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Rooting for cassava: insights into photosynthesis and associated physiology as a route to improve yield potential

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Summary

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As a consequence of an increase in world population, food demand is expected to grow by up to 110% in the next 30–35 yr. The population of sub-Saharan Africa is projected to increase by > 120%. In this region, cassava (*Manihot esculenta*) is the second most important source of calories and contributes c. 30% of the daily calorie requirements per person. Despite its importance, the average yield of cassava in Africa has not increased significantly since 1961. An evaluation of modern cultivars of cassava showed that the interception efficiency (ϵ_i) of photosynthetically active radiation (PAR) and the efficiency of conversion of that intercepted PAR (ϵ_c) are major opportunities for genetic improvement of the yield potential. This review examines what is known of the physiological processes underlying productivity in cassava and seeks to provide some strategies and directions toward yield improvement through genetic alterations to physiology to increase ϵ_i and ϵ_c . Possible physiological limitations, as well as environmental constraints, are discussed.

I. Introduction

The global demand for primary foodstuffs is expected to increase by 60–110% (Tilman *et al.*, 2011; Alexandratos & Bruinsma, 2012; Ray *et al.*, 2013; Long *et al.*, 2015; Tilman & Clark, 2015) as a consequence of increased urbanization and the predicted rise in

global population from c. 7.3 billion today to 9.7 billion by 2050 (United Nations, 2015). The projected increase is particularly high for Africa, where the current population of 1.2 billion is expected to reach 5.6 billion by 2100 (United Nations, 2015). Overlaying this scenario are changes in global climate that will affect crop productivity, primarily increases in temperature, increases in the incidence of drought, rising atmospheric CO₂ and elevated surface ozone. It has been estimated that climate change by mid-century

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will depress aggregated cassava production across sub-Saharan Africa by 18% in the absence of adaptation (Schlenker & Lobell, 2010; Roudier *et al.*, 2011). This is compounded by loss and degradation of agricultural land and exhaustion of water resources for irrigation (Godfray & Garnett, 2014).

Cassava (*Manihot esculenta* Crantz) is a perennial woody shrub of the Euphorbiaceae family and is considered a staple food of more than a billion people in *c.* 105 countries (Chetty *et al.*, 2013). It is typically cultivated by families for their own consumption on small plots of land, although in Asia and some regions of Latin America it is also grown commercially and on large fields (Nassar & Ortiz, 2010). In Africa, cassava is the second most important source of calories. Its tuberous roots provide over a quarter of the daily calorie consumption in some African countries, such as Angola and Mozambique, but for the rural poor it represents a much larger proportion of daily calories (FAO, 2016). In addition to the tuberous roots, the main harvested product, cassava leaves are consumed as a vegetable in at least 60% of the countries in sub-Saharan Africa, providing an important source of proteins, vitamins and micronutrients (Latif & Müller, 2015). Cassava leaves are also used as a protein supplement for livestock (Lukuyu *et al.*, 2014).

Between 2000 and 2013, the amount of cassava harvested in the world increased by *c.* 60% (Howeler *et al.*, 2013). Currently, the largest producer of cassava in the world is Nigeria, followed by Thailand, Indonesia, Brazil and the Democratic Republic of the Congo. Together, these countries account for 52.8% of world production (Table 1). Moreover, it is projected that cassava may become an important replacement for crops that are expected to be more vulnerable to climate change, especially in eastern Africa (Schlenker & Lobell, 2010; Jarvis *et al.*, 2012). This is in part a result of the fact that rising CO₂ concentration ([CO₂]) will have a more positive effect on cassava as a C₃ crop than it will on the major C₄ crops sorghum (*Sorghum bicolor*), maize (*Zea mays*) and millets (*Pennisetum glaucum*) (Roudier *et al.*, 2011; Rosenthal *et al.*, 2012). However, there is great uncertainty in these projections, which range from near complete crop loss to large increases in production (Roudier *et al.*, 2011). This, though, emphasizes the need for the global society to insure against this uncertain future by mobilizing research and development effort to provide germplasm with increased productivity and sustainability potential, under conditions of climate change.

Despite its importance, yield improvement in cassava has received relatively little attention or investment (El-Sharkawy, 2004). This is vividly demonstrated by the fact that between 1961 and 2014 average cassava yields per unit land area did not increase in Nigeria, the largest global producer. Over the same period, maize yields per unit land area in Nigeria increased by 129%, approaching the yield increase of 174% achieved by the world's largest producer of maize, the USA (Fig. 1).

The efforts to improve tuberous root yields made by breeding programs throughout the world have prioritized drought tolerance, cyanogenic content, low soil fertility conditions, and resistance to a wide range of diseases (El-Sharkawy, 2004). Concomitantly, efforts have also been centered on improving cassava nutritional quality (Montagnac *et al.*, 2009; Gonzalez *et al.*, 2011; Sayre *et al.*, 2011;

Table 1 Top 10 producers of cassava in the world and their percentage contribution to total global production in 2014 (FAO, 2016)

Country	Production (millions of tons)	Total world production (%)
Nigeria	54.83	19.9
Thailand	30.02	10.9
Indonesia	23.43	8.5
Brazil	23.24	7.5
Democratic Republic of the Congo	16.61	6.0
Ghana	16.52	6.0
Vietnam	10.21	3.7
Cambodia	8.84	3.2
India	8.14	3.0
Angola	7.64	2.8

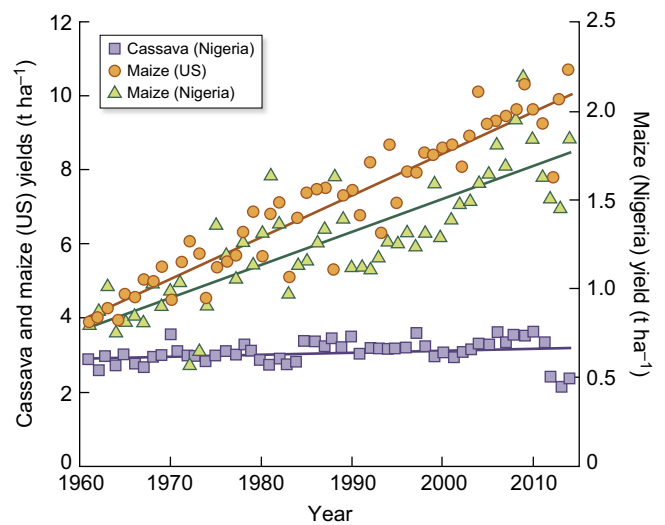


Fig. 1 Yield trends of cassava and maize in Nigeria and the USA, respectively, over the period 1961–2014 (FAO, 2016). Cassava values were converted to dry mass, assuming a 70% water content.

Ceballos *et al.*, 2013) and agronomic practices (CIAT, 2007). Such efforts in Asia, for instance, have increased cassava yields at a rate of 0.138 t ha⁻¹ yr⁻¹ (on a dry weight basis) between 2004 and 2014. However, in sub-Saharan Africa, where cassava is essential in supplying calories to a large proportion of the population, yields have actually been declining by 0.024 t ha⁻¹ yr⁻¹ (Fig. 2). The average yields currently achieved by African farmers are just 2.51 t ha⁻¹ on a dry weight basis, which is lower than the world average of 3.35 t ha⁻¹ and 2.5 times lower than yields attained in Asia (Fig. 3).

Sub-Saharan Africa is predicted to see the largest population growth of all world regions, 123% by 2050 (United Nations, 2015). Cassava is an important crop for subsistence farmers in this region, and, as already mentioned, it is a crucial and favored source of calories by this population, as well as being a cash crop in years of surplus. With limited availability of additional sources of calories, increasing the yield per unit land area of cassava will be critical. Genetic improvement of resource use efficiency, particularly the

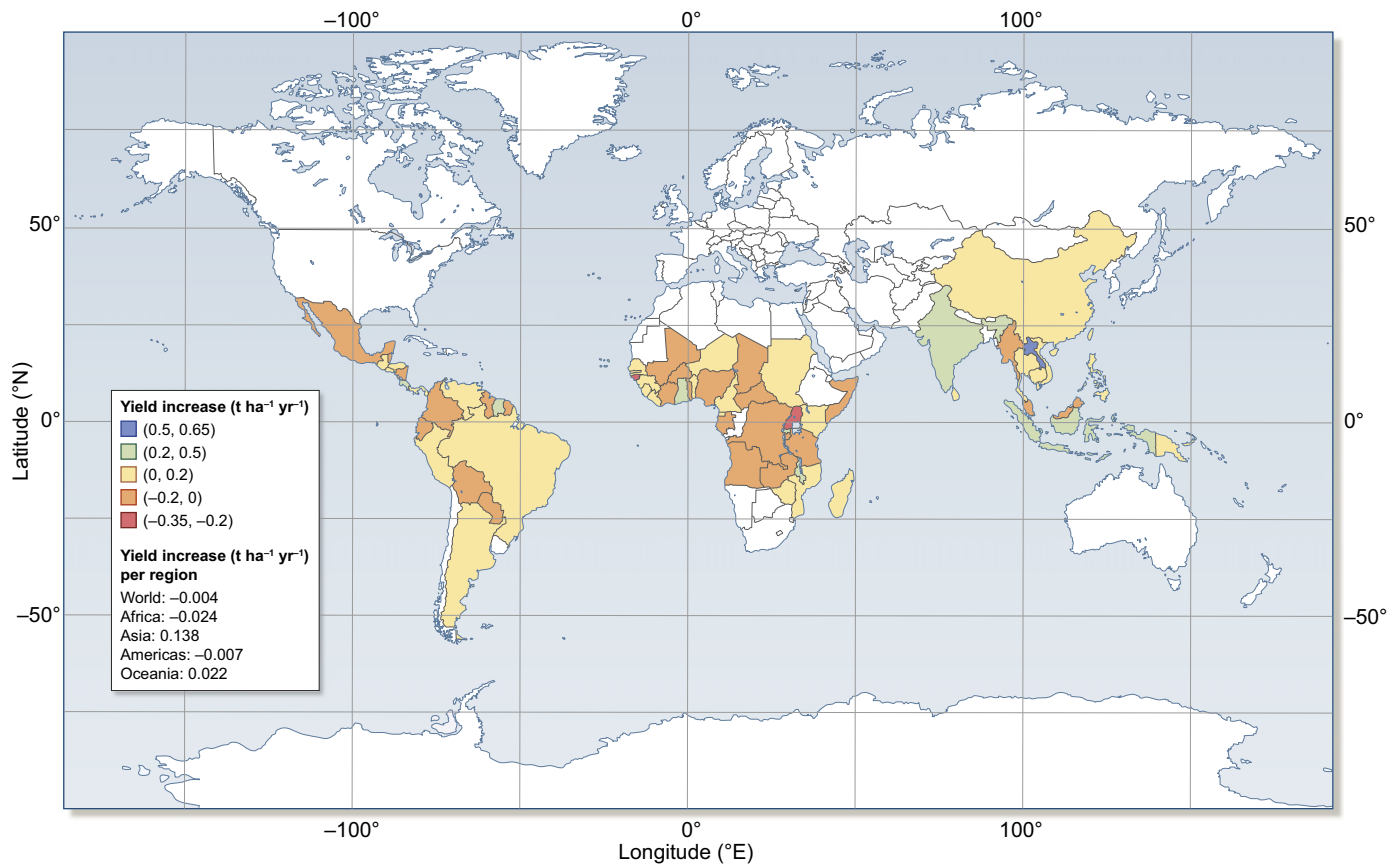


Fig. 2 Change in cassava yields (t ha⁻¹ yr⁻¹) across the world between 2004 and 2014 (FAO, 2016). Values were converted to dry mass, assuming a 70% water content.

conversion of available sunlight into biomass, is one opportunity. This review assembles knowledge of the underlying physiology determining yield potential in cassava, and uses this to suggest ways to increase its genetic yield potential.

II. How might genetic yield potential be increased in cassava?

Improvement of the harvest index, or the proportion of total biomass partitioned into the harvested component, was a key factor driving increased yields in the Green Revolution. Because of this improvement, cassava breeding over the past 30–40 yr has understandably focused upon increasing the harvest index, which proved a successful strategy in increasing rice (*Oryza sativa*) and wheat (*Triticum aestivum*) yields (Ceballos *et al.*, 2010). However, because this strategy increases the proportion of total plant biomass partitioned to the harvested product, the total plant biomass places a limit on the absolute increase in yield that may be achieved. What are the prospects for genetically increasing the total biomass per hectare? The total biomass produced by a crop results from the integral of photosynthetic assimilation over the growing season less all respiratory losses. It depends on the efficiencies with which the crop intercepts light and converts that into biomass over the course of the growing season (Monteith & Moss, 1977; Long *et al.*, 2006a, b; Zhu *et al.*, 2007, 2010; Parry *et al.*, 2011; Reynolds *et al.*, 2011;

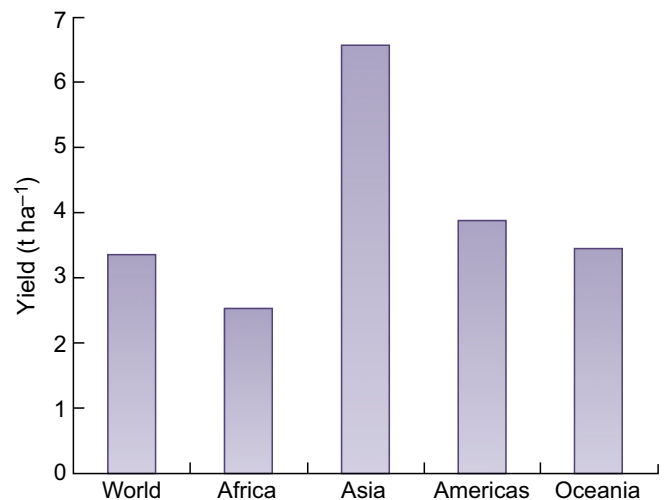


Fig. 3 Cassava yields (t ha⁻¹) in 2014 (FAO, 2016). Values were converted to dry mass, assuming a 70% water content.

Long & Zhu, 2014). Representation of these efficiencies in the form of an equation provides one method to quantitatively assess the opportunity for improvement of yield potential (Monteith & Moss, 1977; Long *et al.*, 2006a,b). Although almost 50 yr old, this simple, but physiologically well-founded approach remains invaluable. It has revealed similarities across photosynthetic types,

allowed evaluation of the effects of atmospheric and climate change on crops, enabled analysis of efficiencies in remote sensing and has shown how genetic improvements of yield potential have been achieved (Beadle & Long, 1985; Zhu *et al.*, 2010). This equation states that yield potential is the product of total incident photosynthetically active solar radiation (PAR) over the growing season (S_p), PAR interception efficiency (ϵ_i), PAR conversion efficiency (ϵ_c) and partitioning efficiency or harvest index (ϵ_p). ϵ_i is affected by canopy size, architecture, duration and speed of ground coverage after planting; ϵ_c is defined by the amount of intercepted PAR that is converted into biomass; and ϵ_p is the proportion of biomass that is partitioned to the harvested plant organ, in the case of cassava, the starchy tuberous roots. Using this equation, the steady increase in soybean (*Glycine max*) yield of 26.5 kg ha⁻¹ yr⁻¹ over the past 80 yr of breeding was shown to be attributable to an improvement in all three efficiencies. However, while ϵ_i and ϵ_p for soybean appear now to be close to their maximum theoretical values, ϵ_c falls far short of its theoretical maximum and has been improved by far the least of the three. Similar conclusions may be drawn for wheat and rice, where a plateauing of improvement in ϵ_i and ϵ_p , as well as failure to improve ϵ_c , coincides with a stagnation of yield increase at the present time. (Long & Ort, 2010; Ray *et al.*, 2012; Long, 2014; Long *et al.*, 2015).

For cassava, the ϵ_p achieved by cultivars (Table 2) is close to that of the crops that have attracted the most attention and investment in breeding, such as maize, rice, wheat and soybean (Long *et al.*, 2006a,b; Fischer & Edmeades, 2010; Fischer, 2011; Koester *et al.*, 2014; Long & Zhu, 2014). For grain and seed crops, ϵ_p is considered to have a theoretical maximum of *c.* 65%, as at harvest some biomass must remain in the stems and floral structures that contain the seed (Zhu *et al.*, 2010). In these crops, however, the stem and floral structure are necessary to hold the harvested plant part. As a root crop, cassava, in theory, does not need any part of the shoot to persist through to harvest, and hence a higher theoretical ϵ_p is conceivable. However, in practice, cassava propagation is predominantly from stem cuttings, which means that a significant amount of live mass must remain in stems under current methods of propagation (El-Sharkawy, 2004).

Table 2 Photosynthetically active radiation (PAR) interception efficiency (ϵ_i), conversion efficiency of intercepted PAR (ϵ_c) and partitioning efficiency or harvest index (ϵ_p) for four cassava cultivars from the International Center for Tropical Agriculture (CIAT), Colombia

Cultivar	ϵ_p (%)	ϵ_i (%)	ϵ_c tuberous root (g MJ ⁻¹)	ϵ_c tuberous root (%)
CM 507-37*	55.3	65.2	0.94	1.6
M Col 1684*	46.3	64.1	0.71	1.2
CM 507-37†	66.1	61.5	0.93	1.6
CM 523-7†	70.5	60.7	0.84	1.4
CMC 40†	53.7	52.3	0.69	1.2
M Col 1684†	69.0	57.9	0.86	1.5

Values used as input for calculations presented in this table and details of the methodology are given in Supporting Information Table S1.

Data used as input for calculations are from El-Sharkawy *et al.* (1992a) (*) and El-Sharkawy & Cadavid (2002)(†).

Although ϵ_p in cassava, like other crops, is probably close to the maximum that could be achieved while still providing stems for propagation, this is not true for ϵ_i . Calculated ϵ_i values from four cassava cultivars were 52.3–64.1% (Table 2), well below those of modern cultivars of major grain and seed crops, as well as the theoretical limit of 90% (Long *et al.*, 2006a,b; Koester *et al.*, 2014). Even for cultivars from Asia, the continent where the greatest increases in yield per unit land area have been achieved (Fig. 3), the cassava season-long ϵ_i is *c.* 64% (Leepipatpaiboon *et al.*, 2009) while for soybean, for instance, ϵ_i may approach 90% (Long *et al.*, 2006a,b). Thus, although ϵ_i seems to be near to its theoretical maximum in the crops that have been most intensively bred (Long & Zhu, 2014), in cassava there is still considerable room for improvement. Based on Table 2, selection or engineering of forms that approach the theoretical 90% could give a 55% increase in yield potential.

The conversion efficiency (ϵ_c), which is determined by canopy photosynthetic carbon uptake less whole-plant respiration, appears to present the greatest opportunity for improving cassava yield potential. In terms of mass per unit intercepted energy, ϵ_c ranges from 0.69 to 0.94 g MJ⁻¹, corresponding to an average ϵ_c in terms of energy transduction of intercepted PAR into biomass of just 1.4%. That is only one-seventh of the theoretical efficiency of C₃ photosynthesis (Table 2; Fig. 4; Zhu *et al.*, 2010). Similar values were reported previously (Beadle & Long, 1985; Pellet & El-Sharkawy, 1997). By contrast, the most productive soybean cultivars can reach an ϵ_c of 2.9–4.3% (Koester *et al.*, 2014). However, even these values are well below the theoretical maximum of ϵ_c predicted for C₃ plants of 9.4% (Zhu *et al.*, 2010) (Fig. 4). It should also be noted that this theoretical maximum assumes typical photorespiratory rates, which, if successfully reduced, would raise this theoretical maximum.

These low values of ϵ_c by comparison both to other crops and to theoretical values highlight the lack of incorporation of photosynthetic traits in breeding and current engineering programs. Although El-Sharkawy & De Tafur (2010) provide a compelling argument for the inclusion of photosynthetic efficiency in breeding traits, the available data for landraces and cultivars suggest that there has been no improvement in photosynthetic rate through breeding (Table 3). This might be partially explained by the fact that there has been little research into cassava photosynthesis compared with the major field and glasshouse crops of the developed world. That improving photosynthesis in cassava will

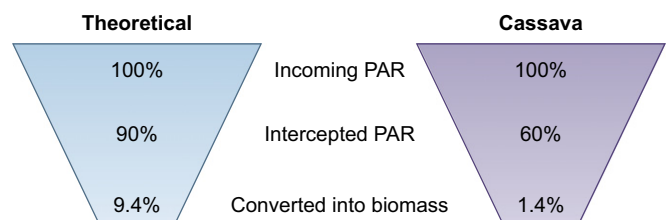


Fig. 4 Comparison between the theoretical maximum conversion efficiency (ϵ_c) for C₃ plants and average values obtained for cassava. Theoretical values are from the analysis of Zhu *et al.* (2010), considering losses of energy at each stage of transduction from the arrival of photosynthetically active radiation (PAR) at the leaf through to net production of carbohydrate.

increase yield is vividly demonstrated by the open-air [CO₂] enrichment study by Rosenthal *et al.* (2012). Here, an average season-long 30% increase in leaf photosynthetic rates under elevated [CO₂] resulted in a 104% increase in tuberous dry mass. This greatly exceeds the *c.* 15% increase in the yields of wheat, rice and soybean observed with similar enhancements of photosynthesis to that seen in cassava, under open-air elevation of [CO₂] (Long *et al.*, 2006a,b; Ainsworth *et al.*, 2008a,b). In reviewing the growth of a wide range of crops under elevated [CO₂], it was observed that, in general, root crops showed a greater stimulation of yield. This may reflect the more indefinite nature of the size and number of roots or tubers in these crops relative to most grain and seed crops. Genetically increasing photosynthetic efficiency might therefore be expected to provide even larger benefits in cassava than in our major grain and seed crops.

III. Modifying the cassava canopy to achieve higher ϵ_i

The ϵ_i of a given crop is defined by the size and architecture of the canopy as well as its duration and speed of closure. In cassava, many parameters related to the canopy, such as leaf area index (LAI), leaf retention and branching habit, have already been shown to positively correlate with yield (Okogbenin & Fregene, 2003; El-Sharkawy & De Tafur, 2010; Lahai, 2013).

The cassava canopy starts to develop *c.* 15 d after planting of the stem section propagules and reaches maximum light interception at *c.* 4–5 months (Alves, 2002; El-Sharkawy, 2004). This would appear slow compared with maize and soybean crops, which can achieve closed canopies within 4 wk (Singer *et al.*, 2011). Yet crops sown from seed have a very small reserve, which clearly limits the speed at which closure can be achieved. Cassava stem segments

should in theory represent a much larger reserve which should power rapid development of leaves and canopy closure. This suggests that there has been little selection for accumulation of reserves in the stem, which could greatly improve the speed of canopy closure in cassava. ϵ_i is determined largely by LAI and leaf angle. ϵ_i shows a rectangular hyperbolic response to LAI, with $\delta\epsilon_i$; δ LAI increasing as the average leaf angle becomes more horizontal (Drewry *et al.*, 2014). Typically, cassava LAI peaks at *c.* 5 months when senescence of lower leaves begins to counteract further leaf production at the top of the canopy. LAI typically begins to decline at 9 months when senescence outpaces new leaf production and ϵ_i declines accordingly (Fig. 5) (El-Sharkawy *et al.*, 1992a; Pellet & El-Sharkawy, 1993; El-Sharkawy & Cadavid, 2002; El-Sharkawy & De Tafur, 2010). Breeding strategies have selected cultivars that have long-lived leaves and individual leaves with an increased leaf area (Lenis *et al.*, 2006; Lebot, 2009).

Cassava shows simultaneous shoot and tuberous root development in which photoassimilates are partitioned between leaves and tuberous root growth (Fukai *et al.*, 1984; Alves, 2002). Tuberous root development starts *c.* 2 months after planting, before maximum investment in leaf biomass (Fig. 5). Although tuberous roots are bulking throughout this period, shoot development is dominant and appears to have priority over root growth (Lian & Cock, 1979). In other words, photoassimilates are not preferentially partitioned to tuberous roots until shoot growth nears completion, which usually occurs *c.* 6 months after planting (Fig. 5). This preference may reflect a delicate balance between shoot and tuber growth, imposing a limit on canopy development for maximum yields. Excessively large canopies may actually reduce yields in cassava (Lahai, 2013). This could result from the fact that the lower leaves might be starved of light to the extent that they respire more

Table 3 Average and highest physiological parameters for improved cultivars and landraces

Physiological parameters	Improved cultivar			Landrace cultivar		
	Average	SE	Highest	Average	SE	Highest
Seasonal A ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	25.36	0.45 (11)	49.70	25.00	0.60 (10)	47.40
$V_{c,\text{max}}$	133.30	6.24 (1)	148.90	–	–	–
J_{max}	225.95	7.133 (1)	247.75	–	–	–
F_v/F_m^*	0.76	0.01 (2)	0.80	0.78	0.02 (3)	0.85
Seasonal $c_i : c_a$	0.48	0.02 (4)	0.71	0.48	0.02 (4)	0.63
Seasonal g_s ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$)	987.40	125.71 (4)	1600.00	1001.50	184.68 (3)	1700.00
WUE _i ($\text{mmol CO}_2 \text{ mol H}_2\text{O}^{-1}$)	0.06	0.0036 (1)	0.10	–	–	–
LAI [†]						
0–3 months	1.10	0.17 (3)	3.10	1.06	0.14 (4)	2.45
3–6 months	2.25	0.11 (5)	4.00	2.82	0.17 (6)	6.16
6–9 months	2.43	0.17 (3)	4.62	2.18	0.18 (3)	3.57
9–12 months	1.72	0.12 (2)	2.42	1.83	0.30 (3)	4.86
Dry root yield (t ha^{-1}) [†]	11.33	0.43 (6)	27.40	8.61	0.49 (8)	17.50
Harvest index [†]	0.56	0.015 (7)	0.84	0.46	0.019 (8)	0.77

Seasonal A , midday photosynthetic rates averaged across the field season; $V_{c,\text{max}}$, maximum carboxylation rate at Rubisco; J_{max} , maximum rate of whole-chain electron transport; F_v/F_m , dark-adapted maximum quantum yield; $c_i : c_a$, ratio of internal [CO₂] to atmospheric [CO₂] averaged across the season; g_s , stomatal conductance averaged across the season; WUE_i, intrinsic water use efficiency calculated from only diurnal values; LAI, leaf area index. Sources of data are detailed in Table S2. –, no reliable data available.

*Studies conducted in glasshouse trials or trials with pots placed outside, as opposed to field trials. SE values are the calculated SE of variation between collected values in at least one study; study counts are in parentheses.

[†]Only parameters with associated photosynthetic rate measurements in field trials were used.

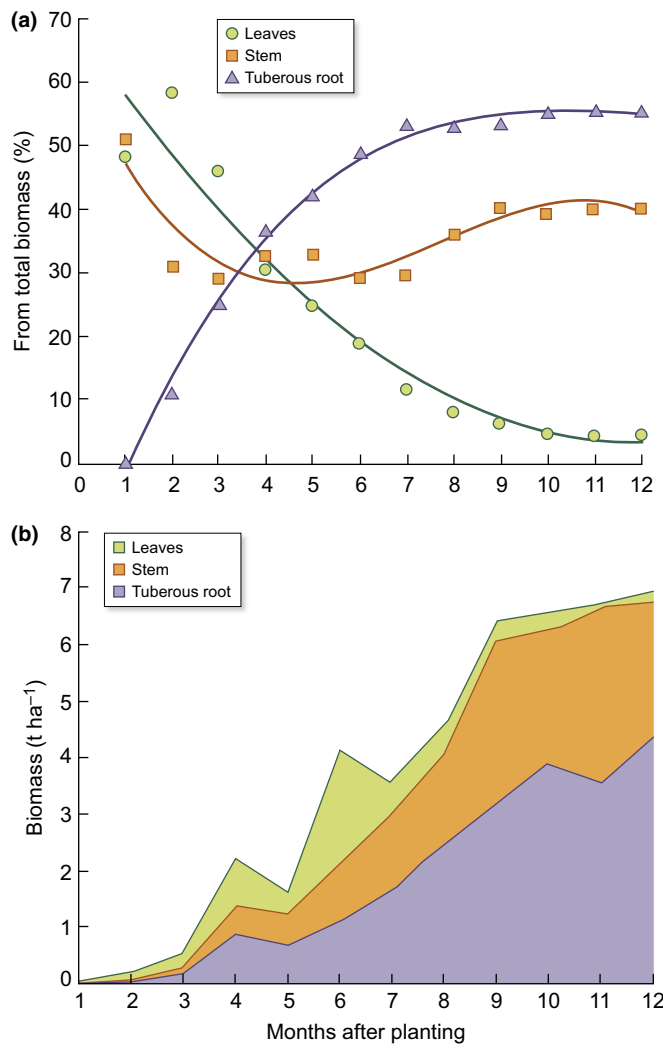


Fig. 5 Percentage (a) and total accumulated biomass (b) of leaves, stem and tuberous roots during 12 months of cassava development under nonstress conditions, that is, watered or without water stress reported, and average temperature between 25°C and 32°C. Data are the average of 36 cultivars. The sources of the data used to produce this figure are detailed in Supporting Information Table S3. All values were converted to dry mass, assuming a 70% water content.

carbon than they assimilate in photosynthesis, and represent investment of resource that could have been used in tuber growth. Conversely, early bulking of tuberous roots will slow canopy development and lower ϵ_i . Selection of genotypes in which bulking does not begin until canopy closure has occurred, followed by a switch to sink dominance by the tuberous roots, could greatly increase yield. Dominance of the shoot would appear to result in an over-investment in leaves. The comparison between improved cultivars and landraces exemplifies this dominance interaction. Improved cultivars have higher tuberous root yields than landraces, yet the LAI of improved cultivars is lower for most of the growing season (Table 3). This suggests that breeders have inadvertently selected for this trait. Maximum yield appears to occur with an LAI between 2.5 and 3.5 (Cock *et al.*, 1979; Ramanujam, 1985; Lebot, 2009), and a leaf longevity of *c.* 100 d has been suggested to be optimal for maximizing yield (Cock *et al.*, 1979).

Canopy architecture in cassava varies considerably with cultivar, ranging from nonbranching types, also called erect types, to bush or highly branched types (Ekanayake *et al.*, 1996). Branching genotypes usually form a better canopy that can intercept more light than nonbranching genotypes, resulting in higher tuberous root yields. However, if branching occurs very early during development, resulting in multiple shoot sinks, competition for photoassimilates between shoot and tuberous root development can reduce the final yield. Indeed, computational simulations suggest that late branching is ideal for maximizing yield (Cock *et al.*, 1979).

In addition to the importance of canopy architecture for photoassimilate partitioning between the shoot and tuberous roots, the canopy is also important in terms of agronomic practices (CIAT, 1985, 2007). For instance, more than one-third of cassava world-wide is intercropped (Lebot, 2009), where an unbranched stem may reduce shading of the adjacent crop. In monocultures, however, improvement may be gained by increasing leaf angles toward the vertical and by selection for lighter green leaves in the upper canopy (Long *et al.*, 2006a,b; Drewry *et al.*, 2014; Ort *et al.*, 2015). This would allow a more effective distribution of light between upper and lower leaves, increasing net canopy photosynthesis and in turn yield. Lighter green leaves would also serve to cool the canopy, relative to the current dark green leaves, as a strategy to deal with rising temperatures (Drewry *et al.*, 2014). The strategy of increasing leaf angle was demonstrated to be effective in other crops such as maize, wheat and rice (Sakamoto & Matsuoka, 2004; Isidro *et al.*, 2012), especially as it allows an increase in plant density which would again allow faster canopy closure.

Although the ideal characteristics for a cassava canopy have been simulated using computational models (Cock *et al.*, 1979; Fukai & Hammer, 1987; Gutierrez *et al.*, 1988; Gijzen *et al.*, 1990; Matthews & Hunt, 1994; Gabriel *et al.*, 2014) with some of those characteristics incorporated into breeding programs, the ϵ_i of modern cassava cultivars is still far below the theoretical maximum (Table 2; Fig. 4). This shortcoming might be because none of these models have succeeded in incorporating an adequate solution to describing the dynamic partitioning of biomass (Gray, 2000), a crucial parameter for cassava. Further, none of these models have considered the link between canopy, leaf-level photosynthesis and productivity. Thus, the inclusion of mechanistic processes such as leaf photosynthesis, stomatal closure, and energy balance in the next generation of models will be vital to identify the best character to select for in improving yield. This will provide a physiological and morphological basis to link with emerging information on gene function and their associated gene networks affecting canopy architecture and leaf properties.

IV. Increasing ϵ_c in cassava through photosynthesis

Carbon assimilation through the photosynthetic process is, of course, crucial for cassava tuberous root production. As mentioned in the previous section, shoots have preference over tuberous root growth in the competition for photoassimilates, so affecting final yield. However, under conditions of increased canopy photosynthesis, it appears that the excess is allocated to the tuberous roots (Rosenthal *et al.*, 2012). Increasing crop photosynthesis may

therefore result in a larger than expected increase in yield, given that a 30% increase in photosynthesis at the leaf level resulted in a more than three-fold increase in the harvested yield of tuberous roots. A very valuable approach to further increase cassava yields would therefore be to increase the efficiency of photosynthesis. Indeed, this has already been recommended by other authors (Pellet & El-Sharkawy, 1993; De Tafur *et al.*, 1997b; Flood *et al.*, 2011), but, to date, genetic improvement of photosynthesis appears a rather unexplored field in cassava research.

Studies of photosynthesis in cassava are limited. Most of the published research on cassava photosynthesis comes from the International Center for Tropical Agriculture (CIAT), in Colombia. Therefore, the available knowledge about photosynthesis in cassava is mostly limited to Latin American cultivars.

Some studies on these cultivars have suggested that cassava uses a C_3 – C_4 intermediate form of photosynthesis on account of high leaf photosynthetic rates, low apparent rates of photorespiration, a chlorenchymatous bundle sheath and a high photosynthetic nitrogen (N) use efficiency (El-Sharkawy & Cock, 1987; El-Sharkawy, 2009, 2016). Parallel work feeding $^{14}CO_2$ to leaves of cassava showed an apparent intermediate pattern of initial C_4 and C_3 products (Cock *et al.*, 1987). However, a subsequent detailed analysis of first products failed to show such an intermediate pattern, but rather a very typical C_3 pattern. This later study also showed that the photosynthetic CO_2 compensation points of 10 different cultivars were between 55 and 62 $\mu mol\ mol^{-1}$, typical of C_3 species, whereas an intermediate would be expected to show a value of *c.* 25 $\mu mol\ mol^{-1}$ (Edwards *et al.*, 1990). Carbon 13 isotope fractionation ($\delta^{13}C$) in cassava is also identical to that of C_3 species, ranging from -23% to -26% (Burns *et al.*, 2012), compared with -12% and -16% found in C_4 plants (O'Leary, 1988). Moreover, although cassava has a chlorenchymatous bundle sheath, unlike C_4 species it is not surrounded by mesophyll cells (Edwards *et al.*, 1990). In total, these findings show cassava to be a typical C_3 species (Edwards *et al.*, 1990; Angelov *et al.*, 1993; Gleadow *et al.*, 2009; Rosenthal *et al.*, 2012). The compilation of data from several studies in which photosynthetic rates were reported shows that the average net photosynthetic rate is significantly smaller than the highest rates observed, calling into question the concept that cassava has unusually high rates for a C_3 species (Table 3). In optimal growing conditions, the highest reported photosynthetic rate for field-grown improved cassava cultivars was 50 $\mu mol\ m^{-2}\ s^{-1}$ at a photon flux of over 1800 $\mu mol\ m^{-2}\ s^{-1}$. However, the seasonal average is about half of this value (Table 3) (El-Sharkawy, 2004) and, although some high values may be observed, photosynthetic rates varied little in the field over the growing season (Bhagsari, 1988; Pellet & El-Sharkawy, 1993; De Tafur *et al.*, 1997a; El-Sharkawy & De Tafur, 2010; Rosenthal *et al.*, 2012). The average *in vivo* capacity for Rubisco carboxylation ($V_{c,max}$) is 133.3 $\mu mol\ m^{-2}\ s^{-1}$ and the maximum rate of whole chain electron transport (J_{max}) is 225.95 $\mu mol\ m^{-2}\ s^{-1}$ for improved cassava cultivars. These are comparable to the $V_{c,max}$ and J_{max} observed for rice in the field (Borjigidai *et al.*, 2006), but somewhat higher than averages observed for other C_3 crops, shrubs, trees, grasses, and legumes (Ainsworth & Long, 2005; Ainsworth & Rogers, 2007). The

significant variation in these parameters within cassava suggests an opportunity for selection.

Several genetic strategies have been proposed for crop and model plants to increase ϵ_c and yield through increasing photosynthesis, and a limited number of these have been realized (Long *et al.*, 2015). One of the most extensively explored strategies has been the optimization of enzyme activity within the Calvin cycle, in particular the up-regulation of sedoheptulose-1,7-bisphosphatase (SBPase) and fructose-1,6-bisphosphate aldolase (Raines, 2011; Rosenthal *et al.*, 2011; Simkin *et al.*, 2015) as predicted by computer simulation (Zhu *et al.*, 2007). In wheat, genetic variation in SBPase expression correlating with leaf photosynthetic rates has been shown, suggesting that conventional breeding in which high expression of SBPase is selected would also increase productivity (Driever *et al.*, 2014). The catalytic properties of the enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) are a key factor determining light-saturated photosynthetic rates of C_3 crops (Portis & Parry, 2007). Variation within and between species suggests an opportunity to engineer or select for improved kinetic properties that would improve canopy photosynthesis without requiring more protein or nitrogen (Zhu *et al.*, 2004b). Under global change-driven conditions of elevated $[CO_2]$ and elevated temperature, efficiency gains could be achieved by altering the balance between the capacity for regeneration of ribulose-1,5-bisphosphate (RubP) and the amount of Rubisco (Kromdijk & Long, 2016). This is particularly relevant to cassava, given the higher temperature conditions of the tropics. Thus, exploring variation in the kinetic properties of Rubisco between cassava cultivars could be of particular value (Galmes *et al.*, 2014; Carmo-Silva *et al.*, 2015).

Synthetic photorespiratory bypass systems engineered into the chloroplast and designed to decrease CO_2 losses, have been shown to effectively increase photosynthesis and production in model species (Kebeish *et al.*, 2007; Peterhansel *et al.*, 2013). Consideration of stoichiometries shows that synthetic photorespiratory bypasses will reduce the energetic costs and increase $[CO_2]$ within the plastid, so also serving to decrease oxygenation and hence photorespiration (Xin *et al.*, 2015). Furthermore, the increase in plastid $[CO_2]$ will increase the temperature optimum of photosynthesis, and increase water use efficiency (Kromdijk & Long, 2016). This approach might be especially relevant in cassava in view of the tropical conditions under which it is cultivated, while serving as a means to counteract the impacts of increasing water vapor pressure deficit with climate change (Lobell *et al.*, 2014; Ort & Long, 2014).

In high light, generation of a trans-thylakoid pH gradient and de-epoxidation of the xanthophyll violaxanthin to zeaxanthin are associated with dissipation of excess excitation energy as heat, termed nonphotochemical quenching (NPQ). This protects the photosynthetic apparatus against the generation of destructive oxidizing radicals (Long *et al.*, 1994). However, on transfer to shade it takes a considerable time, many minutes, for these processes to relax. As a result, even though light is now limiting, a large proportion of the absorbed light energy continues to be dissipated as heat rather than being used to drive CO_2 assimilation. The diurnal course of the sun on a clear day transfers leaves below

the canopy top into and out of shade. This change occurs in a second at the level of individual chloroplasts. Using ray tracing, computational analysis showed that this slow recovery at the canopy level could cost 30% of potential carbon assimilation over the course of a day (Zhu *et al.*, 2004a). The loss would be even greater under intermittent cloud. Selecting or engineering traits for faster relaxation could therefore considerably improve canopy photosynthetic efficiency and ϵ_c . As stomatal conductance adjusts slowly, on transition to shade, this would also significantly increase crop water use efficiency.

V. Does cassava have the sink capacity for an increased influx of photoassimilates?

Limited sink capacity can feed back on any photosynthetic enhancements. Thus, efforts to increase conversion efficiency through improved photosynthetic rates in cassava could be unsuccessful without sufficient sink capacity. Pellet & El-Sharkawy (1993) and Rosenthal *et al.* (2012) found that individual tuberous roots have limited sink capacity, but this is offset by the initiation of additional tuberous roots. Earlier work has suggested that genotypes in which fewer than nine tuberous roots form are sink limited (Cock *et al.*, 1979). This finding has driven interest in analyzing the genes, gene networks and gene products that control tuberous root initiation and bulking. Improving the sink capacity of cassava to increase yield may depend on these molecular targets.

Mitprasat *et al.* (2011), for instance, found a down-regulation of a glyceraldehyde-3-phosphate dehydrogenase with a concomitant up-regulation of a UDP-glucose pyrophosphorylase in cassava leaves after 8 wk, corresponding to initiation of tuberous root development or bulking. The authors hypothesized that changes in these two enzymes will favor sucrose synthesis for sink supply. They also observed a decrease in an antioxidant enzyme from weeks 4 to 7 after planting, and proposed that reactive oxygen species (ROS) formed by this enzyme may be functioning as a signaling molecule for tuber growth regulation through gibberellic acid. Li *et al.* (2010) found a series of differentially expressed genes in cassava roots between 2 and 4 months after planting by using a cDNA microarray. These root-specific genes might be responsible for initiating the root bulking process, given associated changes in transcripts involved in signal transduction, protein metabolism, starch and sucrose metabolism, and glycolysis-related processes.

In addition to sink capacity, sucrose and glucose concentrations in the leaf play a large role in the regulation of expression of genes coding for the proteins of the photosynthetic apparatus. Sucrose and glucose accumulation in source leaves enhance the expression of genes involved in carbon storage and utilization, and cause down-regulation of some key genes coding for the photosynthetic apparatus, including Rubisco (Cho *et al.*, 2009; Kunz *et al.*, 2014). This is clearly illustrated when the leaf petiole is heat-girdled, preventing export and causing a large accumulation of starch and soluble carbohydrates, in turn rapidly down-regulating expression of genes encoding enzymes of photosynthetic carbon metabolism, N metabolism and chlorophyll synthesis. Simultaneously, expression of genes encoding enzymes involved in the tricarboxylic acid (TCA) cycle, mitochondrial electron transport, and flavonoid

biosynthesis were up-regulated. Thus, increasing photosynthetic rates in cassava could also increase the sucrose negative feedback loop unless there is sufficient sink demand and transport capacity to remove the additional sucrose formed in the leaves (Zhang *et al.*, 2015). Strategies to increase sugar transport and reduce carbohydrate accumulation in leaves may involve increasing the expression of sucrose transporters (Ainsworth & Bush, 2011) and the recently discovered SWEET (Sugars Will Eventually be Exported Transporter) transporters (Chen *et al.*, 2015) in sink tissues to optimize sugar flux and increase phloem-loading capacity. Another approach could be to increase capacity for starch formation in leaves. Modeling of leaf photosynthetic carbon metabolism has shown that up-regulation of starch synthesis would also support greater rates of light-saturated CO₂ assimilation (Zhu *et al.*, 2007). This would allow increased export over the dark period, to make more efficient use of phloem capacity. In cassava, the overexpression of AGPase in the tuberous roots increased the amount of starch accumulated in this organ. This modification is also likely to lessen feedback inhibition of photosynthesis by decreasing the risk of accumulation of nonstructural carbohydrates in the leaves (Ihemere *et al.*, 2006). The large increases in tuber yield seen in the one open-air elevated [CO₂] experiment so far conducted may suggest that sink limitation is not a barrier (Rosenthal *et al.*, 2012). However, this experiment concerned one cassava clone over a relatively short growing season. It will be important to establish with a wider range of open-air [CO₂] elevations, ideally within the regions where the crop is normally produced, whether this finding applies more broadly to cassava. If it does, then it suggests photosynthetic improvement would be of great value in increasing yield potential.

VI. Environmental stress effects on photosynthesis and development

Environmental stresses will increase as global climate change unfolds, particularly with respect to temperature and soil moisture in the tropics (IPCC, 2014). In addition, to meet further demand, cultivation may need to expand to poorer soils and more arid regions. Although cassava can withstand challenging conditions with little need for active agronomic management, relative to other food crops (Burns *et al.*, 2010), changes in the environment can still cause significant yield declines and reduce the benefits of increasing photosynthetic efficiency, as proposed in the preceding sections.

One of the most studied environmental stresses acting on cassava is drought (El-Sharkawy *et al.*, 1992b; El-Sharkawy, 1993; Sundaresan & Sudhakaran, 1995; Lokko *et al.*, 2007; Okogbenin *et al.*, 2013; Vandegeer *et al.*, 2013; Hu *et al.*, 2015). Water stress impacts cassava physiology and yield, even though it is generally better adapted to extended periods of drought than most crops. One remarkable physiological adaptation to drought is the ability of cassava leaves to rapidly decrease stomatal conductance, avoiding significant decline in leaf water potential, thus protecting the photosynthetic apparatus and other machinery that is sensitive to a decline in leaf water potential (El-Sharkawy, 2004; Oguntunde, 2005). Cassava leaves may also droop or fold, to decrease interception of sunlight, in turn decreasing, leaf temperature and water loss. This may occur not only during periods of low soil

moisture, but also during periods of low water vapor deficit (VPD) (El-Sharkawy, 2004). With prolonged drought, cassava will protect itself against further water loss by abscission of leaves (Liao *et al.*, 2016). Drought tolerance varies with cultivar (Zhao *et al.*, 2015), as well as the severity and duration of drought. As shown by De Tafur *et al.* (1997a) and El-Sharkawy *et al.* (1992b), while these adaptations allow the crop to survive and result in a water potential similar to that of unstressed plants, they are at the cost of photosynthetic rate in all cultivars studied. The impact of drought is also dependent on developmental stage. When drought occurs either early or mid-season, cassava development is delayed, but the final yield is little affected relative to well-watered plants (El-Sharkawy & Cadavid, 2002). Remarkably, the newly expanded leaves of previously stressed cassava plants often show higher photosynthetic rates than those of unstressed cassava (Cayón *et al.*, 1997), which partially compensates for losses during the drought period and explains the maintenance of tuberous root biomass. However, when drought stress is imposed at ≥ 6 months after planting and continues until harvest, neither LAI nor shoot biomass is impacted, but the biomass of tuberous roots at harvest is lower (El-Sharkawy & Cadavid, 2002). Interestingly, drought seems in general to have a larger relative effect on cultivars with higher photosynthetic rates, while the effect diminishes with lower photosynthetic rates and lower LAI (El-Sharkawy & De Tafur, 2010). This could reflect higher stomatal conductance and a more rapid rate of water loss. The intrinsic water use efficiency (WUE_i) for cassava ranges between 40 and 80 $\mu\text{mol} [\text{CO}_2] \text{mmol} [\text{H}_2\text{O}]^{-1}$ and is quite similar to those of soybean and other C_3 food crops, grown under similar crop-atmosphere water vapor deficits (Gilbert *et al.*, 2011). That cassava has some adaptation to drought is underlined by the fact that it has served as a source of genes that have increased drought tolerance on transfer to rice (Yu *et al.*, 2016). The recent genomic approaches to identifying candidate genes for drought tolerance may facilitate acceleration of marker-assisted breeding for increased drought tolerance (Okogbenin *et al.*, 2013; Turyagyenda *et al.*, 2013). Many of the approaches that have been suggested for increasing the photosynthetic efficiency of C_3 crops more generally, such as increased mesophyll conductance, decreased photorespiration, introduction of algal CO_2 -concentrating mechanisms, and conversion of C_3 to C_4 , would increase water use efficiency at the leaf level, and so could allow more production without demand for more water (Zhu *et al.*, 2010; Long *et al.*, 2015).

Temperature is also critical for cassava development and photosynthetic rates. The optimal temperature for cassava growth is between 25°C and 29°C, but it can tolerate temperatures varying from 16°C to 38°C (Alves, 2002; El-Sharkawy, 2004). For photosynthesis, the optimum temperature ranges from 25°C to 35°C, similar to optima for other tropical crops, with rates declining for temperatures below and above this range (El-Sharkawy *et al.*, 1984). Temperatures above 30°C usually reduce leaf longevity from 200 to 120 d, decreasing LAI and biomass partitioning into tuberous roots (Alves, 2002). Temperatures between 18°C and 16°C delay leaf appearance and expansion, which consequently reduce total plant biomass. Within this range of temperatures, there is a delay in, and reduction of biomass partitioning into tuberous roots, which can decrease yield

to almost zero (Manrique, 1992; Akparobi *et al.*, 2002). A transcriptomic analysis found that, for 44 stress-induced genes in Arabidopsis, 181 genes with significant sequence similarity were identified in cassava. Prevalent among these were heat stress genes, suggesting an important genetic element in the heat tolerance of this crop (Sakurai *et al.*, 2007).

An often overlooked aspect of global atmospheric change is that surface ozone (O_3) concentrations are rising. Although there are few measurements, it appears that pre-industrial levels were < 10 ppb. Surface ozone forms in sunlight from reactions of nitrogen oxides and molecular oxygen in the presence of hydrocarbons. Because nitrogen oxides resulting from high-temperature combustion are long lived in the atmosphere, ozone can form many hundreds or thousands of kilometers from the primary pollution source. Rural areas a great distance from major pollution sources can therefore experience high surface ozone levels, which in the Northern Hemisphere can often exceed 100 ppb (Ainsworth *et al.*, 2012; McGrath *et al.*, 2015). Ozone is one of the most powerful oxidants known and is phytotoxic. It enters the leaf via the stomata and, while too reactive to penetrate beyond the mesophyll cell walls, causes the production of a range of oxidizing radicals and a signal cascade (Overmyer *et al.*, 2000; Morgan *et al.*, 2003; Ainsworth *et al.*, 2012). While extreme concentrations of ozone will cause leaf necrosis, a more common effect is loss of photosynthetic capacity and accelerated leaf senescence (Morgan *et al.*, 2003). Intensive ozone monitoring in the USA coupled with annual county yield records has allowed statistical determination of yield impacts. Over the past 30 yr, ozone was found to have caused a loss of *c.* 10% of maize yield and 5% of soybean yield (McGrath *et al.*, 2015). Globally surface ozone is estimated to cost 79–121 million tons of lost production of primary foodstuffs (Avnery *et al.*, 2011). Although once considered a problem of the Northern Hemisphere temperate zone, industrialization and climate change are now causing high concentrations across much of the tropics. Assuming business-as-usual emissions rates, by mid-century ozone concentrations in sub-Saharan Africa will exceed those seen in North America (Chuwah *et al.*, 2015). Little is known about the impacts of ozone on cassava, but assuming similar levels of damage to temperate root crops a loss of 10% could be expected, possibly rising to 20% by mid-century (Rosenthal & Ort, 2012; Chuwah *et al.*, 2015). However, within temperate crops, considerable intra-specific genetic variability has been found in ozone tolerance (Biswas *et al.*, 2008; Shi *et al.*, 2009; Betzelberger *et al.*, 2010). Given the wide genetic diversity recently revealed within cassava and its wild relatives (Bredeson *et al.*, 2016), similar variation in ozone tolerance should be expected. Identifying this, though, would require the provision of controlled ozone fumigation facilities for breeders in regions relevant to cassava production; technologies for such facilities are feasible (Ainsworth *et al.*, 2008a,b).

Not surprisingly, photosynthesis and development are strongly influenced by soil nutrient availability. In the regions where cassava is currently grown globally, soils are often characterized by low concentrations of N, phosphorus (P) and potassium (K). Furthermore, in sub-Saharan Africa, fertilizer application is strongly limited by high cost, lack of access to fertilizers and slow dispersion of agronomic information on the benefits of fertilization (CIAT,

2011). Although cassava can perform better than most crops on poor soils, it is nevertheless responsive to N, P and K fertilization (Howeler, 2002). The tuberous root biomass is positively correlated with the nutritional status of the stem cuttings used to propagate the next season's crop (Molina & El-Sharkawy, 1995), showing that the nutrient status of the crop not only improves the yield of the current crop, but also affects the next.

Compared with unfertilized soils, the recommended application of fertilizers at 50 kg ha⁻¹ N, 44 kg ha⁻¹ P and 83 kg ha⁻¹ K typically leads to increased photosynthetic rates, growth, final total biomass and tuberous root yield (De Tafur *et al.*, 1997a; El-Sharkawy, 2006). Supra-optimal fertilization with N, however, increases shoot branching, leading to increased partitioning to leaves and stem, at the expense of the tuberous roots (Manrique, 1990; Howeler, 2002). Further, high N concentration also increases the concentration of cyanogenic glucosides in the root while decreasing starch (Obigesan & Fayemi, 1976; Howeler, 2002). The N use efficiency, but not yield, of cassava is often highest when plants are grown on soils with low N (Cruz *et al.*, 2003). Several of the approaches discussed in the previous sections on improving photosynthetic efficiency would also increase N use efficiency, thus increasing production without the need for more N fertilizer (Long *et al.*, 2015).

Cassava yields are very sensitive to P deficiency, especially as a consequence of the high demand for this nutrient for starch accumulation in tuberous roots. Low concentrations of P in the soil may limit cassava yields to a larger extent than K or N deficiencies (Pellet & El-Sharkawy, 1993). For maximum yield, cassava demands a *c.* 10 times higher P concentration than other crops such as maize, rice, common bean (*Phaseolus vulgaris*) and cowpea (*Vigna unguiculata*) (Howeler *et al.*, 1982a). Cassava crops possess a very coarse and poorly branched root system that is very inefficient in soil exploration (CIAT, 2011). However, several studies have shown strong mycorrhizal associations that appear to enhance P uptake from the soil, and greatly decrease the P fertilizer application required (Howeler *et al.*, 1982b). High mycorrhization may explain the poorly branched root system, if the plant has evolved a dependence on the fungus for resource acquisition. This is consistent with evidence that mycorrhizas are essential to achieving high cassava productivity (Howeler *et al.*, 1982b; CIAT, 2011). Although not yet explored in cassava, another strategy to overcome low available P in soils is to improve P use efficiency within the plant. This could be achieved, for example, by enhancing the remobilization of P from senescing tissues, or optimizing the amount of ribosomal RNA used in protein synthesis, which requires 40–60% of the organic pool of P in a plant (Veneklaas *et al.*, 2012).

Given the low fertility of much of the growing area in sub-Saharan Africa and the poor accessibility and high cost of N fertilizers, N fixation would be a very desirable trait in many situations. N fixation in nonleguminous crops has been a goal, which is yet to be achieved, for several decades. However, as plant genomes and partial genomes have been revealed, it has become apparent that much of the signaling pathway required for nodulation, including that required for mycorrhiza formation, is probably present in all flowering plants. Although best known in

leguminous plants (*Fabales*), N-fixing bacteria in nodules have also evolved in the *Rosales*, *Fagales* and *Cucurbitales*, which suggests that engineering this into other dicots may be less of a challenge than previously envisaged (Delaux *et al.*, 2015a; Mus *et al.*, 2016). Indeed, it appears that the ancestor of land plants was already adapted to this symbiosis, such that their descendants may be predisposed for symbiosis with N-fixing microbes (Delaux *et al.*, 2015b). The discovery of transcription factors that co-ordinate nodulation in legumes and the unravelling of other genetic elements underlying nodulation represent key discoveries in the path toward N fixation in other crops (Baudin *et al.*, 2015; Vernie *et al.*, 2015; Shtark *et al.*, 2016; Sinharoy *et al.*, 2016; Yan *et al.*, 2016). However, N fixation in plants is at a high energetic cost derived from respiration. So would it be worthwhile for cassava? A detailed analysis of all costs, including construction and maintenance of nodules as well as the metabolic cost of reduction of atmospheric N to ammonia, suggests that on average in legumes it costs 3–5 kg[C] kg [N]⁻¹ fixed (7–12 mol CO₂ mol N₂⁻¹) (Minchin & Witty, 2005). A cassava crop yielding 25 t ha⁻¹ may remove 57 kg [N] ha⁻¹ if leaves and stems are removed at the same time (Gutierrez *et al.*, 1988). On average across sub-Saharan Africa, crops may mine *c.* 20 kg [N] ha⁻¹ through mineralization in the absence of fertilization (Stoorvogel *et al.*, 1993; Karyotis *et al.*, 2005). This would only allow a yield of 8.8 t ha⁻¹ of tuberous roots. If the crop was N fixing then, assuming that carbon is 40% of the dry mass and the water content is *c.* 70%, an additional 20 t ha⁻¹ could be achieved despite the energetic cost of N fixation. The value of biological N fixation would be enhanced if improved efficiencies of light interception and conversion through crop photosynthesis were achieved by exploiting the opportunities outlined in this article.

VII. Conclusion

It is clear that improvement of cassava yield will be critical to meet the rising demand for primary foodstuffs, especially in sub-Saharan Africa. Although improved pest and disease tolerance would make large differences, as well as informed use of fertilizer, genetic yield potential sets the ceiling on what may be produced at a given location. The genetic yield potential of cassava could be increased by enhancing interception efficiency (ϵ_i) and conversion efficiency (ϵ_c), as both are shown here to be far from their theoretical limits for this crop. The opportunities to increase those efficiencies rely mainly on a modification of canopy structure and architecture, and genetic improvements to increase photosynthetic rates in concert with sink capacity. To be effective, genetic improvements should also enhance the performance of plants under environmental stresses such as drought and nutrient deficiency. If symbiotic N fixation could be introduced, then this would have great synergy with these yield potential enhancement opportunities. The opportunities covered in this review, the timescale on which they might be achieved and the gains they could represent are given in Table 4. These gains are not additive, but there are synergies. Making meaningful advances would be greatly aided by far more intensive studies of the environmental physiology of cassava; specifically, understanding the basis of its variation between

Table 4 The manipulations that could be undertaken to improve the yield potential of cassava, based upon this review and adapted from Long *et al.* (2015); the type of manipulation, and the model estimated improvement in efficiency of conversion of received light energy into crop biomass relative to today's cultivars

Manipulation	Type	Efficiency gain (%)	Timescale	Additional benefits
1 Improved speed of canopy closure (increased ϵ_i)	B	25 ¹	S-M	Synergistic with all changes
2 Optimized dynamic partitioning between leaves, stem and shoot	B	25 ¹	S-M	Synergistic with all changes
3 Transmit more light to lower canopy leaves	B, Syn	15–60 ^{2,3}	S	Synergistic with all changes. Improved WUE, NUE and albedo
4 More rapid relaxation of heat dissipation at PSII	Syn	30 ⁸	S	Synergistic with all changes; improved NUE
5 Convert C ₃ crops to C ₄	Syn	30 ^{3,5}	L	Improved WUE and NUE
6 Add cyanobacterial or microalgal CO ₂ /HCO ₃ pumps	Syn	5–10 ⁴	M	Improved WUE and NUE
7 Add cyanobacterial carboxysome system	CSyn	60 ⁴	L	Improved WUE and NUE
8 Add algal pyrenoid CO ₂ concentrating system	CSyn	60 ⁴	L	Improved WUE and NUE
9 Substitute forms of Rubisco better adapted to today's CO ₂	CSyn, B	15–30 ⁹	L	Improved WUE and NUE
10 Synthetic photorespiratory bypasses	Syn	15 ^{3,6}	L	Improved WUE and NUE
11 Optimize regeneration of RubP	Syn, B	60 ⁷	S	Synergistic with all; improved NUE
12 Transmit more light to lower canopy leaves	B, Syn	15–60 ^{2,3}	S	Synergistic with 1, and 3–9. Improved WUE and albedo. C ₄
13 Introduce N fixation	Syn	> 100 ¹	L	Synergistic with all of the above in low-N environments
14 Breed for ozone tolerance	B	10–20 ¹	S-M	Improved WUE

Source: ¹This review; ²Drewry *et al.* (2014); ³Long *et al.* (2006a,b); ⁴McGrath & Long (2014); ⁵von Caemmerer *et al.* (2012); ⁶Xin *et al.* (2015); ⁷Zhu *et al.* (2007); ⁸Zhu *et al.* (2004a); ⁹Zhu *et al.* (2004b). CSyn includes some synthetic addition of foreign genes to the chloroplast or plastid genome; Syn indicates synthetic addition to the nuclear genome; Sys indicates up- or down-regulation of existing genes, and B indicates that the improvement may be tractable by breeding given adequate molecular markers for the specific genes. The efficiency gains are from modeled estimates and are largely untested; these vary greatly depending on the assumptions and 5–11 are highly temperature dependent, with the greatest benefit in hot climates. Timescale is a speculated time to obtain material that could be used in a breeding program. S represents a 1–5-yr timescale, as this has already been demonstrated in model plants or actual crops to provide some clear improvement; M indicates a 5–10-yr timescale and L a 10–30-yr timescale. These may involve manipulations that require as yet unachieved goals, such as plastid transformation, or a full understanding of what makes an effective N-fixing nodule. It should be noted that with adequate resources there is no reason to believe that these goals cannot be achieved. All timescales are estimates that assume adequate financial investment to resource an intensive effort by relevant expert teams to achieve these goals. Additional benefits indicate synergies, that is, where $1 + 1 > 2$, and simultaneous improvements in either water use efficiency (WUE) or nitrogen use efficiency (NUE) per unit of biomass. Improved albedo implies a more reflective crop surface which would make the canopy cooler, an important adaptation to warming conditions. Manipulation 13 would give a large advantage on soils poor in nitrogen, but would have no benefit where plants have free access to sufficient inorganic nitrogen to support fullrealization of yield potential.

genotypes. This would allow the development of more mechanistic models of productivity, driven by the underlying processes. These in turn could then be used to run optimization routines to gain new insight into genetic traits for increased yield (Zhu *et al.*, 2016). Associating traits with genes can now potentially be greatly aided by the recent genome assembly for cassava and sequencing of a wide diversity of cultivars and wild relatives (Bredeson *et al.*, 2016).

Application of high-throughput phenotyping capabilities will be critical to making full use of the rapidly advancing genomic information for cassava (Lopez *et al.*, 2005; Prochnik *et al.*, 2012; Hu *et al.*, 2015, 2016; Wei *et al.*, 2016). Development or application of high-throughput phenotyping facilities such as those developed for the major grain crops will accelerate realization of the traits outlined in this review in cassava (Trachsel *et al.*, 2011; Winterhalter *et al.*, 2011; Okogbenin *et al.*, 2013; Yang *et al.*, 2013; Kipp *et al.*, 2014; Grosskinsky *et al.*, 2015; Haghhighattalab *et al.*, 2016). There has been much development of controlled-environment and more recently field robotic-assisted phenotyping platforms coupled with computer vision-assisted analysis tools for phenotyping (Kicherer *et al.*, 2015; Parent *et al.*, 2015). Combined use of spectral, thermal and digital sensors can now track plant growth, architecture, phenology, water relations, photosystem II efficiency and chlorophyll content (White *et al.*, 2012; Araus &

Cairns, 2014; Fahlgren *et al.*, 2015; Cabrera-Bosquet *et al.*, 2016) and efficiently assist the correlation of these traits with yield. This is supported by the availability of other noninvasive techniques such as ground-penetrating radar, electrical resistance tomography, and magnetic resonance imaging combined with the established mini-rhizotron technologies (Jeudy *et al.*, 2016). Tracking phenotyping through growth allows selection beyond final yield. This opens the opportunity to identify traits and associated genes that could be combined in breeding to build predicted ideotypes for different environments. For example, combining genes conferring rapid canopy development in early growth with adequate water with genes for drought tolerance in later development, to deal with seasonally dry environments. To date, these technologies have largely been applied to rice and developed-world crops, but they open the opportunity to greatly accelerate improvement of crops that have lacked the attention they deserve, such as cassava.

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Table S1 Inputs used to calculate partitioning efficiency (ϵ_p), photosynthetically active radiation (PAR) interception efficiency (ϵ_i) and PAR conversion efficiency (ϵ_c) in Table 2

Table S2 References of Table 3 values derived from physiology measurements in field trials of improved cultivars and landraces of cassava

Table S3 Cultivars and references used to produce Fig. 5

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