potential for maize and sunflower.

5.3.4. Crop modeling implications

Currently most of crop water uptake models do not account explicitly for differences in water uptake behavior between isohydric and anisohydric species (see Chapter 4). However, with some models there are species-related input adjustments that make it possible to represent the isohydric and anisohydric water uptake behavior using relationships derived from Campbell (1985). Two water stress simulations were performed using CropSyst modeling framework for maize and sunflower (Equation (5.1)
and Table 5.5), with transpiration ratio and cumulative transpiration results reported in Figure 5.6. The shape of the transpiration ratio curve looks similar to what was reported in Moshelion et al. (2014) for sunflower and tomatoes (isohydric). Maize reduces its potential transpiration earlier at day 15, while sunflower’s potential transpiration begins to decrease 15 days later. The slope of this reduction in transpiration also shows species specific risk levels. With these strategies, sunflower transpires more than maize but will have a higher probability of dying earlier than maize in separate soils, as would be the case in a monoculture planting. If an isohydric and anisohydric species were to share the same soil, the water saving strategy of the isohydric would not be effective, and probably detrimental to the isohydric species as the anisohydric species would consume the water regardless.

Table 5.5. Simulation set up for maize and sunflower growing independently.

<table>
<thead>
<tr>
<th></th>
<th>Maize</th>
<th>Sunflower</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daily transpiration demand (mm d⁻¹)</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Number of soil layers</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Soil type</td>
<td>Sandy loam</td>
<td>Sandy loam</td>
</tr>
<tr>
<td>Soil depth (m)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Soil layer thickness (m)</td>
<td>0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Initial soil water potential (J kg⁻¹)</td>
<td>-33</td>
<td>-33</td>
</tr>
<tr>
<td>Onset of stomatal closure leaf water potential (J kg⁻¹)</td>
<td>-500</td>
<td>-1500</td>
</tr>
<tr>
<td>Leaf water potential at permanent wilting point (J kg⁻¹)</td>
<td>-2000</td>
<td>-2000</td>
</tr>
<tr>
<td>Root distribution (fraction per layer)</td>
<td>Figure 5.3</td>
<td>Figure 5.3</td>
</tr>
</tbody>
</table>
Figure 5.6. Transpiration ratio and cumulative transpiration for maize and sunflower.

Other modeling water uptake strategies exist. Tardieu and Simonneau (1998) adapted Campbell’s (1985) method by adding an abscisic acid (ABA) hormonal signaling parameter to explain the variation in water use behavior in sunflower, maize and poplar. The challenge with the hormonal approach is to quantify the signals mechanistically for application in simulation models. This approach puts the emphasis in the messenger rather than in the message. Similarly, Bond and Kavanagh (1999) represented the variation of water use with gradient in \( \psi_L \) and \( \psi_s \) in tree species, finding a correlation with stomatal conductance, soil moisture, and atmospheric demand; further indicating that it is viable to model water used based on known soil, atmospheric and soil conditions. However, simulating stomatal conductance is the key component needed to simulate water use, since in the gradient and resistance framework treats the leaf water potential as a residue of a given flux and resistance in the system.
5.4. Conclusion

This study used soil rhizotrons to investigate competition within and among isohydric and anisohydric crop species. The experimental design appeared to simulate expected soil-plant-water interactions, with no differences in $T$ within the same species, while there was a difference between different species. It was difficult to observe a variation in water content within the rhizotrons’ depth (i.e., no progression of a drying front) since root exploration of the rhizotron was rapid and extensive.

This study shows that the classic isohydric and anisohydric characteristics of maize and sunflower is preserved when plants grow solo or in competition. It also provided the relationships between $T$, $\psi_s$, $\psi_x$, $\psi_L$, $\rho_r$, $A_{lolo}$, and $g_T$ for an anisohydric sunflower plant and isohydric maize plant. Additional research with additional species can provide a larger data set and species with a gradient of root exploration, both of which are needed to reinforce and extend the results (see Chapter 6).

This framework to analyze water use can be used to evaluate multi-species interaction and competition for soil water. No inter-species competition effect was observed in the mixed species rhizotron, which facilitates the development and implementation of multi-species crop models as they can treat each species individually focusing on their respective competitive strategy. The experimental data obtained in this study is rarely collected (Bristow et al., 1984), and includes measurements of $\psi$ at different soil and plant locations, $T$, and conductance/resistance. This data is essential to better understand water uptake under stress situations, and will improve both the mechanistic algorithms and predictive accuracy of crop and soil simulation models.
Chapter 6. Water competition in forage species in a controlled environment

6.1. Introduction

Multi-species pastures and hay crops are key components of sustainable cropping systems (Foley et al., 2005; Malézieux et al., 2009). A common pasture setting is a combination of grasses and legume species, where soil fertility is increased by the legume’s nitrogen fixation (Haynes and Williams, 1993) which is complemented by the grasses ability to grow in a different season or to survive in more stressful conditions. Many forage species combinations exist depending on characteristics such as growing season, plant height, life cycle, drought or flood resistance, and livestock preferences. Orchardgrass (*Dactylis glomerata* L.) and white clover (*Trifolium repens* L.) constitute a typical mixture of pastures in the Northeastern United States. In this chapter I focus our study in these two species.

Since different species share the same soil volume in pasture systems, competition for shared resources arises particularly with solar radiation (Chapter 3), water (Chapter 4) and nutrients. The morphological and physiological features of the different species in a community determine their competitive advantage as well as their spatial and temporal complementarity. Morphologically, species’ competitiveness is determined by characteristics such as shoot height, root depth, and leaf and root density. Physiologically, species competitiveness increases with characteristics such as resistance to pests, resistance to drought, and stomatal behavior. Species stomatal behavior, which relates to water use strategies, is regulated by radiation interception, soil water availability and atmospheric demand (Moshelion et al., 2014). Identifying varying mechanisms of water
use under stress and non-stress situations is critical (Asch et al., 2009; Franks et al., 2007; Moshelion et al., 2014; Tardieu and Simonneau, 1998), since it directly impacts biomass production, consequently affecting the competitive ability of species. Nonetheless, contrasting strategies to cope with water stress may render similar levels of biomass production in different species as shown for fescue (*Lolium arundinaceum* (Schreb.) Darbysh.) and ryegrass (*Lolium multiflorum* Lam) by Halloway-Phillips and Brodribb (2011). Furthermore, morphological diversity such as including a species with contrasting rooting pattern can improve the water relations of contrasting species such as chicory (*Cichorium intybus* L.) and white clover (Skinner et al., 2004).

Assembling the factors that control competition among perennial species in a simulation model must consider both morphological and physiological attributes that are relevant to determine the competition outcome. Among the critical factors that determine a species competitive ability in a community is its pattern of root soil exploration and water use under unlimited water supply and under water stress. Despite its importance, few studies attempt to unravel the patterns of root soil exploration and hydric relations of orchardgrass and white clover mixtures.

Accordingly, the objective of this Chapter was to investigate the hydraulics of orchardgrass and white clover growing alone and in a mixture, focusing on water uptake when the species undergo water stress. I surmise that understanding the hydraulics of these plants will enable modeling competition in comprehensive simulation models. In addition, results from this experiment aim to improve algorithms of water uptake and water stress processes (Chapter 4), which in turn leads to improved simulation of multi-species canopies (Chapter 2).
6.2. Materials and methods

6.2.1. Set up

The experimental approach used in this study was very similar to Chapter 5. Rhizotrons were treated with water sealant to prevent wood from absorbing water. Soil was sieved using a 3 mm mesh to improve the accuracy of soil water potential (\( \psi_s \), J kg\(^{-1} \)) and water content (\( \theta_s \), m\(^3\) m\(^{-3} \)) measurements (see Appendix for detailed soil description).

The experiment had three treatments and five blocks with respect to time (replicates). Each rhizotron hosted one species or two species canopies depending on the treatment. Orchardgrass (\textit{Dactylis glomerata} L.) and white clover (\textit{Trifolium repens} L.) were selected for this evaluation because of their dominance in the pastures planted in the Northeastern U.S. and because of their contrasting growth habit. The treatments were: orchardgrass or white clover growing alone (one species per rhizotron), and orchardgrass and white clover in competition (two species per rhizotron) (Figure 6.1). The rhizotrons were seeded by hand and thinned after emergence to approximately one plant per linear inch.

Treatments were randomly assigned (Table 6.1), and daily solar radiation, temperature, relative humidity, and maximum vapor pressure deficit recorded with sensors installed in a table adjacent to the rhizotrons (Figure 6.2).
Figure 6.1. A diagram representing the pure or mixed stands of orchardgrass (G), white clover (C), and mixture (GGC and CGC). This set up was repeated five times (blocks).

Table 6.1. Rhizotron treatments, blocks and growth periods.

<table>
<thead>
<tr>
<th>Block</th>
<th>Rhizotron</th>
<th>Treatment¹</th>
<th>Unstressed growth (days)</th>
<th>Stressed growth (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>12, 14, 15</td>
<td>C, GC, G</td>
<td>84</td>
<td>3</td>
</tr>
<tr>
<td>2</td>
<td>4, 5, 6</td>
<td>C, G, GC</td>
<td>82</td>
<td>3</td>
</tr>
<tr>
<td>3</td>
<td>1, 2, 9</td>
<td>G, C, GC</td>
<td>84</td>
<td>3</td>
</tr>
<tr>
<td>4</td>
<td>3, 7, 11</td>
<td>C, G, GC</td>
<td>86</td>
<td>3</td>
</tr>
<tr>
<td>5</td>
<td>8, 10, 13</td>
<td>G, C, GC</td>
<td>88</td>
<td>3</td>
</tr>
</tbody>
</table>

¹G: orchardgrass; C: white clover; GC: orchardgrass and white clover mixture in rhizotron.

Figure 6.2. Daily weather data for the three temporal blocks including solar radiation in MJ m⁻² (“solar rad”), maximum (-) and minimum (--), temperature in °C (“Temp”), maximum (-) and minimum (--), relative humidity (“RHI”), and maximum vapor pressure deficit in kPa (“Max VPD”).
As in Chapter 5, to introduce the effect of water competition, plants were allowed to advance progressively towards water stress in pure and mixed stands, keeping light and nutrient conditions at the same level. For this purpose, irrigation was stopped. Stress ensued quickly after three days without irrigation, a time at which the plants were sampled. During the course of this phase, soil evaporation did not occur because the species canopy occupied all of the rhizotron’s soil area. To monitor plant water stress, stomatal conductance \((g_{stom}, \text{mmol} \text{m}^{-2} \text{s}^{-1})\) (SC-1 Porometer Decagon Devices Inc., Pullman, WA) and leaf temperature \((L_T, \text{C})\) were measured during the stress days. The transpiration \((T, \text{kg m}^{-2} \text{leaf day}^{-1})\) was monitored by weighing the rhizotrons daily and dividing the calculated water use by the total leaf area \((A_{leaf}, \text{m}^2)\). The \(A_{leaf}\) consists of leaflets for legumes and leaf blades for grasses. The percentage of leaflets and leaf blades was estimated to be 43% and 58% by weight, respectively. Based on these ratios, the harvested aboveground biomass from each rhizotron was converted to leaflet and leaf blade mass. To convert leaflet and leaf blade mass to area, literature specific leaf area (SLA) values of 230 g cm\(^{-2}\) and 330 g cm\(^{-2}\) were used for orchardgrass and white clover respectively (Nassiri and Elgersma, 1998), which agree with occasional (and not consistent) test samples taken from the rhizotrons. Total plant resistance \((R_T)\) was calculated using eq. (5.1).
6.3. Results and Discussion

6.3.1. Transpiration, water potential, conductance, root density and leaf area

The overall experimental procedure for forage species satisfactorily represented single and multi-species competition settings for $T$, $\psi$, $\rho$, $\theta$, $A_{leaf}$, $R_T$, $g_{stom}$ and $L_T$. The ANOVA showed a treatment effect for all evaluated variables except for $L_T$ (Table 6.2). As in Chapter 5, prior to the ANOVA a regression was performed on data from rhizotrons with single species to estimate the expected average $T$ for each species in the mixture rhizotrons using block and treatment effects. This estimation of $T$ for each of the different species in the mixture rhizotrons was then adjusted to match the measured $T$ value using the leaf area of each species. Regression results were comparable, and allowed five additional data points for each species in the ANOVA analysis.
Table 6.2. Analysis of variance (ANOVA) *P* value and treatment means for transpiration, soil water potential, xylem water potential, leaf water potential, root density, water content, leaf area, plant resistance to water flow, stomatal conductance, and leaf temperature.

| ANOVA |  
|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
|       | $T_{clover}$ | $T_{grass}$ | $\psi_s$ (soil-root) | $\psi_s$ (leaf) | $\psi_x$ | $\theta_s$ | $A_{leaf}$ | $R_T$ | $g_{stom}$ | $L_T$ |
| Block | 0.309  | 0.228  | 0.350  | 0.0323 | 0.5865  | 0.1929  | 0.0954  | 0.4348  | 0.5699  | 0.5362  | 0.0193  | 0.0002 |
| Treatment | 0.798  | 0.923  | 0.0009 | 0.0078 | 0.0211  | 0.0035  | <0.001  | <0.001  | <0.001  | 0.0706  | 0.0275  | 0.312  |
| Covariate | 0.012  | 0.202  | --     | --     | --      | --      | --      | --      | --      | --      | --      | --      |
| Mean   | 1.23   | 1.05   | -1383  | -1050  | -1869   | -2048   | 1.67    | 0.1655  | 0.536   | 3.47×10$^7$ | 386    | 25.7   |
| RMSE   | 0.66   | 0.15   | 272    | 283    | 407     | 297     | 0.410   | 0.0214  | 0.141   | 2.87×10$^7$ | 178    | 1.172  |
| n      | 10     | 10     | 20     | 20     | 20      | 20      | 20      | 20      | 20      | 20      | 20      | 20      |

**Treatment means**

<table>
<thead>
<tr>
<th></th>
<th>kg m$^{-2}$ leaf d$^{-1}$</th>
<th>kg m$^{-2}$ leaf d$^{-1}$</th>
<th>J kg$^{-1}$</th>
<th>J kg$^{-1}$</th>
<th>J kg$^{-1}$</th>
<th>J kg$^{-1}$</th>
<th>J kg$^{-1}$</th>
<th>$\times 10^4$ m m$^{-3}$</th>
<th>m$^3$ m$^{-3}$</th>
<th>m$^2$</th>
<th>$\times 10^7$ m$^4$ kg$^{-1}$ s$^{-1}$</th>
<th>mmol m$^{-2}$ s$^{-1}$</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>1.16</td>
<td>--</td>
<td>-1813</td>
<td>-1033</td>
<td>-1799</td>
<td>-2331</td>
<td>2.26</td>
<td>0.132</td>
<td>1.02</td>
<td>4.557</td>
<td>419</td>
<td>26.5</td>
<td>---</td>
</tr>
<tr>
<td>CGC</td>
<td>1.30</td>
<td>--</td>
<td>-1441</td>
<td>-745</td>
<td>-1804</td>
<td>-1846</td>
<td>2.22</td>
<td>0.152</td>
<td>0.81</td>
<td>2.141</td>
<td>596</td>
<td>25.7</td>
<td>---</td>
</tr>
<tr>
<td>G</td>
<td>--</td>
<td>0.95</td>
<td>-835</td>
<td>-926</td>
<td>-1461</td>
<td>-1621</td>
<td>1.98</td>
<td>0.226</td>
<td>0.24</td>
<td>1.152</td>
<td>328</td>
<td>25.4</td>
<td>---</td>
</tr>
<tr>
<td>GGC</td>
<td>--</td>
<td>1.05</td>
<td>-1441</td>
<td>-1496</td>
<td>-2412</td>
<td>-2392</td>
<td>0.198</td>
<td>0.152</td>
<td>0.07</td>
<td>6.053</td>
<td>201</td>
<td>25.1</td>
<td>---</td>
</tr>
</tbody>
</table>

C: white clover treatment; CGC: white clover in a orchardgrass and clover mixture treatment; G: orchardgrass treatment; GGC: orchardgrass in a orchardgrass and white clover mixture treatment; $T_{clover}$: white clover treatment transpiration per leaf area; $T_{grass}$: orchardgrass treatment transpiration per leaf area; $\psi_s$ (soil-root): soil water potential measured through soil weighted by root density; $\psi_s$ (leaf): soil water potential measured through leaf; $\psi_x$: xylem water potential; $\psi_l$: leaf water potential; $\rho_r$: root density; $A_{leaf}$: leaf area; $\theta_s$: soil water content; $R_T$: total plant resistance; $g_{stom}$: stomatal conductance; $L_T$: leaf temperature; RMSE: root mean square error.

$^1$: $\psi_s$ (soil-root)
To evaluate the different water uptake strategies between species, $T$ should be compared at an equivalent soil water potential; $\psi_{s,\text{soil-root}}$ was used as a covariate to adjust $T$ in the ANOVA analysis for each species. Within the same species, there was no significant $T$ difference among white clover (p=0.8) and orchardgrass (p=0.9). This shows that both species maintained their water uptake strategies regardless of whether they were in a pure species canopy or in a multi-species setting. In addition, since both species presented similar $T$, a similar level of water competition occurred between orchardgrass and white clover when they had comparable leaf area.

Similar to the annual species in Chapter 5, the lack of differences in $T$ between individual plants of the same species in both pure and mixed rhizotrons shows that hydraulic attributes are conserved for a given species whether it is growing in pure or mixed stands. In other words, both species maintained their strategy regardless of whether they were sharing the soil with same species or other species. This behavior allows each species to be treated individually in a simulation model with its particular competition strategies such as stomatal behavior and prioritization of above and below ground biomass production.

Soil water potential measured through soil ($\psi_{s, \text{soil-root}}$) and measured through leaf ($\psi_{s, \text{leaf}}$) were evaluated for white clover and orchardgrass (Figure 6.3). In orchardgrass both measurements followed a similar linear decrease; conversely, white clover $\psi_{s, \text{leaf}}$ measurements were always higher than $\psi_{s, \text{soil-root}}$. These higher soil water potentials measured through the plant show that at night white clover is sensing a wetter soil than what was measured in the rhizotron’s soil and weighted by root density. White clover
seems to compensate sensed soil water potential by prioritizing wetter areas of the soil and increasing the resistance of drier areas (Table 6.3).

![Soil water potential comparison](image)

**Figure 6.3.** Soil water potential comparison when measured through leaf or using potentiometer and root density.

<table>
<thead>
<tr>
<th>Species</th>
<th>( \dot{T}_{inst} )</th>
<th>( \psi_s,\text{soil-root} )</th>
<th>( \psi_s,\text{leaf} )</th>
<th>( \psi_x )</th>
<th>( \psi_L )</th>
<th>( R_{T1} )</th>
<th>( R_{T2} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>White clover</td>
<td>( 4.29 \times 10^{-5} )</td>
<td>-1.627</td>
<td>-889</td>
<td>-1,802</td>
<td>-2,089</td>
<td>1.07 \times 10^7</td>
<td>2.79 \times 10^7</td>
</tr>
<tr>
<td>Orchardgrass</td>
<td>( 3.97 \times 10^{-5} )</td>
<td>-1,138</td>
<td>-1,211</td>
<td>-1,937</td>
<td>-2,007</td>
<td>2.19 \times 10^7</td>
<td>2.00 \times 10^7</td>
</tr>
</tbody>
</table>

\( \dot{T}_{inst} \): instantaneous transpiration at noon; \( \psi_s,\text{soil-root} \): soil water potential measured through soil and weighted through root density; \( \psi_s,\text{leaf} \): soil water potential through leaf; \( \psi_x \): xylem water potential; \( \psi_L \): leaf water potential; \( R_{T1} \): total plant resistance using \( \psi_s,\text{soil-root} \); \( R_{T2} \): total plant resistance using \( \psi_s,\text{leaf} \).

A schematic was made to hypothesize the explanation of white clover’s compensation behavior and also to compare with Campbell’s approach to water uptake (Figure 6.4). To facilitate the explanation, an electrical diagram with \( \psi_L \), \( \psi_s \) and plant conductances (\( g \), i.e., resistance reciprocal) was used to represent nature and the model.

In this example, the soil is drier in the top and wetter in the bottom. To explain the compensation behavior of white clover, variable conductances was assumed in nature for
each soil depth depending on \( \rho_r \) and \( \psi_s \). The drier the soil, the lower is \( g \). In addition, the lower the \( \rho_r \) value, the lower is \( g \). In this case, when a lower soil water potential is measured through the leaf (\( \psi_{s, \text{leaf}} \)) than through soil (\( \psi_{s, \text{soil-root}} \)), I hypothesize that when root density is constant, the conductances of drier layers are reduced, prioritizing the wetter soil and consequently a wetter soil water potential measurement through the leaf. This will also result in an overall reduction conductance of the system. In the model representation, conductances only depend on \( \rho_r \) at each soil layer, and are constant when root growth is zero. Even though the nature and model representations contain variable and constant conductances respectively, the water uptake results should be similar since in both representations water uptake is partitioned according to root density in the soil layers given its water availability. The mechanism that can be invoked to explain variable conductances is a regulation of the cell membranes permeability to water via aquaporins (Moshelion et al., 2014).
6.3.2. Root density, soil water potential and soil water content across rhizotron’s profile

This study created a gradient of $\rho_r$, $\psi_s$ and $\theta$ in the rhizotron soil profile, which provided a more realistic description of plant systems in the field. Orchardgrass had a higher root density gradient than white clover, with about ten times more roots in the top compared to the bottom of the rhizotron (Figure 6.5). White clover had a more uniform root gradient with around two times more roots in the top compared to the bottom of the rhizotron.

![Figure 6.4. Electrical analog representation of plant conductances (g, kg s m$^{-4}$) in nature and model where $\psi_s$ is the soil water potential (J kg$^{-1}$) and $\rho_r$ is the root density (m m$^{-3}$) for each soil layer.](image)
Orchardgrass had a wetter soil than white clover represented as water potential (Figure 6.6) and water content (Figure 6.7). Water uptake correlates to root density of each species in the layer. The drying curve shape is similar to the ones measured in fields and is also similar to CropSyst’s water use profile from Chapter 4.
Figure 6.7. Soil water content means in each soil profile depth for orchardgrass and white clover.

Based on Figure 6.4 discussion and water uptake model usage, $\psi_{s, \text{soil-root}}$ was used as soil water potential in comparison with $\psi_s$, $\psi_L$, $g$, $g_{\text{stom}}$, $T$ and the difference in temperature between greenhouse air and species leaf (Figure 6.8). Overall, orchardgrass used less water than white clover. Both species had a linear decrease of xylem water potential (Figure 6.8 A) and leaf water potential (Figure 6.8 B) as the soil became drier, and show seemingly anisohydric behavior. However, there is no measurement with the soil water potential above approximately -700 J/kg, and thus the ability to detect isohydric behavior might be limited.

White clover showed no significant plant conductance differences ($P=0.9$) as the soil became drier, as opposed to orchardgrass that was significant ($P=0.045$) with plant conductance increasing with soil moisture (Figure 6.8 C). Both species showed a linear decrease of stomatal conductance with soil water potential, and orchardgrass had a steeper slope (0.26 mmol s$^{-1}$ m$^{-2}$ per J kg$^{-1}$) than white clover (0.12 mmol s$^{-1}$ m$^{-2}$ per J kg$^{-1}$). Similarly, transpiration reduced linearly, and orchardgrass had a slope steeper than
white clover (Figure 6.8 E). Lastly, both species had similar greenhouse and leaf temperature difference slopes (Figure 6.8 F).

The main driver of the differences among species was the faster soil exploration by the roots of white clover when compared with orchardgrass. As opposed to white clover, orchardgrass had a slow progression rooting front with a sharp root density distribution with depth. Somewhat unexpectedly, clover showed plasticity colonizing the rhizotron and exploiting the good soil conditions. This seems to reflect an important characteristics of these species. Hydraulically, however, they seemed to display a similar behavior. Therefore, when modeling the water relations of these species, the critical factor to consider is the degree of root exploration in different environments. This conclusion agrees with observations presented by Skinner et al. (2004).

The behavior of white clover resembles that of an early seral species, able to colonize disturbed and fertile environments. The combination of orchardgrass and white clover seems to combine the ability of one species to establish itself slowly but steadily (orchardgrass) and one that can make an opportunistic use of fertile environments. As orchardgrass colonizes the soils with the profuse roots system (top layer in Fig. 6.5) it regulates the ability of clover to access soils resources. While I cannot rule out that white clover can behave as an isohydric species, the putative anisohydric behavior enables aggressive growth, but not the degree of soil water depletion shown by sunflower, allowing therefore the establishment of orchardgrass.
Figure 6.8. Soil water potential ($\psi_{s, \text{soil-root}}$) for orchardgrass and white clover compared to xylem water potential (A), leaf water potential (B), total plant conductance (C), stomatal conductance (D), transpiration (E) and temperature difference between greenhouse and leaf (F).
6.4. Conclusion

This study provided insight on how water uptake occurs in pasture species under drought conditions. The information collected will improve multi-species cropping systems simulation models and water uptake algorithms. This experiment successfully showed a gradient in water potential and root density across the soil profile, allowing further investigation at the field scale.

Orchardgrass and white clover maintained their water uptake strategies when sharing the soil volume with the same species or with a different species. This finding will allow species to be simulated as individuals sharing common resources with their respective competitive and survival strategies. The challenge is to simulate the root distribution properly, particularly when soil properties vary with depth or soil type.

White clover seemed to compensate soil water potential measured through leaf by prioritizing the roots in wetter areas, as opposed to orchardgrass which perceived its water availability as a soil average weighted by roots. This is an interesting results that presents white clover as an opportunistic species highly responsive to the environment, and orchardgrass as a relatively stable colonizer that is unable to respond as quickly to favorable soil conditions. White clover’s compensation can be explained using an electrical analog representation with different soil water potentials and variable conductances in each layer. The prioritization of wet layers occurs by decreasing the conductances in drier layers resulting in a higher (i.e., wetter) soil water potential perception of the plant when measured through the leaf, and an overall lower conductance of the system.
In conclusion, understanding species behavior in drought situations is fundamental to accurately simulate multi-species canopies. Evaluating water relationships experimentally between species in competing and non-competing settings is critical to design, improve and validate multi-species agroecosystem models, as it permits identifying the key ecophysiological factors that explain the differences among species.
Chapter 7. Summary and conclusions

This dissertation was able to accomplish most of its intended goals of improving the understanding of solar radiation and water competition in multi-species agroecosystems systems. In Chapter 2, I was able to dissect existing pasture and multi-species models on each modeling component, compare different approaches, and discuss required improvements. I concluded that processes that explain the competition for light and water have been only partially incorporated in agroecosystem models. More specifically, there was a need for a simple algorithm of solar radiation interception among more than two species with different heights. Also lacking was the ability to quantify the differences of water uptake methods in current agroecosystem models.

In Chapter 3, I evaluated existing solar radiation interception methods in agroecosystem models at different time-steps and introduced a new method. This method can simulate solar radiation interception in each species of a canopy with more than two species of different heights. The new method was robust, yielding comparable results to more complex methods and is readily available to be implemented in most agroecosystem models. The main advantage is that it combines the best properties of earlier models, allowing the simulation of an unlimited number of species that vary in height and leaf area. Earlier models could only handle two species of different height.

In Chapter 4, I evaluated water uptake and water stress methods of current agroecosystem models. I found that methods of modeling water uptake and water stress are different in each method, although depending on parameterization, the methods may render similar results. In the scenarios tested, the main differences among water uptake
methods were in the water use in the subsoil (below 0.5m), which renders differences in the water content in the soil profile. Having accurate estimates of the water content in the soil profile is important since it directly relates to plant water stress, crop growth and development, nutrient cycling, soil temperature, greenhouse gas emissions and other processes. Out of the evaluated methods CropSyst seemed to have the best balance of mechanistic simulation and realistic representation of water use, with a low number of parameters needed. Further improvements in water uptake methods are still needed to account for different species’ strategies of water use (i.e. isohydric vs anisohydric) and to represent variation in soil “weighting” to calculate an average soil water potential, as clearly illustrated in chapter 6 for white clover.

In Chapter 5, I quantified intra and inter species water competition in two model plants, maize and sunflower. Both species showed different water use strategies, with maize saving water when faced with water stress (i.e. isohydric) and sunflower not saving water (i.e. anisohydric). When sharing the same soil both of the evaluated species maintained their water use strategies.

In Chapter 6, I quantified intra and inter species water competition in two pasture species, orchardgrass and white clover. Both species showed similar water use water use strategies (i.e., anisohydric) but orchardgrass was more conservative in terms of water use than white clover owing to a slower exploration of the soil profile by the roots. White clover seemed to prioritize the wetter layers of the soil, which may lead to less conservative water use. Similar to the maize and sunflower in Chapter 5, orchardgrass and white clover maintained similar transpiration rates when sharing the soil with same or different species.
Further investigation is required to gain a full understanding of isohydric and anisohydric mechanisms and their modeling application. In fact, this research indicates that comparative physiology can offer a venue to explore the real potential for water use in the soil-plant system. For example, the behavior of sunflower clearly indicate that water can be used faster, and crop growth can be likely faster, if water is not conserved and is used to match the atmospheric demand. In other words, sunflower showed a profligate use of water that can be helpful when irrigation is available or weather forecasts suggest no water limitation in the future. The slow water use behavior of maize may not capitalize such advantage. On the contrary, drier environments with dry end of season soil or shallow roots may benefit from a slow depletion of soil moisture.

Future research should focus on the creation of an algorithm to characterize isohydric and anisohydric behaviors in agroecosystem models. In Chapter 6, I hypothesized potential methods to represent these water strategies in isohydric and anisohydric plants such as variable plant resistance to water flow. In addition, further investigation is needed in species height determination, which is required in the newly developed solar radiation interception method presented here.

The research presented in this dissertation improved knowledge in the areas of solar radiation interception among plant species and water use among plant species. Specifically, I introduced a new method of solar radiation interception for multiple species, evaluated and compared several water uptake and water stress methods in agroecosystem models, and performed controlled experiments to evaluate water use strategies of different plant species. Together, this research improves the applicability and accuracy of agroecosystem models of both crop and pasture production used in important
efforts including the understanding of climate change, food security, bioenergy production, and environmental impacts of agriculture.
References


Appendix

Table A.3.1. List of abbreviations

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>$f_b$</td>
<td>Fraction of the incoming radiation that is beam</td>
<td>--</td>
</tr>
<tr>
<td>$F_{day,i}$</td>
<td>Fractional radiation interception of each species</td>
<td>--</td>
</tr>
<tr>
<td>$F_{day,T}$</td>
<td>Daily fractional radiation interception by the canopy</td>
<td>--</td>
</tr>
<tr>
<td>$F_i$</td>
<td>Fractional radiation intercepted by each species</td>
<td>--</td>
</tr>
<tr>
<td>$F_{i,d}$</td>
<td>Fractional radiation interception by the dominant species</td>
<td>--</td>
</tr>
<tr>
<td>$F_{i,s}$</td>
<td>Fractional radiation interception by the suppressed species</td>
<td>--</td>
</tr>
<tr>
<td>$F_T$</td>
<td>Fractional radiation interception by the canopy</td>
<td>--</td>
</tr>
<tr>
<td>$h$</td>
<td>Plant height</td>
<td>m</td>
</tr>
<tr>
<td>$i$</td>
<td>Species index</td>
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</tr>
<tr>
<td>$k$</td>
<td>Radiation extinction coefficient</td>
<td>--</td>
</tr>
<tr>
<td>$k_b$</td>
<td>Beam radiation extinction coefficient</td>
<td>--</td>
</tr>
<tr>
<td>$k_d$</td>
<td>Diffuse radiation extinction coefficient</td>
<td>--</td>
</tr>
<tr>
<td>$k_{day}$</td>
<td>Daily radiation extinction coefficient</td>
<td>--</td>
</tr>
<tr>
<td>$k_e$</td>
<td>Effective radiation extinction coefficient of the canopy</td>
<td>--</td>
</tr>
<tr>
<td>$L$</td>
<td>Leaf area index</td>
<td>$m^2_{leaf} m^{-2}_{ground}$</td>
</tr>
<tr>
<td>$m$</td>
<td>Species canopy dominance factor</td>
<td>--</td>
</tr>
<tr>
<td>$n$</td>
<td>Number of species in the canopy</td>
<td>--</td>
</tr>
<tr>
<td>$\zeta$</td>
<td>Height weighting factor</td>
<td>--</td>
</tr>
<tr>
<td>$\tau_T$</td>
<td>Fractional transmitted radiation through the canopy</td>
<td>--</td>
</tr>
<tr>
<td>$\chi$</td>
<td>Parameter representing the canopy leaf angle distribution</td>
<td>--</td>
</tr>
<tr>
<td>$\psi$</td>
<td>Sun zenith angle</td>
<td>degrees</td>
</tr>
<tr>
<td>$\omega$</td>
<td>Dominance weighting factor (or correction of the extinction coefficient to account for dominance)</td>
<td>--</td>
</tr>
<tr>
<td>$\omega_d$</td>
<td>Dominant weighting factor</td>
<td>--</td>
</tr>
<tr>
<td>$\omega_s$</td>
<td>Suppressed weighting factor</td>
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</table>

Source code for solar radiation interception available at:

https://github.com/gcamargo1/SolarRadInterception
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Figure A.4.1. Transpiration ratio comparison between sandy clay and silt loam soil textures with equally and geometrically distributed soil layers for the models CropSyst, DSSAT, APSIM, SWAP and EPIC. Plant available water (PAW) in the layers 1-10 of 50%.

Figure A.4.2. Transpiration ratio comparison between sandy clay and silt loam soil textures with equally and geometrically distributed soil layers for the models CropSyst, DSSAT, APSIM, SWAP and EPIC. Plant available water (PAW) in the layers 1-5 of 50% and in the layers 6-10 of 100%.
Figure A.4.3. Transpiration ratio comparison between sandy clay and silt loam soil textures with equally and geometrically distributed soil layers for the models CropSyst, DSSAT, APSIM, SWAP and EPIC. Plant available water (PAW) in the layers 1-5 of 100% and in the layers 6-10 of 50%.

Figure A.4.4. Cumulative transpiration comparison between sandy clay and silt loam soil textures with equally and geometrically distributed soil layers for the models CropSyst, DSSAT, APSIM, SWAP and EPIC. Plant available water (PAW) in the layers 1-10 of 50%.
Figure A.4.5. Cumulative transpiration ratio comparison between sandy clay and silt loam soil textures with equally and geometrically distributed soil layers for the models CropSyst, DSSAT, APSIM, SWAP and EPIC. Plant available water (PAW) in the layers 1-5 of 50% and in the layers 6-10 of 100%.

Figure A.4.6. Cumulative transpiration comparison between sandy clay and silt loam soil textures with equally and geometrically distributed soil layers for the models CropSyst, DSSAT, APSIM, SWAP and EPIC. Plant available water (PAW) in the layers 1-5 of 100% and in the layers 6-10 of 50%.
Figure A.4.7. Transpiration ratio comparison with different plant available water (PAW) in a silt loam soil with geometrically distributed soil layers for the models CropSyst, DSSAT, APSIM, SWAP and EPIC.

Figure A.4.8. Cumulative transpiration comparison with different plant available water (PAW) in a silt loam soil with geometrically distributed soil layers for the models CropSyst, DSSAT, APSIM, SWAP and EPIC.
Figure A.4.9. Transpiration ratio comparison with different plant available water (PAW) in a sandy clay soil with geometrically distributed soil layers for the models CropSyst, DSSAT, APSIM, SWAP and EPIC.

Figure A.4.10. Cumulative transpiration comparison with different plant available water (PAW) in a sandy clay soil with geometrically distributed soil layers for the models CropSyst, DSSAT, APSIM, SWAP and EPIC.
Source code for Chapter 5 is available at:

https://github.com/gcamargo1/WaterUptakeModels

Table A.5.1. Soil characteristics.

<table>
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<tr>
<th>Rhizotron</th>
<th>Sand</th>
<th>Silt</th>
<th>Clay</th>
<th>Textural class</th>
<th>Soil pH</th>
<th>P</th>
<th>K</th>
<th>Mg</th>
<th>Ca</th>
<th>Acidity</th>
<th>CEC</th>
<th>Organic Matter</th>
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<tbody>
<tr>
<td>#</td>
<td>%</td>
<td>%</td>
<td>%</td>
<td></td>
<td>ppm</td>
<td>ppm</td>
<td>ppm</td>
<td>ppm</td>
<td>meq/100</td>
<td>meq/100</td>
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</tr>
<tr>
<td>15</td>
<td>73.1</td>
<td>19.9</td>
<td>7</td>
<td>Sandy Loam</td>
<td>7</td>
<td>495</td>
<td>149</td>
<td>713</td>
<td>7366</td>
<td>0</td>
<td>21.3</td>
<td>13.1</td>
</tr>
<tr>
<td>2</td>
<td>72.2</td>
<td>20.4</td>
<td>7.4</td>
<td>Sandy Loam</td>
<td>7.1</td>
<td>582</td>
<td>143</td>
<td>724</td>
<td>8436</td>
<td>0</td>
<td>21.4</td>
<td>18.9</td>
</tr>
<tr>
<td>4</td>
<td>75.3</td>
<td>18.1</td>
<td>6.7</td>
<td>Sandy Loam</td>
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<td>470</td>
<td>167</td>
<td>595</td>
<td>7843</td>
<td>0</td>
<td>20.4</td>
<td>17</td>
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<td>AVG</td>
<td>73.5</td>
<td>19.5</td>
<td>7.0</td>
<td>Sandy Loam</td>
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<td>516</td>
<td>153</td>
<td>677</td>
<td>7882</td>
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Figure A.5.1. Rhizotrons in the greenhouse.
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<td>Moisture</td>
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<tr>
<td>LOI (%)</td>
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<td>OM (%)</td>
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<td>P (mg/kg)</td>
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<tr>
<td>Al (mg/kg)</td>
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<td>6.5</td>
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<td>Ca (mg/kg)</td>
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<td>7644.8</td>
</tr>
<tr>
<td>Fe (mg/kg)</td>
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<tr>
<td>K (mg/kg)</td>
<td>215.13</td>
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</tr>
<tr>
<td>Mg (mg/kg)</td>
<td>459.93</td>
<td>586.86</td>
</tr>
<tr>
<td>Mn (mg/kg)</td>
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<td>36.96</td>
</tr>
<tr>
<td>Zn (mg/kg)</td>
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<td>11.13</td>
</tr>
<tr>
<td>NO₃ (mg/kg)</td>
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<td>18.58</td>
</tr>
<tr>
<td>Sand (%)</td>
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<td>40.95</td>
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<td>Silt (%)</td>
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<td>Clay (%)</td>
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<td>Calculated texture</td>
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<tr>
<td>Visual texture</td>
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<td>Loam</td>
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Reference: Cornell Nutrient Analysis Laboratories (2013)
Figure A.6.1. Mixed species (orchardgrass and white clover) rhizotron.
GUSTAVO CAMARGO

EDUCATION

Ph.D. Pennsylvania State University, University Park, PA May 2015
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Dissertation title: Water and Light Competition Among Multiple Species

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Major: Agricultural Engineering

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Graduated Research Assistant Dept. Ag. and Bio. Eng, University Park, PA Aug. 2007-Present
● Create computer models of agro-ecosystems focusing on water competition in pastures
● Conduct water use experiments in plant-root systems
● Develop whole-farm system models including the Farm Energy Analysis Tool (FEAT)
● Evaluate energy and greenhouse gas emissions of cropping, livestock, and bioenergy systems using FEAT
● Assist in development of Penn State’s sustainable dairy cropping systems
● Develop crop growth model for double crop rye biomass production

Agricultural Research Science Engineer Rodale Institute, Kutztown, PA Spring 2011
● Evaluated energy and greenhouse gas emissions of the Farming Systems Trial (FST) cropping systems using FEAT

Agricultural Research Science Engineer USDA, Beltsville, MD Spring 2010
● Assessed emissions of the Farming Systems Project (FSP) cropping systems using FEAT

● Planned and supervised activities of employees engaged in orange oil production
● Coordinated not-from-concentrate (NFC) orange juice production and storage

SELECTED PUBLICATIONS

SKILLS & EXTRACURRICULAR ACTIVITIES
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● Computer languages: Python
● Languages: Portuguese