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Modelling the interindividual variability of organogenesis in sugar beet populations using a hierarchical segmented model

Charlotte Baey[a,*], Anne Didier[b], Sébastien Lemaire[b], Fabienne Maupas[b], Paul-Henry Cournède[a]

[a] École Centrale Paris, Laboratoire de Mathématiques appliquées aux systèmes, Grande Voie des Vignes, 92290 Châtenay-Malabry, France
[b] Institut Technique de la Betterave, 45 rue de Naples, 75008 Paris, France

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ABSTRACT

Modelling the interindividual variability in plant populations is a key issue to enhance the predictive capacity of plant growth models at the field scale. In the case of sugar beet, this variability is well illustrated by rate of leaf appearance, or by its inverse the phyllochron. Indeed, if the mean phyllochron remains stable among seasons, there is a strong variability between individuals, which is not taken into account when using models based only on mean population values.

In this paper, we proposed a nonlinear mixed model to assess the variability of the dynamics of leaf appearance in sugar beet crops. As two linear phases can be observed in the development of new leaves, we used a piecewise-linear mixed model. Four parameters were considered: thermal time of initiation, rate of leaf appearance in the first phase, rupture thermal time, and difference in leaf appearance rates between the two phases. The mean population values as well as the interindividual variabilities (IIV) of the parameters were estimated by the model for a standard population of sugar beet, and we showed that the IIV of the four parameters were significant. Also, the rupture thermal time was found to be non significantly correlated to the other three parameters. We compared our piecewise-linear formulation with other formulations such as sigmoïd or Gompertz models, but they provided higher AIC and BIC.

A method to assess the effects of environmental factors on model parameters was also studied and applied to the comparison of three levels of Nitrogen (control, standard and high dose). Taking into account the IIV, our model showed that plants receiving Nitrogen tended to have a later time of initiation, a higher rate of leaf appearance, and an earlier rupture time, but these differences were not dose-dependent (no differences between standard and high dose of Nitrogen). No differences were found on the leaf appearance rate of the second phase between the three treatments.

1. Introduction

The need for a better description of plant architectural development has been long acknowledged as a key step towards the understanding of plant functional growth (Fourcaud et al., 2008). For this purpose, a new trend in plant growth modelling is the development of individual-based models combining the description of plant architecture and physiological functioning (Vos et al., 2007). However, the extrapolation to population models is yet at its early stages. The main approach consists in simulating all individuals in the population (Fournier and Andrieu, 1999; Wernecke et al., 2007; Sievänen et al., 2008; Cournède et al., 2009).

However, if there is no doubt on the theoretical interest of these approaches to help understand population functioning, they remain quite limited for concrete applications in agriculture or forestry since it is generally not possible to describe all plants in a field or in a forest. Stochastic population models that describe the distributions of individuals' characteristics in the population provide a good way to overcome this difficulty. This approach is well-developed in forestry science at least from a descriptive point of view (Dietze et al., 2008; Vieilledent et al., 2010; Courbaud et al., 2012) to study the variability of allometric relationships.

Such interindividual variability has rarely been taken into account in dynamic plant growth models, even though its impact at the agrosystem level is well acknowledged. For example, Brouwer et al. (1993) showed how soil and crop micro-variability can have

* Corresponding author at: École Centrale Paris, Laboratoire de Mathématiques appliquées aux systèmes, Grande Voie des Vignes, 92290 Châtenay-Malabry, France. Tel.: +33 141 131 559.
E-mail addresses: charlotte.baey@ecp.fr (C. Baey), didier@itbfr.org (A. Didier), lemaire@itbfr.org (S. Lemaire), maupas@itbfr.org (F. Maupas), paul-henry.cournede@ecp.fr (P.-H. Cournède).

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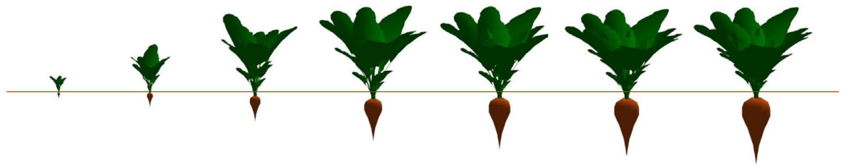

Fig. 1. Sugar beet growth simulated with the DigiPant software (Cournède et al., 2006), at growth cycles 15, 17, 20, 26, 30, 34, 39 and 43.

an impact on yield, as some parts of the field could be more adapted to dryness and could thus compensate poor or less good performances of other parts of the field. Renno and Winkel (1996) also showed how interindividual variability of flowering could prevent from short-term stresses risks.

In sugar beet populations, this variability is well illustrated by the number of leaves, which can be very different from one plant to another, even in the same environmental conditions. In the competition for light occurring between plants, the capacity for some plants to achieve a better and faster ground cover by the leaves will allow them to produce more biomass than their neighbors. Liu et al. (2004) showed how the differences between leaf appearance rates and emergence rates from one individual plant to another can lead to important variations in the final yield. Indeed, as light interception is directly related to biomass production, any factor affecting the speed of leaf area expansion will affect the total leaf surface area and have an impact on the final yield. The leaf appearance rate is thus a crucial parameter of plant development. It is often described through its inverse, the phyllochron, which is then defined as the thermal time (the cumulative sum of daily temperatures above a base temperature) elapsing between two successive appearances of leaves (Wilhelm and McMaster, 1995) (Fig. 1).

The variability of the phyllochron has been studied for various crops, and several environmental factors have proven to have an influence on this crucial parameter of plant development. In their study of sorghum, Clerget et al. (2008) showed that the phyllochron was positively correlated with soil temperature, and negatively correlated with photoperiod and day length. Similar results were shown by Cao and Moss (1989) for wheat and barley, and a short review of factors having an influence on phyllochron was proposed by Wilhelm and McMaster (1995). In the case of sugar beet, Milford et al. (1985a,b) showed that during a first phase of development, the phyllochron was very stable among seasons and experimental treatments (irrigation, fertilizer, plant density and sowing date). They also showed that the duration of this first phase of development, as well as the phyllochron of the second phase of development, were more subject to change. Lemaire et al. (2008) also observed these two linear phases in the development of new phytomers by the sugar beet plant. A first phase stretched from emergence to approximately the 20th leaf, and then a second phase started quite abruptly with a larger phyllochron (corresponding to a slower rate of leaf appearance rate). Different hypotheses were put forward by Milford et al. (1985a) to explain this slowing down, including changes in base temperature and an increasing competition for assimilates between leaves and root compartments. Lemaire et al. (2008) showed that this change in leaf appearance rate corresponded to the beginning of the linear phase of root growth, and to canopy closing, when competition for light increases (Lemaire et al., 2009).

However, even though the mean phyllochron is very stable, there is a strong variability between plants within a cultivar (Frank and Bauer, 1995), leading to a high variability of the total number of leaves of each plant in a given field (Fig. 2). Likewise, variations in seedling emergence can also have an influence on the final number of leaves, as shown by Durr and Boiffin (1995).

However, the effects of the different factors (Nitrogen, density, ...) are usually assessed through the only use of mean population values, without taking into account the interindividual variability, despite its impact at the field scale. Indeed, previous studies of the phyllochron were mainly based on simple linear (or non-linear) models with no random effects. The linear models used were either based on the whole plant population (Xue et al., 2004; Frank and Bauer, 1995; Bauer et al., 1984; Streck et al., 2005; Juskiw et al., 2005), therefore making the very strong assumption that measurements from the same individual are independent, or based on mean values (Lemaire et al., 2009), circumventing the problem of data correlation, but involving a loss of information. Moreover, with these approaches, it is not possible to estimate the phyllochron variability in the population.

One way of analyzing this variability is through the use of mixed models, in which all individuals' profiles follow the same functional form, but with parameters that vary among individuals. In this paper, we propose to study the dynamics of leaf appearance in sugar beet and develop a model accounting for interindividual variability. The number of leaves as a function of thermal time is described by a piecewise-linear mixed model with four parameters: the thermal time of initiation (corresponding to the seedling emergence), the rupture thermal time (corresponding to the setting up of the second phase) and the two rates of leaf appearance in the two phases underlined by Milford et al. (1985a) and Lemaire et al. (2008). Other models can be tested, with a nonlinear relationship between leaf appearance rate and temperature in each phase (Xue et al., 2004).

Taking the example of Nitrogen, even if the literature is abundant about its influence on sugar beet growth and development, its effect on the four parameters defined above has rarely been evaluated. We can cite for example Lee and Schmehl (1988) who reported no significant effect of Nitrogen alone on the leaf appearance rate, but a significant effect of the interactions between harvest date and Nitrogen, and between harvest date, planting date and Nitrogen on the leaf appearance rate. Stout (1961) on the other hand, reported that a high rate of Nitrogen in sugar beets stimulates the

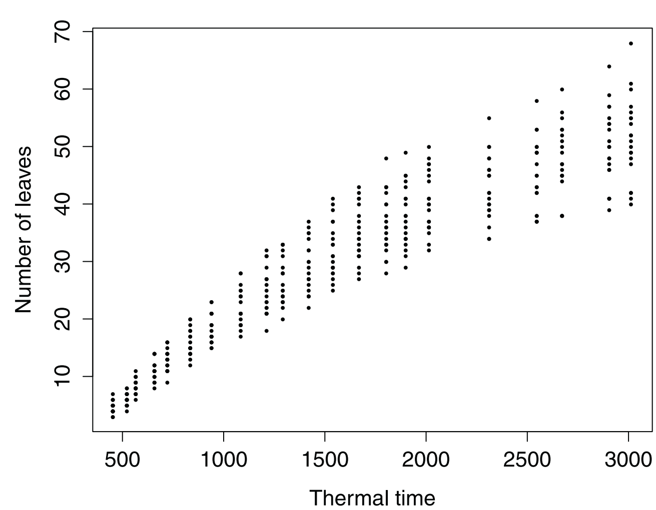

Fig. 2. Number of leaves according to thermal time for 20 plants grown in normal density (10.89 pl/m^2) and with a normal level of Nitrogen (136 kg/ha).