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RELEVANT RESEARCH QUESTIONS ON THE CROP PHYSIOLOGY OF ENSET

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ABSTRACT: Enset is an ideal crop for climate smart, sustainable agriculture, especially in low-input, fragile environments. Its main strengths are: prolonged canopy cover, recycling of nutrients, drought resistance, stable dry matter allocation, large storage capacity of starch, high harvest index, easy vegetative reproduction, and its ability to prevent soil erosion. Enset also has high radiation use efficiency and is tolerant against repetitive removal of leaves and repetitive transplanting. The plant and crop architecture of enset are special and deserve to be investigated in more detail by architectural models, such as functional-structural plant models (FSPMs). Through such FSPMs we can investigate the consequences of (trans) planting and gap filling practices on crop performance. Similarly, FSPMs can be used to assess the effects of repetitive leaf pruning. Moreover, these models should be used for 3D modelling of rainfall interception and water transfer by individual leaves and the entire canopy, enabling the study of water storage in the plant, drought tolerance, water use efficiency and protection against erosion. The influence of leaf tearing and tattering on performance of individual leaves is also relevant. Effects on photosynthesis and transpiration can be either positive or negative at the level of the individual leaves. Upscaling these effects to plant and crop performance is essential. Finally, it is likely that current crop stands are infected by viruses. Quantifying the yield reduction by such infections and the relation between virus titre and crop performance can help to assess the need for virus-free planting material.

Key words/phrases: Functional-structural plant modelling, Leaf pruning, Sustainability, Transplanting, Virus infections.

INTRODUCTION

Enset (*Ensete ventricosum* (Welw.) Cheesman) is a perennial crop plant of great economic and cultural importance in Ethiopia, and is widely used for many different purposes, including food, forage, medicine, building material and fibre (Admasu Tsegaye, 2002) and industrial purposes, such as starch production. While the species widely occurs in tropical Africa, it has only been domesticated in Ethiopia.

In this country, enset has become the main staple for many people, especially in the Southern Nations Nationalities and Peoples Regional State (SNNPR), Oromia and Gambela (Admasu Tsegaye, 2002). Enset has a large

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genetic diversity (Admasu Tsegaye and Struik, 2000a; Admasu Tsegaye and Struik, 2002). Some of the reasons for this diversity may be the fact that the crop is grown in very different agro-ecosystems and contrasting agro-ecologies. However, also the very diverse purposes of its use have contributed to this diversity.

When used for human consumption, enset is a flexible and versatile food source. The plant can be harvested at different growth stages (i.e., over a prolonged period of time and growth) and its products can be stored for long periods (Admasu Tsegaye, 2002).

Enset is exposed to some typical cultural practices, such as frequent transplanting to maximize land use efficiency and frequent leaf pruning to provide forage to domestic animals (Admasu Tsegaye and Struik, 2000b; Admasu Tsegaye and Struik, 2002). Such practices have a strong effect on the crop physiology of the species.

In this contribution, I will first analyse why enset is a productive and climate robust crop. Subsequently, I will describe the need for functional-structural plant models to understand the crop physiology of enset better. I will also discuss the consequences of leaf tearing and tattering and virus infections. Finally, I will list a few research questions for future (crop physiological) research of enset.

Enset is a productive crop

Efficient biomass production is based on effectively capturing incoming light over a prolonged period of time and making maximum use of absorbed light though efficient photosynthesis followed by conversion of the fixed carbon through efficient metabolic pathways. Enset does that very well, for several reasons (see, for example, Admasu Tsegaye and Struik, 2001; Admasu Tsegaye and Struik, 2003).

Enset can capture huge amounts of light during its life cycle. As a perennial crop with continuous renewal of productive leaves, its typical canopy structure with upright leaves, and its long vegetative phase, it produces a long-lasting, highly productive vegetative apparatus with efficient light capture. The efficiency with which that intercepted light (or radiation) is converted into dry matter (the so-called radiation use efficiency, expressed in g of dry matter per MJ light intercepted) can also be high under conditions without stress. Table 1 presents some values for radiation use efficiency of enset.

Table 1. Some examples of the high radiation use efficiency (RUE) of enset (Data from Admasu Tsegaye, 2002).

Site	Clone	RUE (g/MJ)
Awassa	Halla	2.25
Awassa	Addo	2.23
Areka	Halla	1.43
Areka	Nekakia	2.67

The main reasons for that are threefold. First, enset has a very stable dry matter partitioning over the different plant organs, with little investment in plant structures that die at an early stage. The stable dry matter partitioning pattern also guarantees a long period of high fitness for use and therefore high flexibility in harvesting time. Secondly, enset has a large storage capacity of reserves in the corm and pseudostem (i.e., both above- and below-ground). Thirdly, in enset the reserves are stored as starch, which is a relatively "cheap" product for a plant to produce, at least cheaper than oil or proteins. These three reasons result in a high harvest index (expressed in g dry matter harvested per g dry matter of biomass produced), i.e., a large proportion of the dry matter produced is harvestable. The harvestable material is present in an edible form of high quality. The combination of high biomass production, high harvest index, and high-quality storage product makes enset a very productive and reliable staple crop. Table 2 illustrates the high rate of energy production of enset in comparison with other crops with starch as main storage compound.

Table 2. Some data to illustrate that enset has a high rate of energy production in comparison with other crops with starch as main storage compound (Data from Admasu Tsegaye, 2002).

Crop	Energy production rate ($kJ\ m^{-2}\ d^{-1}$)
Enset (transplanting twice)	64.3
Lowest cereal (sorghum)	8.0
Highest cereal (maize)	16.6
Lowest tuber crop (yam)	11.0
Highest tuber crop (sweet potato)	26.5

Enset is a climate smart, sustainable crop for low-input, fragile environments

Some of the crop physiological reasons why enset is a productive crop also make it a climate smart, sustainable crop for low-input environments. These include prolonged vegetative growth and long canopy cover, high radiation use efficiency, stable dry matter allocation pattern (and therefore long period of fitness for use), high harvest index, and large storage capacity of starch (both below- and above-ground), as discussed before. However, enset has a number of other attractive characteristics that make it climate smart and sustainable, including its deep rooting, cold tolerance, drought resistance and its high nutrient use efficiency. Deep rooting allows foraging for water and nutrients over a wide soil volume. Enset's cold tolerance is clearly demonstrated by the wide agro-ecological distribution of the plant and its cultivation at higher altitudes (Table 3). Its drought tolerance is associated with the capture of large amounts of water with its leaves and its capacity to store this water in the pseudostem. The high nutrient use efficiency is associated with nutrient recycling associated with the thick layer of mulch in enset stands consisting of leaf litter, but also with the fact that per unit of nutrient taken up a large quantity of starch can be accumulated in the vegetative storage organs. The combination of drought tolerance and nutrient recycling in association with high water and nutrient use efficiencies makes enset also a sustainable crop for low-input, fragile environments. Moreover, the crop can easily be established making use of its easy vegetative reproduction through numerous and vigorous suckers.

Enset also demonstrates many different ecosystem services, such as soil protection against erosion (based on mulching with leaf litter and continuous and prolonged vegetation cover), providing shading and shelter, and harbouring biodiversity. In addition to food, it produces many other valuable components. Enset is also tolerant to (repetitive) transplanting, allowing more efficient use of land, and leaf pruning and allowing frequent harvesting of leaves for forage.

Important crop physiological issues

Enset has some typical characteristics that require in-depth investigation to assess their physiological and agronomic consequences. First of all, an enset stand has a very characteristic and unique plant and canopy structure, with its stiff and upright leaves that create special vertical light profiles and special pathways of water movement. Moreover, the leaf appearance of enset is slow and leaf longevity potentially long. Due to prevailing strong winds in many enset growing areas, leaf tearing and tattering are frequent and these affect transpiration (and therefore leaf temperature) and leaf photosynthesis. For plants other than enset it has been demonstrated that leaf tattering can help in increasing the transpiration and therefore in cooling the photosynthesis apparatus. Therefore, in conditions in which heat stress effects on photosynthesis are relevant, leaf tattering might be a blessing in disguise. Strong leaf tattering, however, obviously might reduce the photosynthesis efficiency, as it causes physical leaf damage and reduces the longevity of the leaves, but the influence of the extent of tattering on photosynthesis and transpiration requires further research. Upscaling these influences to the canopy level is essential to quantify consequences for plant and crop performance.

Enset is also very diverse in pigmentation. Leaf blades might range from light green to dark green and even dark red. The impact of leaf colour on radiation use efficiency and protection of the plant against too much radiation is an interesting issue to further investigate, preferably at different altitudes.

According to Admasu Tsegaye (2002) and other publications (Admasu Tsegaye and Struik, 2000b; Admasu Tsegaye and Struik, 2003), flowering should be delayed to prolong the starch accumulation in the pseudostem and corm. Flowering can be delayed by repetitive transplanting and perhaps by other traditional cultural practices as well. The mechanisms behind the impact of transplanting on the vegetative and reproductive development of enset require further physiological study.

It is also important to assess nutrient cycling (especially of N, P, and K) and nutrient accumulation, the more so since often households concentrate the nutrients available in their farming system in the enset stands. Equally important is to quantify water storage in enset plant, water flows in enset stands, and water movement in soil underneath these stands. With these water flows, also the nutrient flows are influenced.

We are especially intrigued by the possibilities to investigate the impact of canopy structure making use of functional structural plant models, as will be discussed in the next section.

Functional-structural aspects of enset

Enset growing regions but also individual households differ significantly in the way crop stands of enset are established. Often enset is frequently transplanted, sometimes with clear separation of enset plants of different ages in the home garden. Transplanting is often preceded by leaf pruning and is associated with changes in plant density. The impact of combined leaf pruning and (different frequencies of) transplanting is illustrated in Fig. 1. Note the positive effect of more frequent transplanting on the yield because of delaying flowering (and thereby delayed plant senescence) and the interaction between leaf pruning and transplanting frequency.

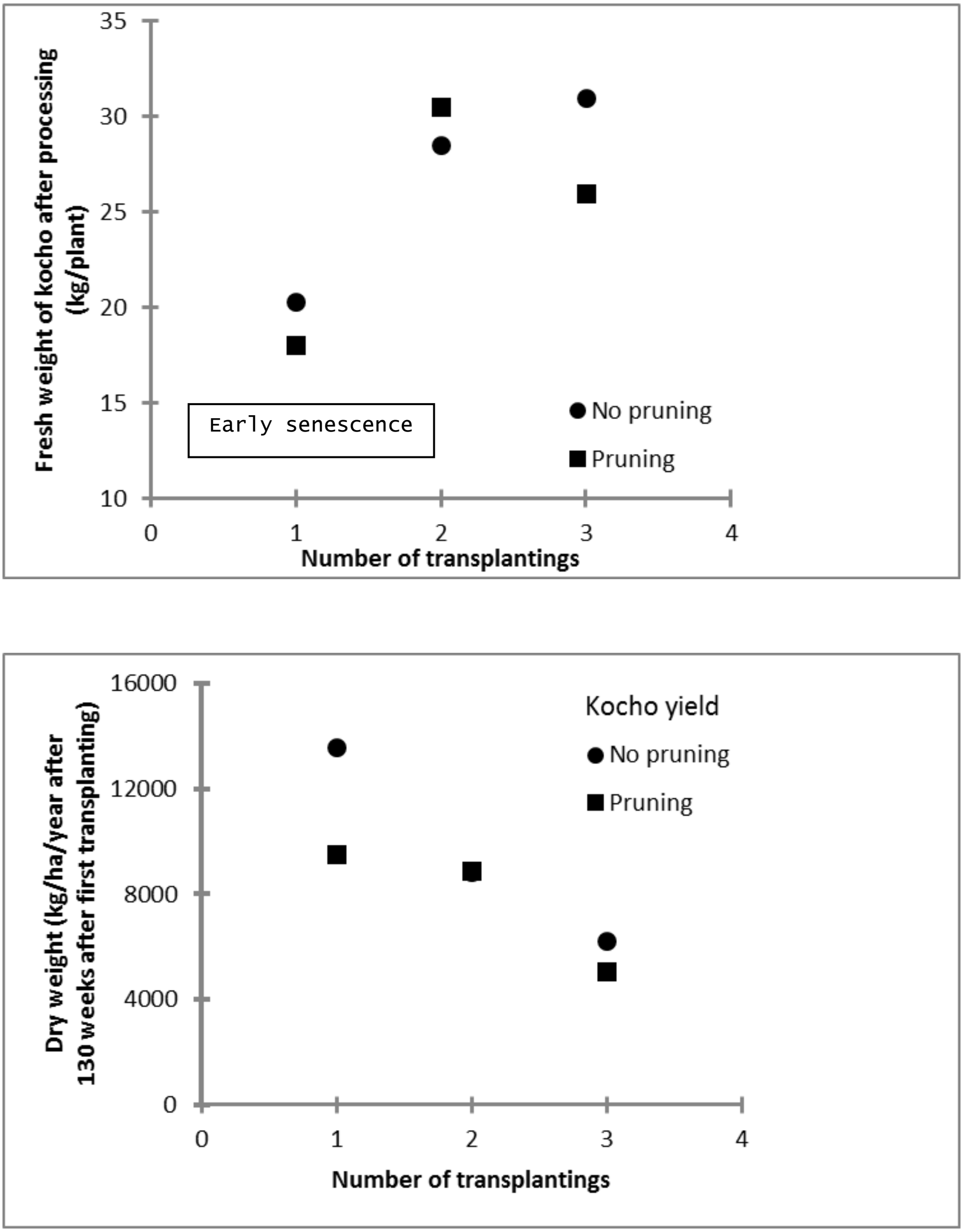

Fig. 1. Effects of transplanting and leaf pruning on fresh kocho yield per plant after processing (assessed 260 days after first transplanting; upper panel) and dry kocho yield per ha per year (assessed 130 days after first transplanting; lower panel) (Data from Admasu Tsegaye, 2002).

There are also mature crop stands where harvested enset plants are replaced by smaller plants and the logics behind the various gap filling strategies in mature stands also need to be unravelled. Even without transplanting, leaf pruning of different levels of intensity is applied.

The traditional practices of transplanting and leaf pruning are not only designed to influence crop physiology, but are triggered by the need to make maximum use of scarce land or by the organization of the home garden (transplanting) or are influenced by the number of animals per household and thus the household's forage needs. Therefore, these common practices of transplanting and leaf pruning can vary a lot among agro-ecologies, and may even be counterintuitively associated with yield potentials as illustrated in Table 3. Table 3 indicates that the logic behind transplanting and leaf pruning are very much based on resource management and not on crop physiology.

Table 3. The frequency of transplanting and the level of leaf pruning for several enset growing regions differing in elevation (After Admasu Tsegaye, 2002).

Region	**Elevation (m asl)**	**Frequency of transplanting**	**Level of leaf pruning**
Sidama	2600-2650	Once	Mild
Wolaita	1750-1820	2-3 times	Very severe
Hadiya	2220-2400	4 times	Moderate

Using general eco-physiological models, the crop physiology and crop ecology of enset have been investigated but many relevant research questions have remained untouched. Because of its upright and rigid leaves, the plant and crop architecture of enset are special and deserve to be investigated in more detail by architectural models, such as functional-structural plant models (FSPMs). Apart from generating a very attractive 3D visualisation of plant growth, these models are particularly suited to analyse problems in which spatial structure of the plant or its canopy is an essential factor to explain performance, or – in other words – to link form and function.

Through such FSPMs we can investigate the consequences of (trans)planting strategies, gap filling practices in mature stands, and plant arrangements of stands of different ages on the performance of the crop, thus evaluating the contrasting approaches in crop management by different tribes in the enset growing regions. Similarly, FSPMs (in combination with ecophysiological approaches of dry matter production and allocation) can be used to assess the effects of repetitive leaf pruning, and the interactions between leaf pruning, (changes in) plant arrangement and/or (repetitive) transplanting. Moreover, these models should be used for 3D modelling of rainfall interception and water transfer by the individual leaves and the entire canopy, which can help to study water storage in the plant, drought tolerance, water use efficiency, nutrient recycling, nutrient use efficiency and protection against erosion by the crop.

Virus infections might reduce yield

Finally, because of the vegetative propagation it is likely that current crop stands are infected by viruses. Although it has not been investigated, the low value of the radiation use efficiency of the clone Halla in Areka in Table 1 might be associated with virus infection. Quantifying the yield reduction by such infections and the relation between virus titre and performance can help to assess the need for virus-free planting material.

Future research questions

Based on the previous sections, I would like to list the following major research questions for further increase in our knowledge on the crop physiology of enset:

1. Are enset leaves designed to be torn and how much does leaf damage matter?
2. What are the exact mechanisms behind the different transplanting benefits?
3. How much leaf removal can the plant or crop tolerate at different agro-ecologies?
4. Is it possible to design improved planting systems based on functional-structural plant models?
5. How can we capitalize on the climate-robustness of enset?
6. How important are viruses to account for variation in radiation use efficiency?
7. Is there a relationship between virus titre and plant vigour or radiation use efficiency?

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