Preliminary studies for modeling diploid potato crop

Estudios preliminares para la modelación de variedades de papa diploide

Tatiana María Saldaña Villota

Universidad Nacional de Colombia – Sede Medellín

Facultad de Ciencias Agrarias, Departamento de Ciencias Agronómicas

Medellín, Colombia

2020

Preliminary studies for modeling diploid potato crop

Estudios preliminares para la modelación de variedades de papa diploide

Tatiana María Saldaña Villota

Tesis presentada como requisito parcial para optar al título de:
Doctora en Ciencias Agrarias

Director:
Doctor. José Miguel Cotes Torres

Línea de Investigación:
Fisiología de la Producción Vegetal

Grupo de Investigación:
Mejoramiento y Producción de Especies Andinas y Tropicales - GIMPEAT

Universidad Nacional de Colombia – Sede Medellín
Facultad de Ciencias Agrarias, Departamento de Ciencias Agronómicas
Medellín, Colombia
2020

Declaración de obra original

Yo, Tatiana María Saldaña Villota declaro lo siguiente:

He leído el Acuerdo 035 de 2003 del Consejo Académico de la Universidad Nacional. «Reglamento sobre propiedad intelectual» y la Normatividad Nacional relacionada al respeto de los derechos de autor. Esta disertación representa mi trabajo original, excepto donde he reconocido las ideas, las palabras, o materiales de otros autores.

Cuando se han presentado ideas o palabras de otros autores en esta disertación, he realizado su respectivo reconocimiento aplicando correctamente los esquemas de citas y referencias bibliográficas en el estilo requerido.

He obtenido el permiso del autor o editor para incluir cualquier material con derechos de autor (por ejemplo, tablas, figuras, instrumentos de encuesta o grandes porciones de texto).

Por último, he sometido esta disertación a la herramienta de integridad académica, definida por la universidad.

TATIANA MARÍA SALDAÑA VILLOTA

16/04/2021

Acknowledgments

A la Universidad Nacional de. Colombia – Sede Medellín, a la Facultad de Ciencias Agrarias, al Área Curricular de Producción Agraria Sostenible y al Departamento de Ciencias Agronómicas.

A la Universidad Nacional de. Colombia – Sede Bogotá, a la Facultad de Ciencias Agrarias.

Al Ministerio de Ciencia, Tecnología e Innovación - MINCIENCIAS (Antes: COLCIENCIAS). Entidad que financió mis estudios doctorales.

A University of Florida. Agricultural and Biological Engineering Department. Gainesville, FL. United States.

Al Sistema de Alerta Temprana de Medellín – SIATA, por la pertinente gestión y suministro de la información climática de las estaciones meteorológicas ubicadas en Medellín, Colombia.

Al profesor José Miguel Cotes Torres. Por su paciencia, dedicación y permanente apoyo. Diez años trabajando juntos y continúo aprendiendo de su experiencia y trayectoria académica.

Gracias a los profesores Kenneth J. Boote y Gerrit Hoogenboom. Por su hospitalidad y dedicación durante mi estadía en el McNair Bostick - Simulation Lab – Agricultural and Biological Engineering Department, University of Florida. Gracias por compartir sus invaluables conocimientos experiencia en fisiología y modelación de cultivos.

Al personal de la Estación Agraria Paysandú y del laboratorio de Fisiología Vegetal de la Universidad Nacional de. Colombia – Sede Medellín.

A Carlos Armando Rivera Moreno, estudiante de Ingeniería Agronómica de la Universidad Nacional de Colombia – Sede Bogotá.

Un agradecimiento especial a Patricia Moreno Cadena. Dejamos de ser "conocidas" por ser colombianas en un mar de gente de todo el mundo. Nos unió la nacionalidad, nos unió DSSAT y nos convertimos en grandes amigas. Gracias por la paciencia para responder cada pregunta que hice sobre SUBSTOR-Potato y DSSAT-CSM. Hoy somos un fuerte apoyo para sobrellevar todos los obstáculos que se nos presentaron durante este proceso. Sin duda, juntas hemos aprendido lecciones valiosas. Hemos sufrido, pero nos hemos divertido.

Resumen

Las variedades de papa diploide (*Solanum phureja* Juz. *et* Buk.) se cultivan en diferentes regiones de América del Sur, principalmente en Colombia, Ecuador, Perú y Bolivia. Estas variedades se destacan por sus características organolépticas y nutricionales. Sin embargo, no se han realizado suficientes estudios para mejorar la comprensión de la dinámica de crecimiento y desarrollo de este cultivo y mejorar las condiciones agronómicas del mismo. Con el objetivo de mejorar el conocimiento sobre estas variedades y su uso en estudios de modelación de cultivos, en esta investigación se evaluó el modelo SUBSTOR-Potato, y aunque el modelo predice bien el crecimiento de los tubérculos, no logra simular variables relacionadas con la parte vegetativa. Este estudio explica que las dificultades de SUBSTOR-Potato para simular la parte vegetativa se deben a fallas en la estimación del índice de área foliar y del uso eficiente de la radiación (RUE) en cultivos de papa. Por lo tanto, esta investigación también se llevó a cabo con el objetivo de estimar la fracción de radiación solar interceptada a partir del porcentaje de cobertura de follaje mediante el uso de fotografías. También muestra cómo estimar el índice de área foliar a partir de la cobertura del follaje aplicando la ley de Beer-Lambert. La expectativa, es que este conocimiento pueda usarse para desarrollar un modelo de cultivo de papa diploide. Finalmente, de acuerdo con las características del crecimiento en diferentes momentos fenológicos y de la importancia del RUE para comprender la productividad del cultivo, este estudio también tuvo como objetivo estimar el RUE del cultivo de papa diploide involucrando no solo la biomasa total acumulada respecto a la cantidad de PAR interceptada, sino que también tomó en cuenta las pérdidas de carbohidratos por respiración.

Palabras clave: Modelación de cultivos; evaluación de modelos; calibración de modelos; RUE; interceptación de la radiación; LAI; cobertura de follaje.

Abstract

The diploid potato cultivars (*Solanum phureja* Juz. et Buk.) are grown in different South American regions, mainly in Colombia, Ecuador, Peru, and Bolivia. These cultivars stand out for their organoleptic and nutritional characteristics. However, not enough studies have been carried out to improve the understanding of this crop growth and development dynamics and improve its agronomic conditions. With the aim of increase knowledge about these cultivars and their use in crop modeling studies, in this research, the SUBSTOR-Potato model was evaluated. Although the model predicts well the tuber growth, it has some issues simulating variables related to the vegetative part. This study explains that the difficulties of SUBSTOR-Potato to simulate the vegetative part are due to failures in the estimation of the leaf area index and the radiation use efficiency (RUE) in potato crops. Therefore, this research was also carried out with the objective of estimating the fraction of intercepted solar radiation from the foliage cover by using photographs. It also shows how to estimate the leaf area index from the foliage cover applying the Beer-Lambert law. The expectation is that this knowledge can be used to develop a diploid potato crop model. Finally, according to the growth characteristics at different phenological moments and the importance of the RUE to understand the productivity of the crop, this study also aimed to estimate the RUE of the diploid potato crop involving not only the total biomass accumulated concerning the amount of PAR intercepted, but also took into account the carbohydrate losses per respiration.

Keywords: Crop modeling; model evaluation; model calibration; RUE; radiation interception; LAI, foliage cover.

Table of Contents

List of figures

1.Introduction

The potato crop is original from the Andes (South America), and during the sixteen century, it was brought to Europe, and in a short time, the crop has been distributed worldwide (Sukhotu & Hosaka, 2006). Many civilizations adopted the crop, making it the primary source of daily energy and nutrients (Birch et al., 2012). After grain crops, potatoes are the most important food in the world (Lutaladio & Castaldi, 2009). The global impact of the potato crop on food security was first noticed with the Irish famine in 1845 when a disease, "late blight," wiped out all potato fields causing the death of more than one million people and the migration of other five million (Birch et al., 2012).

The potato cultivars of the species *Solanum tuberosum* L. and *Solanum tuberosum* subsp. *andigena* are the most important for the area planted and productivity; however, diploid potato cultivars (*Solanum phureja* Juz. *et* Buk.) are especially important for their good taste, high culinary and nutritional quality (high content of dry matter, proteins, vitamin C, carotenoids, and total phenols), also for its suitability for industrial processes, its low production cost compared to tetraploid cultivars of *S. tuberosum* (Burgos et al., 2009; Dobson et al., 2004; Ligarreto & Suárez, 2003). Besides, *S. phureja* cultivars are a source of resistance genes for late blight and other limiting diseases, which have been used for the genetic breeding of potato crops (Cadena et al., 2005; Escallón et al., 2005; Guzmán & Rodríguez, 2010; Moslemkhani et al., 2012).

The problem we are facing now is that despite the potential that diploid potato cultivars have, research on this species is still insufficient. Also, many environmental, social, and economic factors affect crop production for food security like this. In this sense, agriculture and research in crop sciences have the challenge of generating strategies to overcome limitations and take advantage of research opportunities in food security crops.

The knowledge about potato crops, particularly their physiology, has been widely developed based on tetraploid species that can be easily applied to the two main subspecies, *S. tuberosum* subsp. *tuberosum* and *S. tuberosum* subsp. *andigena*, but this valuable knowledge is not adaptable to a different species like *S. phureja*. The *tuberosum* and *andigena* subspecies came from a common species (*S. tuberosum* L.), and in this sense, they share many characteristics of their genome as they came from the same group of germplasm (Ovchinnikova et al., 2011; Spooner et al., 2014).

Although *S. tuberosum* and *S. phureja* originated about 8000 and 5000 BC near Lake Titicaca, which is located at 3,800 m above sea level on the border between Bolivia and Peru (Reddy et al., 2018), the tetraploid subspecies *tuberosum* was distributed in temperate zones around the world and adapted to long days (Gutaker et al., 2019). The species *S. phureja* does not tuberize in latitudes where the day length is higher than 12 h (Bukasov, 1933; Hawkes, 1990). Thus, its distribution was located in the tropics and is adapted to altitudes in frost-free Andean mountains of Venezuela, Colombia, Ecuador, and northern Peru (Correll, 1962; Hawkes, 1956; Lutaladio & Castaldi, 2009). Most of the available studies in potato crop physiology have been carried on *S. tuberesum* subsp. *Tuberosum* under temperate conditions. These can be applied to the cultivars of *S. tuberosum* subsp. *andigena* adapted to the Andes and because, as has been said, they have the same genetic base. However, these studies cannot be applied to the physiology of *S. phureja* because they are different species, with different genotypes and consequently with different phenotypic expressions and different metabolisms and physiological processes. In addition to the differences in their ploidy, some differences in physiological aspects between the subspecies of *S. tuberosum* and *S. phureja* that stand out the most are:

- *S. phureja* possesses no dormancy period (Dodds & Paxman, 1962). Tubers intended as seeds for the next cycle should be sown within a few days so that they do not lose viability. When a tuber of *S. phureja* is delayed in sowing, the plant from that aged seed accelerates its metabolic processes with consequences in the growth and development, in such a way that as soon as it is sown, the plant emerges and flowers very quickly, altering the reproductive demands and the accumulation of carbohydrates. *S tuberosum* tubers can be stored for months without losing viability or altering the crop phenological phases (Alamar et al., 2017).

- *S. phureja* has decumbent growth pattern, and this could represent its ancestral condition (Hariharan et al., 2016). Meanwhile, S. tuberosum has erectus growth pattern.

- There are no clear studies that make a punctual marking of the beginning and end of the phenological stages in *S. phureja*. And without this information, it is complicated to predict these stages, and consequently, it is not so easy to propose improvements to the production system if the dynamics of growth are not yet known integrally. *S. tuberosum* has clearly determined growth. The onset and duration of the phenological stages are known with outstanding precision, the growth of plants in the crops is very homogeneous.

- *S. phureja* does not have uniform tuberization, unlike *S. tuberosum*. Tetraploid cultivars have uniform tuberization, and tubers are harvested at the same maturation stage for marketing and consumption or storage for later planting (Hawkes, 1990). Diploid cultivars of S. *phureja* tuberize with non-established order; while the crop reaches the maximum tuber fill, those which matured faster start their metabolic processes of germination. This indicates that the crop is not necessarily fully domesticated (Hariharan et al., 2016).

- *S. phureja* grows faster than *S. tuberosum* (Hawkes, 1990; Spooner et al., 2014). Morphologically, *S. phureja* corresponds to smaller plants of accelerated and unrestrained growth. Leaves of diploid potato cultivars grow indeterminately, turning the row of plants into a vine, making it impossible to establish spaces for each plant.

Given the need to provide studies that contribute to the improved understanding of *S. phureja*, we set a long-term goal of developing an initial crop model of diploid potato cultivars as a Research Group. To reach that goal, we needed to start with studies that would allow us to explore and more clearly address the existing knowledge on *S. phureja* and address gaps that we found in that exploration towards a simulation model.

Crop modeling is one of the disciplines in crop physiology that has advanced the most in recent years to offer alternatives to creating different crop production scenarios (Jones et al., 2003; Wallach et al., 2019). The properly evaluated and calibrated crop models allow

the creation of experiments where the effects of factors such as environmental, nutritional, and water stresses can be evaluated during the cycle and based on the evaluation of the possible responses of the crop; the models allow exploring and developing management strategies to achieve better performance under different conditions (Haverkort & Top, 2011). However, the vast majority of crop modeling studies focus on grain crops (White et al., 2011), while tubers and roots crops have received less attention in model testing, model improvement, and applications (Raymundo et al., 2014).

SUBSTOR-Potato (Griffin et al., 1993; Ritchie et al., 1995), available in DSSAT-CSM (Hoogenboom et al., 2019), is one of the most used or applied models in potato crops. However, the model has been developed using information from tetraploid potato cultivars and under temperate conditions. SUBSTOR-Potato has not been tested to simulate the growth and yield of diploid potato cultivars in the tropics. In this sense, it is crucial to carry out this kind of research to include this type of cultivars in the improvements of SUBSTOR-Potato routines and other models such as APSIM-Potato (Brown et al., 2011), INFOCROP-Potato (Singh et al., 2005), LINTUL Potato DSS (Haverkort et al., 2015), NPOTATO (Wolf, 2002), GLAM-Potato Crop Model (Jennings et al., 2020), among others.

One of the most critical aspects of developing crop models is the accurate determination of the crop physiological level assumptions. And the interception of radiation is an essential input to the model mechanisms. Basically, the photosynthesis, respiration, and adequate translocation and allocation of the carbohydrates produced will depend on solar energy entry into the system. Based on this fact, during the research carried out in the second chapter of this dissertation, we exposed that the SUBSTOR-Potato model has difficulty simulating the plants aboveground part (LAI and vegetative dry weight). If the model does not represent these variables well, the interception of photosynthetically active radiation would also have failures, and consequently, the carbohydrate production processes, their translocation, and final yield are also affected.

Nevertheless, the SUBSTOR-Potato model simulates well the tuber dry weight and variables closely related to this organ (total dry weight and the harvest index), suggesting that the manual calibration of the genetic coefficients leads to equifinality; that is, the model reaches a desirable final state (outputs) even if the path does not necessarily have reasonable assumptions and physiological principles. This issue can be explained by one

of the difficulties in the potato crop simulation (not only of SUBSTOR-Potato model); the method usually employed to estimate the leaf area index (LAI) and the ability to capture the incoming radiation and convert it into biomass (RUE).

There is a clear need to establish non-destructive methods for estimating LAI that also allow being more accurate in potato crops, which is an oversight to apply the relationship between the total leaf area and the area occupied by the soil due to the potato plant architecture and the distribution of the leaf area through the canopy (Jonckheere et al., 2004). Also, through destructive methods, there is difficulty obtaining large amounts of input data; this is one of the main limitations of exhaustive sampling, which is undoubtedly laborious and time-intensive (Luo et al., 2020). Thus, the second chapter of this dissertation offers an alternative to destructive methods for estimating LAI in potato crops from the foliage cover. The proposed method would be the closest to the potato crop conditions. The foliage cover depends on the architecture, and the crop simulation model would approximate the plant architecture and biomass production and yield with suitable assumptions. Furthermore, with an adequate estimation of LAI as an essential parameter in PAR interception and absorption, it is possible to estimate an adequate conversion rate into biomass (RUE).

Most crop models use RUE to determine crop productivity, and many studies on this topic have been published. The studies have followed an estimation method that states that the RUE corresponds to a single value that comes from the slope of the linear regression between the total biomass and the PAR accumulated during the crop season (Murchie et al., 2019; Sinclair & Muchow, 1999; Stöckle & Kemanian, 2009). This method assumes the plants have a single and constant RUE without considering ontological variations and respiratory processes that make the ability to convert light energy into biomass variable over time. A significant loss of carbon is considered as mitochondrial respiration, a vital process divided into growth and maintenance respiration under the associated physiological process. Respiration as a whole can vary from 30% to 60% of total carbon exchange, and consequently, it has a significant impact on RUE (Murchie et al., 2019). However, many approaches do not consider respiratory processes in RUE calculations because it is difficult to measure and define respiration in field conditions and practice (Amthor, 2000). This was the aim of the third chapter of this dissertation; the estimation of a changing RUE over time, considering respiratory processes during the crop development.

The SUBSTOR-Potato performance and finding the model difficulties simulating the LAI and the vegetative part showed us that there are still failures in the conceptualization of the principles that explain the dynamics of potato crop growth, the estimation of LAI, and the adequate estimation of the RUE during the crop cycle. These parameters become the keys to improving the existing crop models or the key to generating new routines that incorporate these proposals and improvements. Thus, according to characteristics of the potato crop, particularly diploid potato cultivars with unique characteristics such as their accelerated growth rate, their non-existent dormancy period, and their smaller size compared to tetraploid cultivars, they call for attention to studies of the physiology of the growth of this crop.

Finally, the calibration and evaluation of the SUBSTOR-Potato model also showed us that there are still misunderstandings in using statistical parameters to evaluate the quality of the simulations when representing the observed data. For this reason, a brief review of the most used statistics in the evaluation of models was made. This revision clarifies that the statistics that work best in crop modeling evaluation studies are the RMSE, the rRMSE, and the new index of agreement (d_1). These indices should be used together, and by themselves, they are insufficient to establish the quality of a simulation model. This revision is presented as Appendix A.

1.1   Goals and objectives

Given the deficiency of knowledge on crucial aspects of *S. phureja* physiology, this research aimed to carry out preliminary studies that begin to supply the demand for knowledge on *S. phureja* with a view to the development of a simulation model.

In order to begin to fill the gap in knowledge about *S. phureja*, especially in the area of crop modeling, this work developed three main secondary objectives:

- Assess the SUBSTOR-Potato model's performance (calibration and evaluation) for simulating the growth of five new diploid potato cultivars.

- Estimate the fractional radiation interception from fractional foliage cover by using photographs. This study also shows how to obtain the LAI from fractional foliage

cover as a secondary objective by applying the Beer-Lambert law. Thereby, the expectation is that this knowledge can be used to develop a diploid potato crop model.

- Estimate the RUE of the diploid potato crop involving not only the total biomass accumulated concerning the amount of PAR intercepted but also took into account the losses by respiration.

2. Radiation interception and leaf area index from foliage cover in diploid potato[*]

ABSTRACT

The leaf area index (LAI) is defined as the proportion of leaf area per unit of land area. It is also considered as an essential factor in the crop's ability to capture solar energy. Destructive methods of LAI estimation involve significant areas of cultivation and individually measuring the total leaf area, which is not an accurate method to assess the LAI in diploid potato (*Solanum phureja* Juz. et Buk.) cultivars. The objective of this study was to evaluate a practical method for determining the fractional radiation interception and the LAI based on the fractional foliage cover in diploid potato cultivars found using digital photographs and applying open-source software. Then, we compared the results of this method with the results obtained using a canopy analyzer. The results obtained allow us to estimate foliage and obtain the fractional radiation interception properly, and with these two variables, it is possible to make reasonable estimates of the LAI. It is common to model the LAI, and from this value estimate, the fractional radiation interception. We propose to model the architecture of the plant to know how the diploid potato plant covers the soil in a given space and how much radiation it intercepts, then estimate LAI. This method of estimation would be the closest to the cultivation conditions. Foliage cover depends on the architecture, and the crop simulation model would approximate the plant architecture and not just biomass production and yield.

2.1. Introduction

One of the main functions of the foliar area is to intercept the incident solar radiation, an essential factor in crop growth and development. Light interception is the required energy input in vital processes such as photosynthesis and its subsequent production, allocation, and partition of biomass (Gifford et al., 1984). Thus, the productivity of crops can be understood as the product of light energy intercepted during a crop cycle and the efficiency to convert that energy to biomass (Monteith, 1977).

Therefore, estimating the fraction of intercepted solar radiation (i) is an important source of information that can be used to estimate the radiation use efficiency (RUE), to analyze the differences between varieties in terms of their capability to capture energy, and to determine the influences of environmental factors in productivity (Hatfield, 2014; Sinclair & Muchow, 1999).

The foliage cover (f) that absorbs the fraction of the incident photosynthetically active radiation (PAR) depends on the canopy structure. However, the weather conditions can be important; for example, in cloudy weather, radiation is received from all angles, and as a result, it penetrates further into the canopy (Russell et al., 1989). Foliage cover and leaf area index (LAI) are related and depend on each other to intercept the incident radiation (De la Casa et al., 2007, 2008).

It is possible to estimate LAI from foliage cover with a known value of radiation-extinction coefficient (k), which is specific for crops and cultivars (Vose et al., 2008). Leaf area index was defined for the first time by Watson (1947) as the ratio of leaf area per ground area unit. This index determines and controls canopy radiation interception and extinction, water, and gas exchange. Any change in LAI (defoliation, drought, pest, and diseases) means changes in crop productivity (Bréda, 2003). Leaf area index is also used in many growth analysis and crop modeling studies (El-Sharkawy, 2011; Hoogenboom et al., 2019; Jones et al., 2003; Zhao et al., 2019).

Usually, LAI is obtained through destructive methods with which direct measurements of the total leaf area (TLA) with planimeters or leaf area meters are taken. Total leaf area is divided by the area that, theoretically, is occupied by the plant according to crop planting

density. In diploid potato crops (*Solanum phureja* Juz. et Buk.), the destructive method does not work accurately due to the plant architecture, because unlike tetraploid potato crop (*Solanum tuberosum* L.), the leaves extend outside the assigned area for its growth and development, occupying different spaces (Figure **2-1**). This field condition is why quantifying the TLA and dividing by the area of land occupied by the plant is not a real approximation of LAI on this crop. The definition of LAI, according to Watson (1947), is suitable for trees or plants that have one main stem and flat individual leaves. However, if the leaves and their leaflets are not flat, and there is no stem as a principal axis from which the leaves are attached, the relation between TLA and the land area to estimate the LAI is not clearly defined (Jonckheere et al., 2004). Besides, direct LAI measurement methods require time and large field areas are required to have enough material to sample over time during the crop cycle.

Figure 2-1. Overlapping leaf area between diploid potato plants on field conditions from different points of view: (a) from two hills, note that the leaf area of the left plant uses the area assigned to the right plant and vice versa; (b) between plants over one hill, note the overlap between leave of plants is higher than among plants over different hills; and (c) a bird's-eye view of crop, note that the leaf area always uses a higher area than the assigned by the crop planting density.
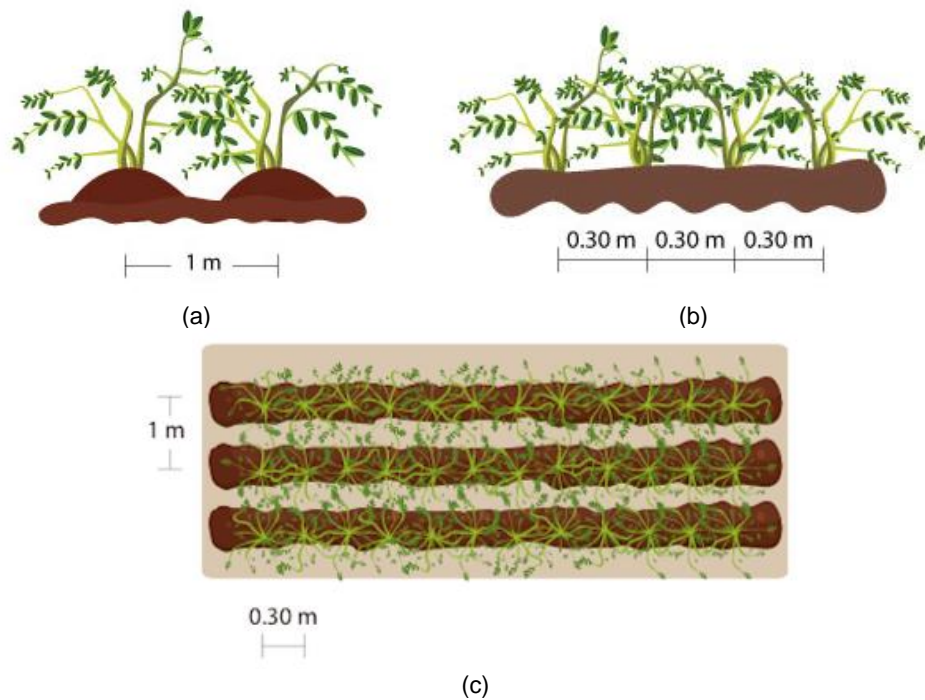
Beer–Lambert law allows relating the total leaf area and the solar radiation intercepted by the crop. Therefore, the intercepted radiation or LAI can be measured in the field, and through *k*, it is possible to estimate *i* or LAI, respectively.

Due to the architecture of diploid potato plants, intercepted solar radiation would be a better option to measure than LAI. There are more precise methods to measure the intercepted solar radiation, but they are more expensive and have more requirements and limitations (such as a canopy analyzer), and more straightforward methods exist such as the use of digital cameras (Figure **2-2**).

Figure 2-2. Estimating the leaf area index (LAI) and fraction of intercepted solar radiation (a) by using a canopy analyzer; (b) from digital photographs, and (c) destructive method for estimating LAI, where the total leaf area is measured and divided by the area of soil that is theoretically assigned by the crop planting density. Parts (a) and (b) use the Beer Lambert law to obtain the leaf area index, and require an appropriate ellipsoidal leaf angle distribution parameter to generate the correct values of LAI
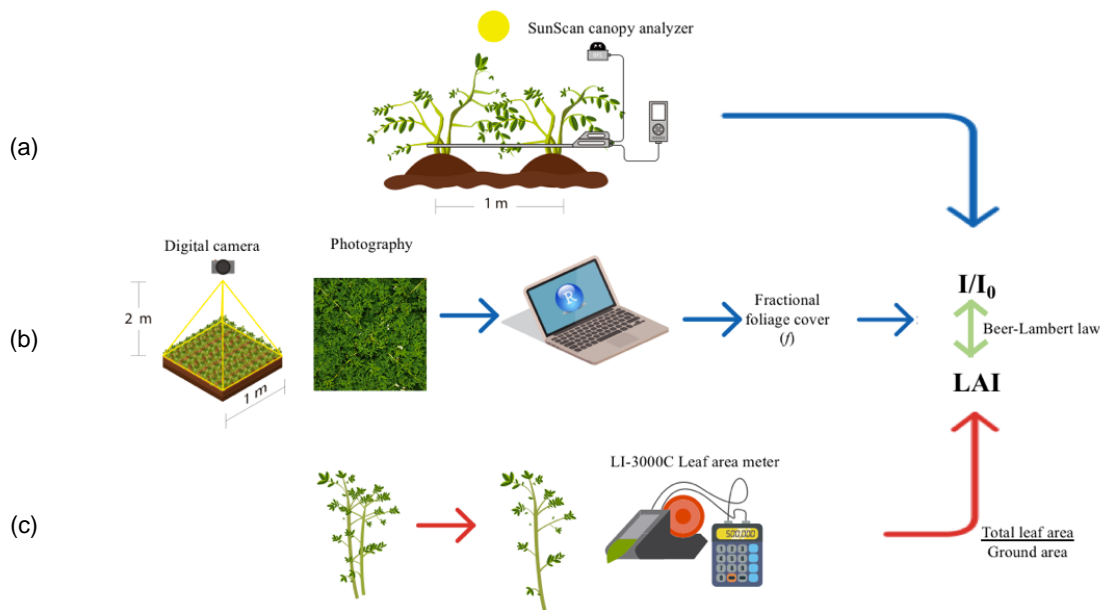
Nondestructive methods to estimate LAI are welcome to obtain values closer to the true value for crop. With nondestructive methods, LAI is computed based on the transmitted light through the canopies. The principle to indirectly estimate foliage cover, and consequently LAI, is that the transmittance of radiation intercepted by a canopy layer could be represented by analogy with Beer–Lambert law (Equation [[2-1]), that states the attenuation of radiation in a homogeneous medium depends on the incident irradiation, the canopy architecture, and the optical properties (Monsi & Saeki, 1953).

$$I = I_0 \, e^{(-\mathrm{k}_i * LAI)}$$

[2-1]

where I is transmitted light, I_0 is the incident light, and k is the radiation-extinction coefficient. Taking into account that f is defined by the vertical projection of the canopy on the ground surface:

$$f = 1 - I_v$$

[2-2]

where I_v is the direct transmittance of light reflected from the soil surface along a vertical path through the canopy. The fraction of intercepted radiation (i) by the canopy is:

$$i = 1 - I_i$$

[2-3]

where I_i is the mean transmittance of radiation into the plant canopy along all the possible ways, weighted according to the geometric distribution of direct and diffuse radiation. In this sense, f and i are determined by the same process, mainly controlled by leaf angle distribution (Steven et al., 1986).

The theoretical relationship between cover and LAI could be computed from Equation [[2-1]. Thus, f is given by:

$$f = 1 - e^{(-\mathrm{k}_f * LAI)}$$

[2-4]

And the theoretical relationship between fractional radiation interception and LAI could be computed as follows:

$$i = 1 - e^{(-\mathrm{k}_i * LAI)}$$

[2-5]

By combining Equations [2-4] and [2-5], we obtain the relationship between f and i:

$$i = 1 - (1 - f)^{\mathrm{k}_{ratio}}$$

[2-6]

where k_{ratio} is calculated by ${\mathrm{k}_i} / {\mathrm{k}_f}$.

This research was carried out with the aim to estimate the fractional radiation interception from fractional foliage cover by using photographs. As a secondary objective, this study also shows how to obtain the LAI from fractional foliage cover by applying the Beer–

Lambert law. Thereby, the expectation is that this knowledge can be used for the development of a diploid potato crop model.

2.2. Materials and Methods

2.2.1.   Location and plant material

An established crop in an area of 500 m^2 with five cultivars of diploid potato (Paola, Colombia, Paysandú, Primavera, and Violeta) in Medellín, Colombia (6°12'36'' N, −75°30'25'' W) was used. The distance between the plants was 0.25 m, and the distance between rows was 0.90 m. Thus, the plant density was 44,444 plants ha^{-1}. The field was at 2,539 m above the sea level, with an average temperature of 13.2°C. In this field crop, original incoming radiation and the shaded light intensity under the leaf area were measured. Photographs of the top of the canopy were also taken to estimate the fractional foliage cover.

2.2.2.   Fractional foliage cover (*f*)

A 1 by 1 m, square PVC tubing frame was set up between two hills along with the field crop. Thirty-three sites were randomly selected throughout the field crop; four sites corresponded to 'Colombia', six sites to 'Paysandú', seven to 'Paola', eight to 'Primavera', and the last eight sites corresponded to 'Violeta'. A total of 105 photographs were taken throughout the field crop as follows: seven photos of Colombia, 32 of Paola, 14 of Paysandú, 27 of Primavera and, 25 of Violeta. The photographs were taken using a commercial camera (NIKON® 5300, Nikon, Tokio, Japan) from a distance of 2 m above the frame.

The photographs were taken around noon, coinciding with the measurement of incoming radiation and the shaded light intensity. Capture NX-D Software (NIKON®, 2019) was used to correct lens distortion, to adjust distortion due to the point of view, and to cut the area that was outside the frame. These measurements were taken at 70 d after planting. One value of *f* was obtained for each photograph, and the values for each site were averaged.

We used two methods to obtain the fractional foliage cover. The first one was the RGBmax approach (Campillo et al., 2010), and the second one was the method proposed by

Patrignani and Ochsner (2015) in their mobile application CANOPEO, a tool used for measuring the percentage of green canopy cover.

The JPEG library (Urbanek, 2014) of R environment (R Core Team, 2020) was used to decompose the photograph into R, G, and B channels. RGBmax counts pixels when R < G, B < G, G is ≤0.9, and when G ≥0.1. The CANOPEO method counts the pixels when R < 0.9G, B < 0.9G, and when 2G > (20/255)(B + R).

2.2.3.   Fractional radiation interception (*i*)

Intercepted radiation and LAI measurements were taken directly on the field using the SunScan Canopy Analysis System (Delta-T Devices, Cambridge, UK) (Webb et al., 2008). The data were recorded around solar noon, perpendicular to the crop hill in the same area (1 m^2) where the photographs were taken. Eight records of incident radiation (I_0) and transmitted radiation (I) were taken per square frame, and the fraction of radiation intercepted (*i*) by the canopy was calculated as Equation [2-3] where $I_i = {}^I\!/_{I_0}$. Finally, the average of these eight points was obtained to estimate the *i* value for 1 m^2.

2.2.4.   *k$_{ratio}$* estimation

With thirty-three data values obtained, a regression without intercept between log(1 − *i*) and log(1 − *f*) was computed, and *k$_{ratio}$* corresponds to the β obtained in the regression, and *k$_{ratio}$* was estimated by both methods, RGBmax and CANOPEO.

2.2.5.   Ellipsoidal leaf angle distribution parameter and LAI estimation

Because in our research it is necessary to obtain a nondestructive LAI value, the most accurate method currently is the one used internally by the canopy analyzer (SunScan), in which ellipsoidal leaf angle distribution parameter (ELADP) is a way to characterize the horizontal or vertical trend of the leaves in the canopy (Campbell, 1986).

It is assumed that the leaves in the canopy are distributed in the same direction and proportion as the surface area of an ellipsoid, that is, symmetrical about the vertical axis. This parameter can be described by the ratio of the horizontal to vertical axes of the

ellipsoid. An ELADP of 1.0 gives a spherical leaf angle distribution where all leaf angles are equally represented. A high ELADP (e.g., 1,000) represents a broad flat ellipsoid, that is, the leaf elements are all horizontal, and a low ELADP (0.0) represents a tall thin ellipsoid, that is, all the leaf elements are vertical.

Both LAI and *k* depend on the estimation of ELADP. This parameter has a crucial role in plant development because it regulates energy balances, microclimate, and light competition (Campbell, 1990). The direction of the angles of inclination and the azimuthal angles of the leaves are the factors that determine leaf angle distribution (Sinoquet & Andrieu, 1993). Information about leaf angle distribution in diploid potato varieties does not exist in the literature. Even in tetraploid potato varieties, the information available is limited. Therefore, seven plants from each cultivar in the field crop were randomly selected to measure their height and the horizontal distance to achieve an approximation to an ELADP value according to the method proposed by (Campbell, 1990).

To estimate the radiation penetration through the canopy, the model developed by Campbell (1986) was followed. The model uses the model of light penetration developed by Mann, Curry, DeMichele, and Baker (1980) and stated that *k* depends on the ELADP as follows:

$$k(\text{ELADP}, \theta) = \frac{\sqrt{\text{ELADP}^2 + \frac{1}{(\tan\theta)^2}}}{\text{ELADP} + \frac{1}{2 \times \text{ELADP} \times e_1} \log\frac{1+e_1}{1-e_1}}, \qquad \text{ELADP} \geq 1 \qquad [2\text{-}7]$$

$$k(\text{ELADP}, \theta) = \frac{\sqrt{\text{ELADP}^2 + \frac{1}{(\tan\theta)^2}}}{\text{ELADP} + \frac{\arcsin e_2}{e_2}}, \qquad \text{ELADP} \leq 1 \qquad [2\text{-}8]$$

where

$$e_1 = \sqrt{1 - \frac{1}{\text{ELADP}^2}} \qquad [2\text{-}9]$$

and

$$e_2 = \sqrt{1 - \text{ELADP}^2} \qquad\qquad [2\text{-}10]$$

When ELADP = 1, Equations [2-7] and [2-8] reduce to:

$$k = \frac{1}{\sin\theta} \qquad\qquad [2\text{-}11]$$

For the estimation of LAI, an iterative procedure was used as follows:

1.   Set a higher initial value for LAI (e.g., 20).
2.   Set a lower initial value for LAI (e.g., 0).
3.   Calculate the mean between the upper and lower values and obtain LAI.
4.   Calculate the numerical integral:

$$\tau_{diff}(\text{ELADP}, LAI) = \frac{1}{\pi}\int_0^{\frac{\pi}{2}} 2\pi \sin(\theta)\cos(\theta)\; e^{(-k(\text{ELADP},\theta)LAI)}d\theta \qquad [2\text{-}12]$$

5.   Obtain the estimate (I / I$_0$) value.
6.   Calculate the difference between the estimated value and the value observed by SunScan.
7.   If the absolute value of the difference is less than 0.00001, then LAI obtained in Step 3 is the estimated LAI. Otherwise, follow Step 8.
8.   If the difference is greater than 0, the upper initial LAI is updated by estimate LAI in Step 3, and Step 1 is restarted. If the difference is less or equal to 0, the lower initial LAI is updated by the LAI estimate at Step 3, and Step 2 starts again.

In the previous algorithm, the output is obtained in Step 7. This procedure was used to estimate LAI with the original data obtained with the SunScan and with the data estimate by the foliar cover model.

2.3. Results and Discussion

### 2.3.1. Ellipsoidal leaf angle distribution parameter

The average ELADP value obtained for diploid potato cultivars was 0.75, with a minimum of 0.60 and a maximum of 0.85. This value is lower than the values proposed by (Campbell

and van Evert (1995) for tetraploid potato crops, which are between 1.70 and 2.47, and consequently, the value is less than the values recommended by Webb et al (2008) for the use of SunScan. When devices like SunScan or any canopy analyzer use a higher ELADP, the LAI obtained is underestimated. That is, if high ELADP values are used, the estimated LAI values would be lower, whereas with low ELADP values, higher LAI values are obtained. By using the ELADP values suggested by SunScan, the researcher will obtain underestimated LAI values, which will consequently generate errors in the following analyzes where LAI is required.

2.3.2.   *k_{ratio}* **estimation**

The estimated *k_{ratio}* values were 0.74 and 0.93 for RBGmax and CANOPEO, respectively. The values obtained are statistically different because the confidence intervals do not overlap each other (Figure **2-3**). The adjusted r^2 of the models were higher than 0.90.

Figure 2-3. Logarithmic transformations of the relationship between interception and cover in diploid potato cultivars. The slopes of the regressions are *k_{ratio}*. The green line represents the CANOPEO method, and the red line represents the RGBmax method. The limits of confidence at 95% are shown next to the *k_{ratio}* values.
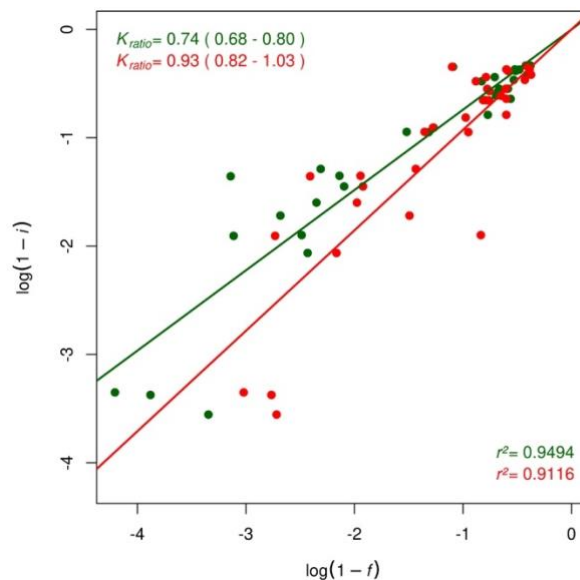

Determining foliage cover through photographs allows us to estimate the transmittance (I/I_0) appropriately, and with this information, it is possible to obtain a more accurate approximation of LAI. This method is practical; the photographs are taken in a short time and the required elements are accessible. On the other hand, SunScan also estimates LAI

through measuring (I/I_0) and applying Beer–Lambert law internally, but the equipment is too expensive and has several limitations: measurements can only be taken within 3 h around the solar noon, and full sun in the blue sky is required to obtain satisfactory measurements results. Besides, the SunScan used in this research has the limitation that the measurements are not suitable if the incident radiation is less than 200 µmol m^{-2} s^{-1} (Webb et al., 2008). Finally, obtaining LAI through destructive methods does not offer a good approximation in diploid potato, because as explained before, the leaves take up more space than the corresponding one based on crop planting density (Figure **2-1**).

In diploid potato, we can observe that when foliar coverage is 0.9, the fractional radiation intercepted is 0.78, and the LAI predicted is 2.5, while when $f = 0.4$, $i = 0.3$ and LAI = 0.8. Higher LAI is expected when foliage cover has higher values. (Figure **2-4**).

Figure 2-4. Fractional radiation interception i (left ordinate axis) and leaf area index (right ordinate axis) predicted from fractional foliage cover in diploid potato cultivars. The green line represents the CANOPY method to estimate k_{ratio}, and the red line represents the RGBmax method. The limits of confidence at 95% are shown next to the k_{ratio} values
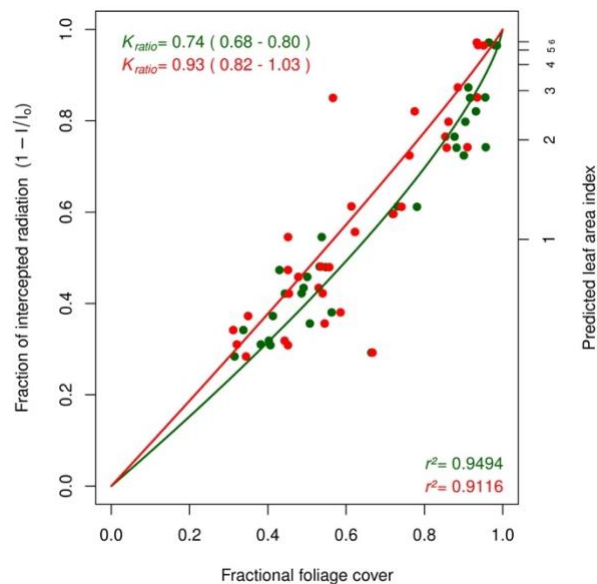
It is common to model the LAI, and from this value estimate, the fractional radiation interception. We propose to model the architecture of the plant to determine how the plant covers the ground in a given space and how much radiation intercepts and then estimate LAI, because as explained before, this method would be the closest to the growing conditions of the crop. Foliage cover depends on the architecture, and the crop simulation

model would approximate to the plant architecture and not just biomass production and yield.

2.4. Conclusion

Currently, the fastest way to estimate LAI in diploid potato crops is using the canopy analyzer. The resulting outputs (LAI) also correspond to an internal calculation from variables such as incident radiation, transmittance, ELADP, and k. Following the same algorithm described in the SunScan user manual (Webb et al., 2008) and also described in the materials and methods section, LAI was estimated on a computer making a more significant number of iterations. We used an epsilon of 1×10^{-5}, and the number of steps of the numerical integral was 1×10^{5}, while the SunScan has an epsilon of 0.1 and only does 1,000 iterations. Thus, the SunScan estimate is less accurate than that obtained through the same algorithm on a computer, and the requirements correspond to good quality photographs of the canopy and the incident radiation.

3. General discussion, conclusions and recommendations

It is crucial to increase the knowledge of diploid potato crop growth dynamics, basically because there are very few studies on this species and what has been done wrongly is to apply the knowledge of other species such as *Solanum tuberosum* L., leading us to make wrong inferences. In this sense, we started to work on existing tools to study potato crop growth and development, so we calibrated and evaluated one of the most used models worldwide: the SUBSTOR-Potato model, one of the submodels available on DSSAT-CSM (Griffin et al., 1993; Hoogenboom et al., 2018).

We know that many models simulate the growth of the potato crop, such as APSIM-Potato (Brown et al., 2011), AquaCrop (Steduto et al., 2009), CropSystVB-CSPotato (Alva et al., 2010), DAISY (Hansen et al., 2012), DANUBIA (Lenz-Wiedemann et al., 2010), Expert-N-SPASS (Gayler et al., 2002), INFOCROP-Potato (Singh et al., 2005), LINTUL-Potato DSS (Haverkort et al., 2015), NPOTATO (Wolf, 2002), POMOD (Kadaja & Tooming, 2004), GLAM-Potato Crop Model (Jennings et al., 2020), Potato Calculator (Jamieson et al., 2006), SIMPOTATO (Hodges et al., 1992), WOFOST (Boogaard & Kroes, 1998), among others. The SUBSTOR-Potato model was chosen because of its wide application and acceptance by the scientific community and because it considers in its routines management aspects such as water and nitrogen balances and also allows hypothetical evaluations to be made in the face of climate change scenarios such as increases in environmental temperature and variations in CO_2 concentration (Saqib & Anjum, 2021).

Tuber growth of the five diploid potato varieties was generally well simulated by the SUBSTOR-Potato model. (**Error! Reference source not found.** and **Error! Reference source not found.**) with rRMSE ranged between 1.741% and 56.417%; although the range of the rRMSE is wide, it is considered adequate for growth variables with high biomass

accumulation, such as tubers (Li et al., 2015; Willmott et al., 1985; Yang et al., 2000). Adequate predictions were also observed for total plant dry weight (rRMSE 6.006% and 43.904%) (**Error! Reference source not found.** and **Error! Reference source not found.**) and the harvest index (6.226% and 41.570%) (**Error! Reference source not found.** and **Error! Reference source not found.**). Considering that total dry weight and harvest index are directly affected by tuber weight, the good performance of SUBSTOR-Potato is understood and accepted.

But what happened to the variables related to the vegetative part of the plant? Despite the exhaustive calibration and modification of the LALWR and extinction coefficient in the model routines, the model did not adequately predict the vegetative dry weight and LAI where in some cases, rRMSE values were higher than 90% (**Error! Reference source not found.** and **Error! Reference source not found.**), (**Error! Reference source not found.** and **Error! Reference source not found.**). When the model apparently achieves a good simulation in these variables, it is because the measured data corresponds to low stem and leaf productivities.

We consider that achieving a good simulation of tubers, but a poor simulation of the vegetative part was a result obtained by equifinality, i.e., the calibration and combination of genetic and ecotype parameters allowed a result of interest for the type of crop by simulating well the growth of tubers, but leaves doubts regarding the functionality of the model for its performance in predicting the growth of the leaves and stems.

If one of the inputs to the model is solar radiation and the interception and absorption of that energy are regulated by the LAI and also converted into biomass through the RUE, it is expected that the first variables to be well simulated are LAI and the vegetative dry weight. The SUBSTOR-Potato model assumes a very rigid leaf area growth. In the PT_GROSUB.for routine between lines 392 and 398, where the relative leaf growth rate (RLGR) is defined, the value of 0.5 (value taken from Ingram and McCloud (1984)) should be a user-modifiable ecotype or species coefficient, as well as 0.75 of leaf growth (GROLF) for the stem growth conversion (GROSTM). Ingram and McCloud (1984) evaluated *Solanum tuberosum* cv Sebago at locations in Florida, US, where temperatures above 30ºC during the crop cycle were reported. Besides, the cultivar Sebago yields more than 30 t ha^{-1} (Pregno & Armour, 1992); Thus, the SUBSTOR-Potato model uses the leaf and stem

conversion rate of a single variety evaluated under subtropical conditions with very different growing conditions than *S. phureja* cultivars and even *S. tuberosum* cultivars cultivated in the tropics.

As highlighted in the discussion of the chapter "Adapting the SUBSTOR-Potato model for simulating diploid potato cultivars", different authors claim that failures in the simulation of vegetative growth of potato crops are due to possible failures in the measurement of LAI. Failures in the estimation of LAI as the ratio of total leaf area to the soil area occupied by the plant is an issue of great importance. It is assumed that the destructive method is the most accurate in plants with clearly determined growth patterns. In plants such as *S. phureja* with decumbent growth patterns, where stems and leaves continue to grow after flowering (Ovchinnikova et al., 2011), and occupy the area of neighboring plants with their growth, the usual LAI estimation method is not as suitable (Figure 2-1). This problem justifies the second chapter of this dissertation entitled "Radiation interception and leaf area index from foliage cover in diploid potato", which proposes a non-destructive alternative for LAI estimation from leaf cover exposed to incident solar radiation. This method solves the issue with soil area occupied by the plants and does not require costly and time-consuming destructive sampling. The method only requires good quality photographs of the canopy top and adequate measurements of incident radiation.

Having solved one of the problems in the attempts to model the growth and development of *S. phureja* came the effort to find an estimated RUE with more realistic assumptions. We hypothesized that the RUE is not a constant value for the entire crop cycle, and its estimation as the slope of the linear relationship between intercepted PAR and total accumulated biomass is not a value that truly reflects the capacity to convert light energy into biomass. Much of the efficiency of plant growth is affected by the respiratory processes of growth and maintenance. These processes are relative to plant growth over time (Amthor, 1984, 2000; Thornley, 2011; Yamaguchi, 1978). Thus, the energy conversion capacity cannot be a constant value throughout the crop cycle. The RUE varies with the plant age and is stimulated by significant events in the life cycle, in potato, with such a carbohydrate-demanding event as the tuber initiation and tuber filling (**Error! Reference source not found.**).

This work is entitled "Preliminary studies for modeling diploid potato crop", corresponding to the need to have a clear basis for the dynamics of growth and development of the diploid potato crop. With an adequate LAI estimation method and a RUE calculation with correct assumptions, we have the first step of building a simulation model, which is the correct energy input to the system. With the appropriate assumptions of solar energy interception and absorption through leaf cover and the correct transformation of energy into biomass, it is possible to begin to think about organ growth rates and photoassimilates translocation rates.

Taking into account that the construction of a model has different levels, the first step would consider:

- PAR interception, absorption, and transformation into biomass through the RUE.

A second level would involve:

- The effect of environmental factors in addition to solar radiation, such as temperature, on physiological processes (photosynthesis, respiration, transpiration, photorespiration).
- The effect of temperature on the rates of growth and translocation of assimilates to the plant component organs.

A third level would involve nitrogen and water balances:

- The effect of nitrogen on plant growth and development. The effect on vegetative development and tuber filling.
- The effect of water deficit on growth and development.

To reach each stage or level in the approximation of a model and insisting on the lack of information on the basic physiology of *S. phureja*, the recommendations we make are to propose studies and research in basic physiology such as the following:

- Studies on water stress in *S. phureja*.

- In *S. phureja*, the exact time of onset of tuberization is uncertain. In *S. tuberosum*, tuberization coincides with flowering. *S. phureja* flowers before the onset of tuber filling. Furthermore, tuberization occurs very early in the cycle. It is possible to measure the onset of tuberization, but currently we are not able to predict this event.

- Studies on the effect of temperature on development, respiratory rates, leaf expansion, and photoassimilates translocation.

- The effect of soil nutritional conditions and fertilization on the growth and development of *S. phureja*. The fertilization plan of *S. tuberosum* is clear and concrete, and attempts have been made to manage *S. phureja* based on this fertilization management. However, probably much of the fertilizer is wasted due to the rapid tuberization of diploid materials.

- Studies on yield components under the effect of variation in abiotic factors.

- Studies on the senescence of *S. phureja*. This species does not have programmed senescence as does *S. tuberosum*; in this topic, the questions that should be resolved are: How to understand and then how to predict the growth of stems and leaves that would continue to grow indeterminately if not for the effect of *P. infestans*? Is the rate of leaf senescence a function of temperature in *S. phureja*? How does the rate of leaf emission change in a hypothetical scenario where phytosanitary management never stops?

- Studies on tuber filling cohorts of *S. phureja*. In *S. tuberosum*, it is known that at harvest time, all tubers are mature and in dormancy. In *S. phureja*, this does not occur. A few days after maturity, the tubers start germination processes. How to model this "non-dormancy" and the quick germination of the sprouts even when they have not even been harvested?

These studies of basic biology and physiology would allow us to know how the system works so that when the knowledge is well mastered, improvements to the productive system can be made. It would be irresponsible to propose improvements when the knowledge base is incomplete.

The use of models and their development allows to improve the understanding of plant growth in cultivation; by improving the understanding, predicting the effect of the main factors on productivity and yield is possible. This research allows us to solve the technical problem of LAI estimation (which does not necessarily solve a scientific problem but rather a technical one) and highlights that the knowledge we currently have on *S. phureja* is too limited. We still have a lot to understand and improve, and without the knowledge, a direct

application of this work to the production system is not possible. Once the effects of the factors (at least the abiotic factors) on diploid potato growth and development are known and quantified, field validations should be made, and based on these corroborations, improvements to the system could be proposed.

4. References

Alamar, M. C., Tosetti, R., Landahl, S., Bermejo, A., & Terry, L. A. (2017). Assuring potato tuber quality during storage: A future perspective. *Frontiers in Plant Science*, *8*(2034), 1–6. https://doi.org/10.3389/fpls.2017.02034

Alva, A. K., Marcos, J., Stockle, C., Reddy, V. R., & Timlin, D. (2010). A crop simulation model for predicting yield and fate of nitrogen in irrigated potato rotation cropping system. *Journal of Crop Improvement*, *24*(2), 142–152. https://doi.org/10.1080/15427520903581239

Amthor, J. S. (1984). The role of maintenance respiration in plant growth. *Plant, Cell and Environment*, *7*(8), 561–569. https://doi.org/10.1111/j.1365-3040.1984.tb01856.x

Amthor, J. S. (2000). The McCree-de Wit-Penning de Vries-Thornley respiration paradigms: 30 Years later. *Annals of Botany*, *86*(1), 1–20. https://doi.org/10.1006/anbo.2000.1175

Birch, P. R. J., Bryan, G., Fenton, B., Gilroy, E. M., Hein, I., Jones, J. T., Prashar, A., Taylor, M. A., Torrance, L., & Toth, I. K. (2012). Crops that feed the world 8: Potato: Are the trends of increased global production sustainable? In *Food Security* (Vol. 4, Issue 4). https://doi.org/10.1007/s12571-012-0220-1

Boogaard, H. L., & Kroes, J. G. (1998). Leaching of nitrogen and phosphorus from rural areas to surface waters in the Netherlands. *Nutrient Cycling in Agroecosystems*, *50*(1–3), 321–324. https://doi.org/10.1007/978-94-017-3021-1_35

Bréda, N. (2003). Ground-based measurements of leaf area index: A review of methods, instruments and current controversies. *Journal of Experimental Botany*, *54*(392), 2403–2417. https://doi.org/10.1093/jxb/erg263

Brown, H. E., Huth, N., & Holzworth, D. (2011). A potato model built using the APSIM Plant.net Framework. *MODSIM 2011 - 19th International Congress on Modelling and Simulation - Sustaining Our Future: Understanding and Living with Uncertainty*, 961–967. https://doi.org/10.36334/modsim.2011.b3.brown

Bukasov, S. M. (1933). The potatoes of South America and their breeding possibilities. (According to data gathered by expeditions of the Institute of Plant Industry to Central and South America.). *Bull. Appl. Bot*, 58–192.

Burgos, G., Salas, E., Amoros, W., Auqui, M., Muñoa, L., Kimura, M., & Bonierbale, M. (2009). Total and individual carotenoid profiles in Solanum phureja of cultivated potatoes: I. Concentrations and relationships as determined by spectrophotometry and HPLC. *Journal of Food Composition and Analysis*, *22*(6), 503–508. https://doi.org/10.1016/j.jfca.2008.08.008

Cadena, M., Naranjo, A., & Ñústez, C. (2005). Evaluating the response of 60 Solanum phureja (Juz. et Buk.) genotypes to attacks by the Guatemalan moth (Tecia solanivora Povolny). *Agronomía Colombiana*, *23*(1), 112–116.

Campbell, G. S. (1986). Extinction coefficients for radiation in plant canopies calculated using an ellipsoidal inclination angle distribution. *Agricultural and Forest Meteorology*, *36*(4), 317–321. https://doi.org/10.1016/0168-1923(86)90010-9

Campbell, G. S. (1990). Derivation of an angle density function for canopies with ellipsoidal leaf angle distributions. *Agricultural and Forest Meteorology*, *49*, 173–176.

Campbell, G. S., & van Evert, F. K. (1995). Light interception by plant canopies: Efficiency and architecture. In *Resource Capture by Crops* (pp. 35–52). University Press.

Campillo, C., García, M. I., Daza, C., & Prieto, M. H. (2010). Study of a non-destructive method for estimating the leaf area index in vegetable crops using digital images. *HortScience*, *45*(10), 1459–1463.

Correll, D. (1962). *Potato Its Wild Relatives* (First Edit). Texas Research Foundation.

De la Casa, A., Ovando, G., Bressanini, L., Martínez, J., & Ibarra, E. (2008). Leaf Area Index in Potato Estimate From Canopy Cover. *Agronomía Trop.*, *58*(1), 61–64.

De la Casa, A., Ovando, G., Bressanini, L., Rodríguez, Á., & Martínez, J. (2007). Use of leaf area index and ground cover to estimate intercepted radiation in potato. *Agricultura Técnica*, *67*(1), 78–85.

Dobson, G., Griffiths, D. W., Davies, H. V., & McNicol, J. W. (2004). Comparison of fatty acid and polar lipid contents of tubers from two potato species, Solanum tuberosum and Solanum phureja. *Journal of Agricultural and Food Chemistry*, *52*(20), 6306–6314. https://doi.org/10.1021/jf049692r

Dodds, K. S., & Paxman, G. J. (1962). The Genetic System of Cultivated Diploid Potatoes. *Evolution*, *16*(2), 154. https://doi.org/10.2307/2406194

El-Sharkawy, M. A. (2011). Overview: Early history of crop growth and photosynthesis modeling. *BioSystems*, *103*(2), 205–211. https://doi.org/10.1016/j.biosystems.2010.08.004

Escallón, R., Ramirez, M., & Ñústez, C. E. (2005). Evaluating potential yield and resistance to Phytophthora infestans (Mont. de Bary) in the Solanum phureja (Juz. et Buk.) yellow potato collection. *Agronomia Colombiana*, *23*(1), 35–41.

Gayler, S., Wang, E., Priesack, E., Schaaf, T., & Maidl, F.-X. (2002). Modeling biomass growth, N-uptake and phenological development of potato crop. *Geoderma*, *105*, 367–383. https://doi.org/10.1016/S0016-7061(01)00113-6

Gifford, R. M., Thorne, J. H., Hitz, W. D., & Giaquinta, R. T. (1984). Crop productivity and photoassimilate partitioning. *Science*, *225*, 801–808. https://doi.org/10.1126/science.225.4664.801

Griffin, T. S., Johnson, B. S., & Ritchie, J. T. (1993). A simulation model for potato growth and development: SUBSTOR-Potato version 2.0. Department of Agronomy and Soil Science, College of Tropical Agriculture and Human Resources, University of Hawai, Honolulu. *Soil Science*, 32.

Gutaker, R. M., Weiß, C. L., Ellis, D., Anglin, N. L., Knapp, S., Luis Fernández-Alonso, J., Prat, S., & Burbano, H. A. (2019). The origins and adaptation of European potatoes reconstructed from historical genomes. *Nature Ecology and Evolution*, *3*(July). https://doi.org/10.1038/s41559-019-0921-3

Guzmán, M., & Rodríguez, P. (2010). Susceptibility of Solanum phureja (Juz. et Buk.) to potato yellow vein virus. *Agronomía Colombiana*, *28*(2), 219–224.

Hansen, S., Abrahamsen, P., Petersen, C. T., & Styczen, M. (2012). DAISY: Model, use, calibration and validation. *Transactions of the ASABE*, *55*(4), 1315–1333.

Hariharan, I. K., Wake, D. B., & Wake, M. H. (2016). Indeterminate growth: Could it represent the ancestral condition? *Cold Spring Harbor Perspectives in Biology*, *8*(2), 1–17. https://doi.org/10.1101/cshperspect.a019174

Hatfield, J. (2014). Radiation use efficiency: Evaluation of cropping and management systems. *Agronomy Journal*, *106*(5), 1820–1827. https://doi.org/10.2134/agronj2013.0310

Haverkort, A. J., Franke, A. C., Steyn, J. M., Pronk, A. A., Caldiz, D. O., & Kooman, P. L. (2015). A Robust Potato Model: LINTUL-Potato-DSS. *Potato Research*, *58*(4), 313–327. https://doi.org/10.1007/s11540-015-9303-7

Haverkort, A. J., & Top, J. L. (2011). The potato ontology: Delimitation of the domain, modelling concepts, and prospects of performance. *Potato Research*, *54*(2), 119–136. https://doi.org/10.1007/s11540-010-9184-8

Hawkes, J. G. (1956). Taxonomic studies on the tuber ‑ bearing Solanums. 1: Solanum tuberosum and the tetraploid species complex. *Proceedings of the Linnean Society of London*, *166*(1–2), 97–144. https://doi.org/10.1111/j.1095-8312.1956.tb00754.x

Hawkes, J. G. (1990). *The Potato: Evolution, biodiversity and genetic resources*. Smithsonian Institution Press.

Hodges, T., Johnson, S. L., & Johnson, B. S. (1992). A Modular Structure for crop simulation models: Implemented in the SIMPOTATO model. *Agronomy Journal*, *84*(5), 911–915. https://doi.org/10.2134/agronj1992.00021962008400050027x

Hoogenboom, G., Porter, C. H., Boote, K. J., Shelia, V., Wilkens, P. W., Singh, U., White, J. W., Asseng, S., Lizaso, J. I., Moreno, L. P., Pavan, W., Ogoshi, R., Hunt, L. A., Tsuji, G. Y., & Jones, J. W. (2019). The DSSAT crop modeling ecosystem. In K. J. Boote (Ed.), *Advances in Crop Modeling for a Sustainable Agriculture* (pp. 173–216). Burleigh Dodds Science Publishing.

Hoogenboom, G., Porter, C. H., Shelia, V., Boote, K. J., Singh, U., White, J. W., Hunt, L. A., Ogoshi, R., Lizaso, J. I., Koo, J., Asseng, S., Singels, A., Moreno, L. P., & Jones, J. W. (2018). *Decision Support System for Agrotechnology Transfer (DSSAT). Version 4.7.2* (4.7.2). www.DSSAT.net

Ingram, K. T., & McCloud, D. E. (1984). Simulation of Potato Crop Growth and Development 1. *Crop Science*, *24*(1), 21–27. https://doi.org/10.2135/cropsci1984.0011183x002400010006x

Jamieson, P. D., Zyskowski, R. F., Sinton, S. M., Brown, H. E., & Butler, R. C. (2006). Potato calculator: A tool for scheduling nitrogen fertiliser applications. *Agronomy New Zealand*, *36*(July 2015), 49–53.

Jennings, S. A., Koehler, A. K., Nicklin, K. J., Deva, C., Sait, S. M., & Challinor, A. J. (2020). Global Potato Yields Increase Under Climate Change With Adaptation and CO2 Fertilisation. *Frontiers in Sustainable Food Systems*, *4*(December). https://doi.org/10.3389/fsufs.2020.519324

Jonckheere, I., Fleck, S., Nackaerts, K., Muys, B., Coppin, P., Weiss, M., & Baret, F. (2004). Review of methods for in situ leaf area index determination Part I. Theories, sensors and hemispherical photography. *Agricultural and Forest Meteorology*, *121*,

19–35. https://doi.org/10.1016/j.agrformet.2003.08.027

Jones, J. W., Hoogenboom, G., Porter, C. H., Boote, K. J., Batchelor, W. D., Hunt, L. A.,
Wilkens, P. W., Singh, U., Gijsman, A. J., & Ritchie, J. T. (2003). The DSSAT
cropping system model. *European Journal of Agronomy*, *18*(3–4), 235–265.
https://doi.org/10.1016/S1161-0301(02)00107-7

Kadaja, J., & Tooming, H. (2004). Potato production model based on principle of
maximum plant productivity. *Agricultural and Forest Meteorology*, *127*(1–2), 17–33.
https://doi.org/10.1016/j.agrformet.2004.08.003

Lenz-Wiedemann, V. I. S., Klar, C. W., & Schneider, K. (2010). Development and test of a
crop growth model for application within a Global Change decision support system.
Ecological Modelling, *221*(2), 314–329.
https://doi.org/10.1016/j.ecolmodel.2009.10.014

Li, T., Hasegawa, T., Yin, X., Zhu, Y., Boote, K., Adam, M., Bregaglio, S., Buis, S.,
Confalonieri, R., Fumoto, T., Gaydon, D., Marcaida, M., Nakagawa, H., Oriol, P.,
Ruane, A. C., Ruget, F., Singh, B., Singh, U., Tang, L., … Bouman, B. (2015).
Uncertainties in predicting rice yield by current crop models under a wide range of
climatic conditions. *Global Change Biology*, *21*(3), 1328–1341.
https://doi.org/10.1111/gcb.12758

Ligarreto, G., & Suárez, M. (2003). Evaluation of the potential of genetics resources of
creole potato (Solanum phureja) for industrial quality. *Agronomía Colombiana*, *21*(1–
3), 83–94.

Luo, S., He, Y., Li, Q., Jiao, W., Zhu, Y., & Zhao, X. (2020). Nondestructive estimation of
potato yield using relative variables derived from multi-period LAI and hyperspectral
data based on weighted growth stage. *Plant Methods*, *16*(1), 1–14.
https://doi.org/10.1186/s13007-020-00693-3

Lutaladio, N., & Castaldi, L. (2009). Potato: The hidden treasure. *Journal of Food
Composition and Analysis*, *22*(6), 491–493. https://doi.org/10.1016/j.jfca.2009.05.002

Mann, J. E., Curry, G. L., DeMichele, D. W., & Baker, D. N. (1980). Light Penetration in a
Row-Crop with Random Plant Spacing1. *Agronomy Journal*, *72*(1), 131.
https://doi.org/10.2134/agronj1980.00021962007200010026x

Monsi, M., & Saeki, T. (1953). Über den Lichtfaktor in den Pflanzengesellschaften und
seine Bedeutung für die Stoffproduktion. *Jap. Journ. Bot.*, *14*, 22–52.

Monteith, J. L. (1977). Climate and the efficiency of crop production in Britain.

Philosophical Transactions of the Royal Society B: Biological Sciences, *281*, 277–294. https://doi.org/10.1098/rstb.1977.0140

Moslemkhani, K., Mozafari, J., Shams-Bakhsh, M., & Mohamadi, E. (2012). Expressions of some defense genes against Ralstonia Solanacearum in susceptible and resistant potato genotypes under in vitro conditions. *Iran. J. Plant Path.*, *48*(2), 57–60.

Murchie, E. H., Townsend, A., & Reynolds, M. (2019). Crop Radiation Capture and Use Efficiency. In R. Savin & G. Slafer (Eds.), *Crop Science* (pp. 73–106). Springer. https://doi.org/10.1007/978-1-4939-8621-7

NIKON®. (2019). *Capture NX-D Reference Manual* (pp. 1–58).

Ovchinnikova, A., Krylova, E., Gavrilenko, T., Smekalova, T., Zhuk, M., Knapp, S., & Spooner, D. M. (2011). Taxonomy of cultivated potatoes (Solanum section Petota: Solanaceae). *Botanical Journal of the Linnean Society*, *165*(2), 107–155. https://doi.org/10.1111/j.1095-8339.2010.01107.x

Patrignani, A., & Ochsner, T. E. (2015). Canopeo: A powerful new tool for measuring fractional green canopy cover. *Agronomy Journal*, *107*(6), 2312–2320. https://doi.org/10.2134/agronj15.0150

Pregno, L. M., & Armour, J. D. (1992). Boron deficiency and toxicity in potato cv. Sebago on an Oxisol of the Atherton Tablelands, North Queensland. *Australian Journal of Experimental Agriculture*, *32*(2), 251–253. https://doi.org/10.1071/EA9920251

R Core Team. (2020). R: A Language and Environment for Statistical Computing. *R Foundation for Statistical Computing*. https://www.r-project.org/

Raymundo, R., Kleinwechter, U., & Asseng, S. (2014). *Virtual potato crop modeling: A comparison of genetic coefficients of the DSSAT-SUBSTOR potato model with breeding goals for developing countries*. *January*, 1–15. https://doi.org/10.5281/zenodo.7687

Reddy, B., Mandal, R., Chakroborty, M., Hijam, L., & Dutta, P. (2018). A review on potato (Solanum tuberosum L.) and its genetic diversity. *International Journal of Genetics*, *10*(2), 360–364. https://doi.org/10.9735/0975-2862.10.2.360-364

Ritchie, J. T., Griffin, T. S., & Johnson, B. S. (1995). SUBSTOR: Functional model of potato growth, development and yield. In P. Kabat, B. Marshall, B. J. van der Broek, J. Vos, & H. van Keulen (Eds.), *Modelling and Parameterization of the Soil-Plant-Atmosphere System: A Comparison of Potato Growth Models* (pp. 401–435). Wageningen Pers.

Russell, G., Marshall, B., & Jarvis, P. . (1989). *Plant canopies: their growth, form and function* (G. Russell, B. Marshall, & P. G. Jarvis (eds.)). Cambridge University Press.

Saqib, M., & Anjum, M. A. (2021). Applications of decision support system: A case study of solanaceous vegetables. *Phyton - International Journal of Experimental Botany*, *90*(2), 331–352. https://doi.org/10.32604/phyton.2021.011685

Sinclair, T., & Muchow, R. (1999). Radiation Use Efficiency. *Advances in Agronomy*, *65*, 215–265. https://doi.org/10.1016/s0065-2113(08)60914-1

Singh, J., Govindakrishnan, P., Lal, S., & Aggarwal, P. (2005). Increasing the efficiency of agronomy experiments in potato using INFOCROP-POTATO model. *Potato Research*, *48*(3–4), 131–152. https://doi.org/10.1007/BF02742372

Sinoquet, H., & Andrieu, B. (1993). The geometrical structure of plant canopies : characterization and direct measurement methods. In *Crop structure and light microclimate* (Issue June, pp. 131–158).

Spooner, D. M., Ghislain, M., Simon, R., Jansky, S. H., & Gavrilenko, T. (2014). Systematics, Diversity, Genetics, and Evolution of Wild and Cultivated Potatoes. *Botanical Review*, *80*(4), 283–383. https://doi.org/10.1007/s12229-014-9146-y

Steduto, P., Hsiao, T. C., Raes, D., & Fereres, E. (2009). Aquacrop-the FAO crop model to simulate yield response to water: I. concepts and underlying principles. *Agronomy Journal*, *101*(3), 426–437. https://doi.org/10.2134/agronj2008.0139s

Steven, M. D., Biscoe, P. V., Jaggard, K. W., & Paruntu, J. (1986). Foliage cover and radiation interception. *Field Crops Research*, *13*(C), 75–87. https://doi.org/10.1016/0378-4290(86)90012-2

Stöckle, C. O., & Kemanian, A. R. (2009). Crop Radiation Capture and Use Efficiency. *Crop Physiology*, 145–170. https://doi.org/10.1016/b978-0-12-374431-9.00007-4

Sukhotu, T., & Hosaka, K. (2006). Origin and evolution of Andigena potatoes revealed by chloroplast and nuclear DNA markers. *Genome*, *49*(6), 636–647. https://doi.org/10.1139/G06-014

Thornley, J. H. M. (2011). Plant growth and respiration re-visited: Maintenance respiration defined it is an emergent property of, not a separate process within, the system and why the respiration: Photosynthesis ratio is conservative. *Annals of Botany*, *108*(7), 1365–1380. https://doi.org/10.1093/aob/mcr238

Urbanek, S. (2014). *Package jpeg: Read and write JPEG images*. 1–5. https://cran.r-project.org/package=jpeg

Vose, J. M., Clinton, B. D., Sullivan, N. H., & Bolstad, P. V. (2008). Vertical leaf area distribution, light transmittance, and application of the Beer–Lambert Law in four mature hardwood stands in the southern Appalachians. *Canadian Journal of Forest Research*, *25*(6), 1036–1043. https://doi.org/10.1139/x95-113

Wallach, D., Makowski, D., Jones, J. W., & Brun, F. (2019). *Working with dynamic crop models. Methods, tools and examples for agroculture and environment* (Third edit). Academic Press. https://doi.org/10.1016/c2011-0-06987-9

Watson, D. J. (1947). Comparative Physiological Studies on the Growth of Field Crops. I. Variation in net assimilation rate and leaf area between species and varieties, and within and between years. *Annals of Applied Biology*, *11*(41), 41–76. https://doi.org/10.1111/j.1744-7348.1953.tb02364.x

Webb, N., Wood, J., & Nicholl, C. (2008). *User Manual for the SunScan Canopy Analysis System Delta-T Devices Ltd*.

White, J. W., Hoogenboom, G., Kimball, B. A., & Wall, G. W. (2011). Methodologies for simulating impacts of climate change on crop production. *Field Crops Research*, *124*(3), 357–368. https://doi.org/10.1016/j.fcr.2011.07.001

Willmott, C. J., Ackleson, S. G., Davis, R. E., Feddema, J. J., Klink, K. M., Legates, D. R., O'donnell, J., & Rowe, C. M. (1985). Statistics for the evaluation and comparison of models. *Journal of Geophysical Research*, *90*(5), 8995–9005.

Wolf, J. (2002). Comparison of two potato simulation models under climate change. I. Model calibration and sensitivity analyses. *Climate Research*, *21*, 173–186.

Yamaguchi, J. (1978). Respiration and the growth efficiency in relation to crop productivity. *J. Fac. Agric. Hokkaido Univ.*, *59*, 59129.

Yang, J., Greenwood, D. J., Rowell, D. L., Wadsworth, G. A., & Burns, I. G. (2000). Statistical methods for evaluating a crop nitrogen simulation model, N_ABLE. *Agricultural Systems*, *64*(1), 37–53. https://doi.org/10.1016/S0308-521X(00)00010-X

Zhao, C., Liu, B., Xiao, L., Hoogenboom, G., Boote, K. J., Kassie, B. T., Pavan, W., Shelia, V., Kim, K. S., Hernandez-Ochoa, I. M., Wallach, D., Porter, C. H., Stockle, C. O., Zhu, Y., & Asseng, S. (2019). A SIMPLE crop model. *European Journal of Agronomy*, *104*(January), 97–106. https://doi.org/10.1016/j.eja.2019.01.009