PHYSIOLOGICAL CAUSES OF YIELD VARIATION IN CASSAVA (*MANIHOT ESCULENTA* CRANTZ)

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Physiological causes of yield variation in cassava (*Manihot esculenta* Crantz)

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CONTENTS page

STELLINGEN

1. Als selectie parameters bij cassave verdienen de ESRP (de 'efficiency of storage root production') en de AISS ('apparent initial start of starch accumulation') de voorkeur boven de HI (harvest index).

   Dit proefschrift

2. Onderzoek naar kloonverschillen bij cassave voor wat betreft de fotosynthese snelheid van bladeren met het doel de resultaten te gebruiken in een kruisingsprogramma gericht op de verhoging van de opbrengst aan verdikte wortels is momenteel niet zinvol.

   Mahon, J.D., S.B. Lowe and L.A. Hunt (1977). Variation in the rate of photosynthetic CO_2 uptake in cassava cultivars and related species of *Manihot*. Photosynthetica 11 (2) 131 - 138.
   Palta, J.A. (1982). Gas exchange of four cassava cultivars in relation to light intensity. Expl. Agric. 18 : 373 - 382.

3. Meer nog dan nieuwe, verbeterde klonen kan op korte termijn toepassing van verbeterde teeltmethoden bijdragen aan de verhoging van de opbrengst aan verdikte wortels van cassave.

   De Vries, C.A., J.D. Ferwerda en M. Flach (1967). Choice of food crops in relation to actual and potential production in the tropics. Neth. J. of agric. Sc. 15 : 241 - 248.

4. Verhoging van de harvest index voor verdikte wortels leidt bij cassave tot een toename van de nutrienten efficiency.

   Veltkamp, H.J. Publication in preparation.

5. De waarheid van het gezegde 'Wie schrijft die blijft' dient men zich bij het landbouwkundig onderzoek en de landbouwvoorlichting in tropische landen veel meer aan te trekken.

6. Adviezen voor de teelt van cassave waarbij bemesting, in welke vorm dan ook, niet nodig wordt geacht dienen als onjuist ter zijde te worden gelegd.

   Toro, J.C. and C.B. Atlee (1980). Agronomic practices for cassava production: a literature review. In: Weber, E.J. et al. (eds.), Cassava cultural practices. Proceedings of a workshop, Salvador, Bahia, Brazil, 18-21 March 1980. International Research Development Center, Ottawa, IDRC - 151e, pp. 13 - 28.

7. Veel meer nog dan nieuwe onderzoeksresultaten dienen overzichten van resultaten van reeds verricht onderzoek in voor de tropen 'toegankelijke' tijdschriften te worden gepubliceerd. Zij zullen bijdragen tot een versnelling van het beschikbaar komen van voor de praktijk bruikbare resultaten.

8. Voor een goede overdracht van resultaten van landbouwkundig onderzoek naar de boeren via de Landbouwvoorlichtingsdienst is het gewenst dat ieder onderzoeksstation in de tropen ook een afdeling Kontakten-met-de-Landbouwvoorlichting kent die daar zorg voor kan dragen en tevens bij kan dragen aan de gewenste informatiestroom vanuit de praktijk naar de onderzoeksstations.

9. Landbouwbladen in de tropen dienen veel meer aan te sluiten bij de dagelijkse gang van zaken op de boerenbedrijven.

10. Het CIAT Cassave onderzoeksprogramma richt zich niet in de eerste plaats op het gebruik van de verdikte wortels van cassave in de voeding van de mens, ofschoon dat gezien het gebruik voor de hand zou liggen.

11. Onderzoek op het gebied van de onkruidkunde en de onkruidbestrijding in de tropen dient extra te worden gestimuleerd vanwege de grote arbeidsbehoefte voor de bestrijding van onkruid.

12. De introductie van de aardappel in Oost Nederland heeft plaatsgevonden vóór 1700. De verspreiding van de aardappelteelt over Nederland behoeft niet vanuit het zuiden te hebben plaatsgevonden.

    Roessingh, H.K. (1976). Het begin van de aardappelteelt en de aardappel consumptie in Gelderland. Gelders Oudheidkundig Contactbericht nr. 68: 1 - 9.
    Vooys, A.C. de (1954). De verspreiding van de aardappelteelt in ons land in de 18e eeuw. Geografisch tijdschrift 7: 1 - 5.

13. Voor het verrichten van een promotie-onderzoek op teeltkundig gebied verdient voor een uitvoering binnen de daarvoor door de Landbouwhogeschool geboden periode van 3 jaar bij de gewaskeuze tuinkers veruit de voorkeur boven cassave.

14. Toevoegen van niet plezierig geurende stoffen aan bestrijdingsmiddelen die worden gebruikt in de land- en tuinbouw zal leiden tot een voorzichtiger en zorgvuldiger omgaan met die middelen in de tropen.

15. Een peul van kouseband *(Vigna unguiculata* var. *sesquipedalis)* lijkt meer op een yardlong bean dan op een haricot kilomètre.

Proefschrift van H.J. Veltkamp
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Wageningen, 18 september 1985.

page

1 INTRODUCTION

Cassava, *Manihot esculenta* Crantz, a perennial shrub, is an important crop in many parts of the tropics. It is not known in a wild state (Purseglove, 1968) and it is almost exclusively cultivated for its storage roots, which consist mainly of starch. Furthermore, the leaves, which have a high protein content (Rogers and Milner, 1963), are consumed as a vegetable in some regions (Terra, 1964), but on the whole their use is of minor importance.

There are four distinctly identifiable markets for storage roots of cassava. Foremost among these is the demand for cassava as a staple food for human consumption. Other markets are the animal feed market, the industrial starch market and the power alcohol ('gasohol') market. Cock (1982) estimated that about 65% of the total cassava production was used for direct human consumption in the period 1975 to 1977.

Cassava is indigenous to America, together with all other species of the genus *Manihot*. Rogers and Appan (1973) defined 98 species. The exact area of origin of cassava as a crop plant is unknown, although several theories have been put forward. De Candolle (1886) suggested that cassava was first cultivated in north-eastern Brazil; he based this theory on the abundance of wild *Manihot* species in that region. This view was supported by Vavilov (1951), who pointed out that the longer a group has been established in an area the larger will be the number of species found. Rogers (1963) favoured Mexico and Central America as one of the centres of domestication. Northern South-America was suggested by Sauer (1952), largely on the basis of the presence of ceramic platters and stone chips presumably derived from grater boards, also associated with the processing of cassava storage roots. These ceramic platters and stone chips have been dated at around 1000 B.C. (Cruxent and Rouse, 1961; Reichel-Dolmatoff, 1965; Schwerin, 1970). Remains of cassava storage roots have been found in many sites on the coast of Peru; the radiocarbon date has been placed at approximately 750 B.C. (Towle, 1961).

These data certainly indicate that cassava was already being cultivated in many parts of America during the first millennium B.C. The time of initial cultivation is assumed to be considerably more ancient (De Boer, 1975). By the time of Columbus's discovery of America cassava had reached its present limit of cultivation in America (Purseglove, 1968).

The cassava plant spread from the American continent in post-Columbian times. At different times it was carried by the Portuguese from the east coast of Brazil to their stations on the entire west coast of Africa from Senegal to Angola (Ross, 1975). The earliest successful introductions were probably made on the islands São Tomé, Príncipe and Fernando Poo in the Bight of Benin, and in the area around the mouth of the Congo river during the latter half of the sixteenth century (Jones, 1959). It is only since the beginning of the twentieth century that the cultivation of cassava has spread rapidly into the interior of West Africa. In East Africa cassava was absent or unimportant in most of the region in 1850, except right along the coast (Ross, 1975). The main expansion has taken place since 1920. Cassava was encouraged, as in West Africa, as a famine reserve. The most likely period of introduction of cassava into Java is around 1810 (Koch, 1934). The introduction of cassava into India has been set at 1794 (François, 1938; Kiok, 1934). As at most African locations, in India and Java the adoption of cassava was also slow at first.

The present-day distribution of cassava is worldwide in regions between latitudes 30° north and south. According to FAO (1982) cassava is now cultivated in more than 80 countries in Africa, Latin America, the Far East and Oceania.

In 1981 the total area cultivated with cassava was approximately 14.1×10^6 ha, an increase of 3.3×10^6 ha since the period 1969-1971. World production of storage roots increased from 97 to 127 million tons in the same period (FAO, 1982). In 1981 nearly 70% of the world production came from only six countries (Brazil, Thailand, Indonesia, Zaire, Nigeria and India), while 90% of the total production came from 17 countries (FAO, 1982). In 1981 Africa was still the continent producing most cassava: 38% of the total production, against 37% in the Far East and 24% in South America (Table 1).

Table 1 Area and production of cassava in 1981 in the most important cassava-producing countries, in some continents and in the world

	area ($\times 10^3$ ha)	production	
		$\times 10^6$ tons	as % of world production
world	14054	127.3	100
Africa	7433	47.8	37.5
South America	2577	30.7	24.1
Asia	3866	47.6	37.4
Brazil	2093	25.1	19.7
Thailand	1050	17.9	14.1
Zaire	1853	13.0	10.2
Indonesia	1412	13.7	10.8
Nigeria	1200	11.0	8.6
India	346	5.8	4.6

Source: FAO production yearbook 1981 (FAO, 1982)

The average storage root yield of cassava has not changed much during the last 20 years. In 1981 the global average was 9.1 tons per ha (FAO, 1982). It has been estimated that less than 10% of the production increase in the last decade can be accounted for by higher yields per unit area. The production increase is therefore mainly a result of the use of new areas (Hahn et al., 1979).

There are great differences in yield between individual countries (FAO, 1982), but for all countries the average yield level is far below the potential one, which has been estimated at 30-32 tons dry storage roots per ha per year (equivalent to 80-90 t ha^{-1} $year^{-1}$ on fresh weight basis) (Cock et al., 1979; Boerboom, 1978b; Cock, 1974). Very high yields (all on fresh weight basis) have been obtained in some experimental plots. On Java (Indonesia) 53.3 tons were obtained in 270 days (APL, 1937). At CIAT (Colombia) the highest yield in 1977 was 79.2 t ha^{-1} $year^{-1}$ and in 1978 82.2 t ha^{-1} $year^{-1}$ (CIAT, 1979, 1980). Enyi (1973) obtained a yield of 84.6 tons in 16.5 months, whereas De Bruijn and Dharmaputra (1974), referring to Indonesian literature data on yield of Mukibat cassava (*Manihot glaziovii* grafted onto cassava), reported a yield of about 96 t ha^{-1} $year^{-1}$.

Several constraints to higher yields have been reported: lack of adequate clones, poor weed control, poor disease and pest management, lack of fertilizers and generally poor agronomic practices (Cock, 1979; Hahn et al., 1979).

Until recently, cassava was neglected in agricultural research. In their study of the choice of food crops in relation to actual and potential production in the tropics, De Vries et al. (1967) concluded that root and tuber crops, including cassava, should play an important role in the search for increasing food production.

In the early 1970s, two international research centres, the International Institute of Tropical Agriculture (IITA) at Ibadan (Nigeria) and the Centro Internacional de Agricultura Tropical (CIAT) near Cali (Colombia), started extensive research programmes on cassava. One of the objectives of the CIAT Cassava programme was formulated as: 'To study the problems associated with the production of energy in the form of roots and hence to develop varieties and cultural practices that will give high levels of productivity' (CIAT, 1972).

Breeding for the improvement of cassava has received very little attention in the past compared with many other crops (Hahn et al., 1979; Kawano, 1978). Serious breeding of cassava was probably started in Indonesia by Van der Stok (1910) in approximately 1908.

The aim of CIAT's cassava breeding programme is to obtain new genotypes that give maximum caloric yield per unit area per unit time over a wide range of climatic conditions and with limited use of chemical inputs, by genetic modification of the plant structure, including protection against pests and diseases. In recent years, achieving the highest potential yield has been the primary interest (Kawano, 1978).

In order to modify the plant structure of cassava in such a way that new promising genotypes can be obtained by breeding, the construction of a model plant or ideotype of cassava was initiated by the cassava physiology programme of CIAT (CIAT, 1974; Cock et al., 1979).

The approach of constructing model plants or ideotypes was originally proposed by Donald (1968). An ideotype was defined as 'a biological model which is expected to perform or behave in a predictable manner within a defined environment'. The following steps for the construction of an ideotype can be distinguished (e.g. Adams (1973)):

- identifying those morphological and physiological components related to yield, for which genetic variation exists
- formulating one or more plausible plant-type models
- constructing plausible ideotypes by suitable breeding processes
- testing the constructed cultivars against standard cultivars
- after testing, reassessing of the models to determine whether adjustments in particular components would lead to better performance. If so, a reformulation followed by new constructions will proceed.

Under optimal growing conditions the growth of a root crop such as cassava is mainly determined by:

- rate of photosynthesis per unit leaf area
- magnitude of the leaf surface available for photosynthesis ('source')
- capacity of the plant to translocate assimilates from the leaves to the storage roots
- capacity of the storage roots to accept assimilates ('sink')
- respiratory activity.

In cassava the storage roots are the predominant sink during the root-filling period and the photosynthetically active parts of the plants act as the 'source'. Early in the growth period the shoots form an important sink (Mason, 1972; CIAT, 1978; Tan and Cock, 1979a).

The aim of this study was to obtain more information on physiological determinants of storage root and total dry matter production of cassava in order to get a better insight into how storage root yield can be increased. Furthermore, the variation in morphological characteristics in a selected number of clones was investigated. The research, the results of which are reported in the following chapters, was done from August 1978 to July 1981. In the next chapter the literature on physiological determinants of cassava storage root yield is reviewed. In Chapter 3 the ecological conditions under which the field experiments were conducted are described and questions related to the general methods followed and materials used are discussed. The results of a study on photosynthesis and transpiration of attached leaves of four cassava clones are reported in Chapter 4. Interrelationships between LAI, light interception and total dry matter yield are discussed in Chapter 5. Canopy characteristics of different cultivars are described in Chapter 6. Chapter 7 comprises a study of the partitioning of produced dry matter in cassava. In Chapter 8 the effects of daylength on growth, total dry matter production and its partitioning are described. A general discussion of the results follows in Chapter 9, especially with respect to their implications for improving cassava production.

2 REVIEW OF LITERATURE ON PHYSIOLOGICAL DETERMINANTS OF CASSAVA STORAGE ROOT YIELD

Hunt et al. (1977) have reviewed the information on the growth physiology of cassava contained in research published up to circa 1974. Since 1974 considerable physiological data on cassava growth have been collected. All data available until 1983 have been reviewed in this chapter.

2.1 PLANTING AND RATE OF SPROUTING

In commercial production, cassava is propagated exclusively by stem cuttings of varying length (generally 15 to 35 cm), which are planted horizontally, vertically, or at slant. The basal part of cuttings planted vertically or at a slant is inserted 5 to 10 cm deep in the soil (Purseglove, 1968). Toro and Atlee (1980) have reviewed the literature on the effect on the storage root yield of the size of the cuttings, the planting position and the planting depth.

Cours (1951) reported that under the climatic conditions of the Malagasy Republic the first leaves appeared 10 days after planting. Keating and Evenson (1979) found that the minimum temperature for sprouting ranged from 12°C to 17°C, with the optimum temperature being from 28.5°C to 30°C. Time to 50% sprouting was 150-210 degree-days above a base of 13°C. Cock and Rosas (1975) observed large clonal differences in rate of sprouting at a site 2300 m above sea level, near the equator (mean temperature circa 17°C).

2.2 DEVELOPMENT OF THE LEAF AREA

The development of the leaf area per unit ground area depends on number of plants per unit area, number of active apices (branches), number of leaves formed per apex, leaf size, and leaf life.

2.2.1 Leaf formation rate per apex

Cassava plants produce new leaves continuously. The pattern of leaf formation rate per apex has been detailed in several publications (CIAT, 1976; CIAT, 1977; Irikura et al., 1979; Cock et al., 1979). With one exception (MCol 72), little variation was found between the clones studied (CIAT, 1977; Tan and Cock, 1979b). The leaf formation rate per apex decreased with plant age. Leaf formation rate was lower at 20°C than at 24°C and 28°C (Irikura et al., 1979).

2.2.2 Number of apices and branching patterns

After a certain number of nodes (leaves) have been formed (the number depends on the clone, the climate and the soil (CIAT, 1979; Irikura et al., 1979; De Bruijn, 1977; Van der Stok, 1910;), the growing point becomes reproductive. At the same time a number of axillary buds sprout and develop into similarly sized branches (generally two to four, sometimes up to six (Van der Stok, 1910)) (see also Fig. 3). Later on in the growth period this process can be repeated, thus giving the second branch level. In all, up to six branch levels have been observed for plants younger than one year (Van der Stok, 1910). On the other hand, a clone that did not branch at all in a growth period of one year has been observed (CIAT, 1979). Miège (1957) showed that the length of the planted cuttings (which ranged from 16 to 60 cm in his study) did not influence the length of the period from planting until the first or second branch level was reached. Neither did the planting method have any significant effect on the length of the period to the first branching. Cuttings taken from the main stem branched later than cuttings obtained from the first to the third branch levels. Unfortunately, in his study Miège gave no information on the rate of leaf formation, so it is not clear whether the observed differences in time to branching were caused by differences in that rate.

2.2.3 Leaf size

Leaf size has been found to increase to a maximum and then to decline in all clones studied and under different ecological conditions. The maximum average size of a mature leaf was generally observed at 3 to 4 months after planting. Large clonal differences were observed in maximum leaf size (CIAT, 1976). At higher temperatures (means of 24°C and 28°C) leaves were larger than at 20°C

(Irikura et al., 1979). Moreover, soil fertility influenced the average leaf size, the leaves being smaller in less fertile soil (CIAT, 1979). It has been found that changing the branching pattern by clipping apices results in bigger leaves when only one apex is retained (Tan and Cock, 1979a).

2.2.4 Leaf life

Mutual shading of leaves greatly limits leaf life. Rosas et al. (1976) reported that when light absorption by a leaf lamina was prevented, a quick abscission of that leaf resulted (in about 10 days). Leaf life also varies with clone and environmental conditions (Irikura et al., 1979). It has been found that leaf life is not negatively influenced by rapid storage root growth (Rosas et al., 1976) and that leaf life is longer when the number of active apices is reduced (Tan and Cock, 1979a); the latter is presumably a result of reduced shading. The maximum leaf life is 210 days (Irikura et al., 1979); the minimum leaf life approximately 40 days (CIAT, 1978).

2.2.5 Leaf area index (LAI) and leaf area duration

Generally, the leaf area index (leaf area per unit ground area) increases slowly during the first 1 to 2 months of the growth period. Then follows a rapid increase and a decline thereafter (Cours, 1951; Enyi, 1972c; Cock, 1976). Until recently, the maximum reported leaf area indices were about 7 to 8 (Enyi, 1973; Cock, 1976; CIAT, 1979), but these values were maintained during relatively short periods only. Keating (1982) reported leaf area indices up to and exceeding 10.0 in periods with long days in Queensland, Australia, although maximum leaf area indices of 3 to 4 were more normal, although only during short periods.

Doku (1965) reported that clones that gave high yields had the ability to retain a large number of leaves and had a large leaf area and a large area of green stem. Sinha and Nair (1971) concluded that the leaf area duration is an important factor contributing to the storage root yield of cassava. They found that the clones that had a large leaf area duration and relatively high leaf area indices (in their study the leaf area indices of the clones varied from 0.7 to 2.7) were high yielders. Enyi (1972b,c) reported a positive relationship between leaf area duration and storage root yield in one study, but not in another (Enyi, 1973). An optimal leaf area index for storage root growth of 3.0 - 3.5 has been suggested (CIAT, 1976; Cock et al., 1979).

Williams and Ghazali (1969) suggested that storage root yield is associated with the leaf angle, so clones with vertically orientated leaves should have a higher yielding ability than those that possess horizontally disposed leaves. Cock (1976), however, found that there was little, if any advantage of a more vertical leaf orientation over a horizontal leaf orientation for clones that had leaf area indices up to about 4.

2.3 PHOTOSYNTHESIS IN ATTACHED LEAVES

Several studies have been done on photosynthetic CO_2 uptake of attached leaf parts of cassava clones and wild *Manihot* species (Mahon et al., 1976; Mahon et al., 1977a,b; Aslam et al., 1977; CIAT, 1978). Large variations in net photosynthetic rate were observed, ranging from 15 to 29 mg CO_2 $dm^{-2}h^{-1}$ at a photon flux density of 165 nEinstein $cm^{-2}s^{-1}$ (400-700 nm) (Mahon et al., 1977b) and from 27 to 33 mg CO_2 $dm^{-2}h^{-1}$ at 100 nEinstein $cm^{-2}s^{-1}$ (400-700 nm) for plants grown outdoors (CIAT, 1978). Photosynthesis was already light-saturated at a photon flux density of 110 nEinstein $cm^{-2}s^{-1}$ (Mahon et al., 1977a). A high CO_2 compensation point (68 vppm at 25°C) was found, and also a high ratio of H_2O efflux/CO_2 uptake (109 to 138), suggesting a C_3 photosynthetic pathway in cassava (Mahon et al., 1977a). The temperature optimum for CO_2 assimilation was 25°C (Mahon et al., 1977a). Data from CIAT suggest a very broad optimal range of temperature (nearly 20-40°C) (Cock, personal communication 1982). The net photosynthetic rate decreased with leaf age, especially at saturating light intensities. Significant clonal differences were observed in the pattern of decline (Aslam et al., 1977). At CIAT (1979, 1980), however, for one clone no decrease in photosynthetic rate was observed with leaf ages up to 100 days.

2.4 INITIATION AND GROWTH OF STORAGE ROOTS

Planted cuttings start to root some 5 days after planting (Cours, 1951). In cassava the development of storage roots starts with the initiation of secondary growth of the roots. This process has been observed in plants only three weeks old. The deposition of starch grains starts some days later and takes place mostly in the secondary xylem parenchyma cells in the central part of the roots (Indira and Sinha, 1970; Indira and Kurian, 1977). The starch grains formed first have a diameter of only 2-6 µm, but they grow relatively rapidly during the first two months of the growth period, although less rapidly thereafter (Cours, 1951). New starch grains are formed continuously. Cours (1951) found that the mean diameter of starch grains in storage roots of 7- to 27-month old plants of 19 clones varied from 12.9 to 14.6 µm.

Under field conditions it is difficult to define the moment at which storage root growth starts. Sometimes storage roots are arbitrarily distinguished from others by their thickness, i.e. those thicker than 0.5 cm (Boerboom, 1978a). A thickness of 0.5 cm is generally reached 2-4 months after planting.

Boerboom (1978a) assumed that during the root filling phase the partitioning of dry matter in cassava over different plant parts (storage roots, stems) is constant. To describe this phenomenon he introduced two terms: the 'efficiency of storage root production (ESRP)', being the regression coefficient of the linear equation between the storage root weight and the total dry weight; and the 'initial start starch accumulation (ISS)', being the plant weight at which storage root production starts. For the latter parameter Flach (1982) proposed the more exact term 'apparent initial start of starch accumulation (AISS)', as it is a calculated point. Boerboom's ESRP, however, does not represent the true efficiency of storage root production because the weight of the fallen leaves is not included in the total weight.

The relation between ESRP and harvest index (proportion of root weight of the total plant weight and a much used selection criterion (Kawano et al., 1978)), can be described with the help of an asymptotic function (Boerboom, 1978a). For cassava, a large variation in harvest indices has been observed. Kawano et al. (1978) reported a range of 0 to 0.75 in an evaluation study of CIAT's germ plasm accessions. In Indonesia, Van der Stok (1910) found a range of 0.23 to 0.61 for 52 clones.

2.5 SINK-SOURCE RELATIONSHIPS

In cassava, sink-source relationships have been studied by changing the sizes of source and sink, varying the branching pattern, removing apices, removing laminae, girdling plants, removing different numbers of storage roots at the beginning of the root filling period and by experimenting with grafts (Cours, 1951; Mason, 1972; De Bruijn and Dharmaputra, 1974; Dharmaputra and De Bruijn, 1977; Cock et al., 1979; Tan and Cock, 1979a; IITA, 1980).

Changing the branching pattern by clipping young apices led to significantly higher dry root yield (Cock et al., 1979; Tan and Cock, 1979a). But, because both late branching clones (first branching at six months after planting, with three branches at each branch level) and early branching clones (with two branches at each branch level) were found to give high storage root yields (Tan and Cock, 1979a), it is questionable whether the branching pattern per se caused the dry root yield increase. At IITA (1980) the highest root yield was obtained in a plant type that branched at one metre.

In a tracer experiment with $^{14}CO_2$ Hume (1975) found that in a period of rapid growth of storage roots 60% of the labelled assimilates had been translocated to the storage roots in the seven days after labelling, whereas after labelling in a dry period with a low bulking rate the assimilates were mainly recovered in above-ground parts. An active root sink apparently leads to a stimulation of the translocation of assimilates to it. An increase in net assimilation rate has been linked with an increased root growth rate (Enyi, 1972b,c). Williams (1972) suggested that in cassava the activity of the root sink affects the photosynthesis. However, Cock et al. (1979) reported that small reductions of the number of storage roots did not result in lower yields of storage roots or of total dry matter, as long as at least 9 storage roots per m^2 were present. A further reduction of the storage root number resulted in lower dry root yields (Cock et al., 1979), so it seems unlikely that storage roots have a large excess storage capacity and can accept more assimilates if available (Tan and Cock, 1979a). De Bruijn (1971) found a correlation coefficient of 0.69 between the number of storage roots and the storage root yield.

The effect on total dry weight and root dry weight of stem girdling to prevent the translocation of assimilates from the aboveground parts to the roots was studied by Mason (1972), CIAT (1974) and Cock et al. (1979). Mason (1972) reported a lower total dry weight for the girdled plants. The root weight was 25% of that of the ungirdled plants, whereas the stem weight of girdled plants was more than 12 times higher. The same tendency was reported by CIAT (1974). In another experiment Cock et al. (1979) found that the total dry weight of the plants was not affected by girdling; the distribution pattern, however, changed in the same way as reported by Mason (1972) and CIAT (1974). Girdling stems had no effect on total leaf area per plant, on leaf area per leaf (Cock et al., 1979), nor on rate of leaf formation per apex (CIAT, 1974). This suggests that a strong limitation of the root sink, induced by girdling, does not affect the source size. When as induced by girdling, the roots are unable to accept assimilates from the source, these assimilates are accepted by the stem. Data from Cock et al. (1979) suggest that the stem is as effective at accepting assimilates as the root sink. In contrast, in the experiments by Mason (1972) and CIAT (1974), total dry weight increase was less in girdled plants than in ungirdled ones.

Hahn (1977) stated that the treatments as mentioned above, to change sink and source size have the disadvantage that they may have adverse effects on internal physiological processes. By using grafting or budding techniques, interference with these processes can be minimized.

Cours (1951) grafted *Manihot glaziovii* onto cassava and observed that the stock functioned as if the whole plant were cassava. The reciprocal graft with *Manihot glaziovii* as stock formed fibrous roots only, as happens with a complete *M. glaziovii* plant. Mogilner et al. (1967), who made grafts between cassava and *Manihot flabellifolia*, also concluded that the scion does not have any effect on the formation of storage roots. So the capacity of a grafted plant to form storage roots is inherent to the stock.

Grafting a scion of a clone with a low root fraction (0.38) onto a stock of a clone with a relatively high root fraction (0.54) resulted in plants with a root fraction similar to that of the stock (Cours, 1951). This suggests that the distribution of assimilates is controlled by the stock.

De Bruijn and Dharmaputra (1974) and Dharmaputra and De Bruijn (1977) reported very high storage root yields with grafted planting material using *Manihot glaziovii* as scion and cassava as stock. This system (the Mukibat system, named after its inventor) is practised in East Java (Indonesia), where an increasing number of cassava growers have adopted it since 1952 (De Bruijn and Dharmaputra, 1974). The majority of them came to use this system because they felt it increased yield (Nugroho, 1976). It is most improbable that these high yields were caused by a high photosynthetic rate of the individual leaves, because the CO_2 uptake rate of *Manihot glaziovii* leaves has been found to be lower than the mean photosynthetic rate of leaves of ten cassava clones (Mahon et al., 1977b).

2.6 GROWTH PERIOD

The growth period of cassava varies in practice from about six months to two years (Purseglove, 1968; Jones, 1959; Ezeilo et al., 1975). Ezeilo et al. (1975) reported that in a survey of 190 cassava-cultivating farmers in Nigeria it was found that on 47% of the harvested fields the cassava was less than one year old, on 19% it was between 1 and 1.5 years old and on 33% it was between 1.5 and 2 years old. In Colombia the average growth period was found to be 11 months, or longer at altitudes above 1000 m (Diaz and Pinstrup-Andersen, 1977). Van der Stok (1910) stated that plants nearly three year olds were still in good condition, although storage roots were partly woody and were therefore unsuitable for human consumption.

3 MATERIALS AND GENERAL METHODS

This chapter provides the background for the more detailled description of the individual experiments that are described in Chapters 4-8 inclusive.

3.1 LOCATION

All the field experiments described in this thesis were conducted at the experimental farm of the Centro Internacional de Agricultura Tropical (CIAT) in Palmira, near Cali (Colombia) (Fig. 1), situated 1000 m above sea level at 3°31'N and 76°21'W. One pot experiment was conducted to measure photosynthesis and transpiration. (see Chapter 4). These experiments were carried out from December 1978 to March 1981.

Two additional experiments were carried out in a greenhouse at the Department of Tropical Crops, Agricultural University in Wageningen, The Netherlands. These experiments were conducted in the period October 1980 to July 1981. They are described in Chapter 8.

Meteorological data at Palmira for the period December 1978 to March 1981 are presented in Table 2.

The soil, a fertile clay loam, has been classified as a Mollisol (Howeler et al., 1978). Some chemical properties and data on the particle size distribution of the topsoil (0-20 cm) of the experimental fields are given in Table 3.

3.2 CLONES

All the clones used in these experiments were taken from CIAT's germ plasm bank. In this germ plasm bank (which contains approximately 2400 accessions (Kawano, 1978)) the clones have been catalogued as follows: first an M, which refers to *Manihot esculenta*, followed by a code of three letters indicating the country where the clone was collected and finally a number representing the CIAT accession number for that country.

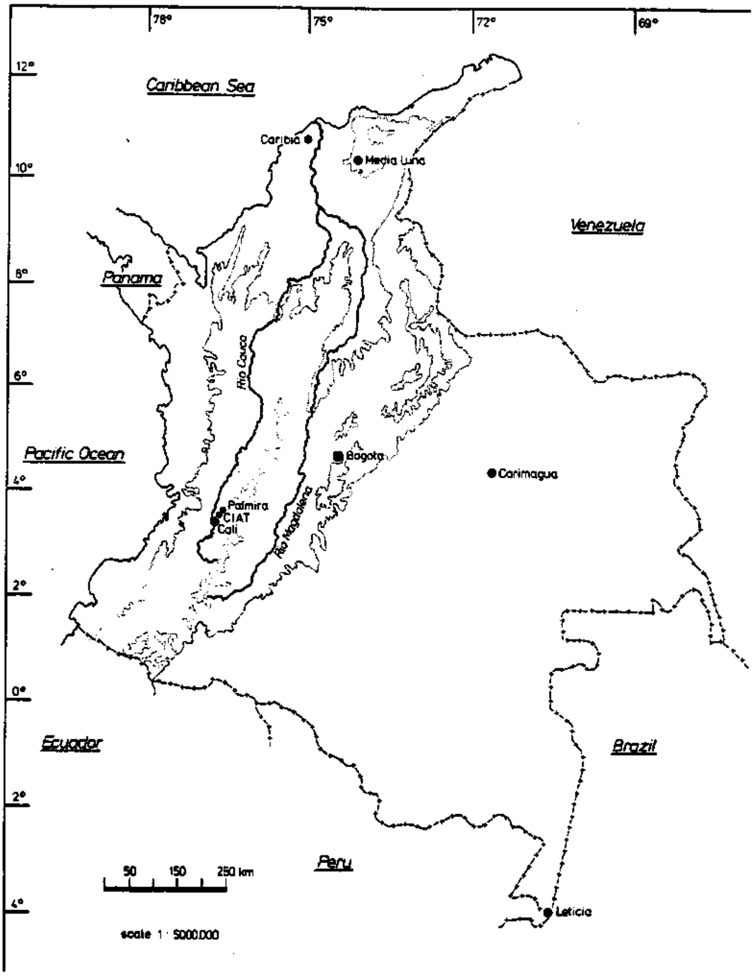

Fig. 1 Sketch map of Colombia.

Table 2 Meteorological data at CIAT experimental farm in Palmira (Colombia) for the period December 1978 - March 1981

	temperature (°C)			precipitation (mm)	class A pan evaporation (mm)	relative humidity (%)	global radiation ($Jcm^{-2}day^{-1}$)
	mean	maximum	minimum				
1978							
December	23.4	28.4	19.5	133	154	76	2012
1979							
January	23.9	29.5	19.0	23	168	71	2201
February	24.3	30.4	18.8	4	173	68	2092
March	24.2	29.4	19.6	70	169	74	1995
April	24.1	29.1	19.6	123	153	75	1894
May	23.8	28.8	19.3	117	141	76	2037
June	23.7	28.9	19.2	43	135	76	1705
July	24.3	30.3	18.7	46	181	71	2003
August	23.9	29.4	18.6	112	165	71	1823
September	23.6	28.8	18.6	79	155	74	2218
October	23.8	29.0	19.2	62	145	74	1701
November	23.3	28.4	19.1	122	151	76	1810
December	23.6	29.0	18.9	37	145	75	1945
1980							
January	24.1	30.0	19.2	40	173	74	1924
February	24.1	29.7	19.7	42	163	74	2192
March	24.8	30.7	19.8	94	173	71	2617
April	24.2	29.6	19.6	62	157	74	2848
May	23.9	29.3	19.7	72	146	76	1882
June	23.9	29.0	19.4	79	130	75	1882
July	24.1	30.4	19.2	8	173	71	2108
August	24.5	30.8	18.7	20	185	68	2276
September	24.5	30.5	19.5	37	185	70	2113
October	23.3	28.7	19.2	129	152	75	2142
November	23.2	28.6	19.0	43	147	76	2302
December	23.1	28.9	18.8	71	148	75	1739
1981							
January	23.8	30.4	19.0	13	194	71	1823
February	23.9	29.6	19.6	107	151	76	1823
March	24.3	29.7	19.4	98	188	75	1940

Table 3 Chemical characteristics and particle size distribution of the soil in the experimental fields, sampled in the 0-20 cm layer

Characteristic	Range	Average
particle size distribution		
% clay	36 - 57	44
% silt	34 - 42	40
% sand	1 - 26	16
% O.M. (Walkley-Black)	3.2 - 4.2	3.7
P-Bray II (ppm)	34 - 67	53
Ca*	10.1 - 15.0	12.5
Mg*	6.9 - 13.8	9.2
K*	0.40 - 0.64	0.49
Na*	0.14 - 0.28	0.21
CEC*	20.2 - 29.3	23.8
pH (H_2O)**	5.9 - 7.3	6.6
pH (KCl)***	5.0 - 6.6	5.9

* me/100 g; extracted with 1 N NH_4-acetate at pH 7
** 1:1 soil-water
*** 1:1 soil-KCl solution (1 N).

In all field experiments the clones MCol 1684 and MPtr 26 were used. MCol 1684 (Fig. 2a) was selected for its reported excellent yielding ability at different locations and its high harvest index. It is regarded as the best among all germ plasm accessions in terms of yield and wide adaptability (Kawano et al., 1978; CIAT, 1980). MCol 1684 was originally collected by the ICA (Instituto Colombiano Agropecuario) from the Leticia area, the southernmost area of Colombia (see Fig. 1), a tropical lowland region, with a mean temperature above 25°C, a high annual rainfall (above 2000 mm) without a pronounced dry season, and a constant high relative humidity (CIAT, 1980).

In order to obtain a sufficient diversity of plant types the following clones were also selected:

MPtr 26 (Fig. 2b): A late branching clone which was originally collected in Puerto Rico, but which is very similar to clones such as MVen 218 from Venezuela and MMex 11 from Mexico. MCol 22 was used in three experiments (experiment 1, 2 and 4). MVen 77 was used in experiments 1 and 2. MMex 59 and MCol 638, both used in experiment 3, complete the list of clones used in the field experiments. MCol 22 was collected in the north coast area of Colombia, a region with a

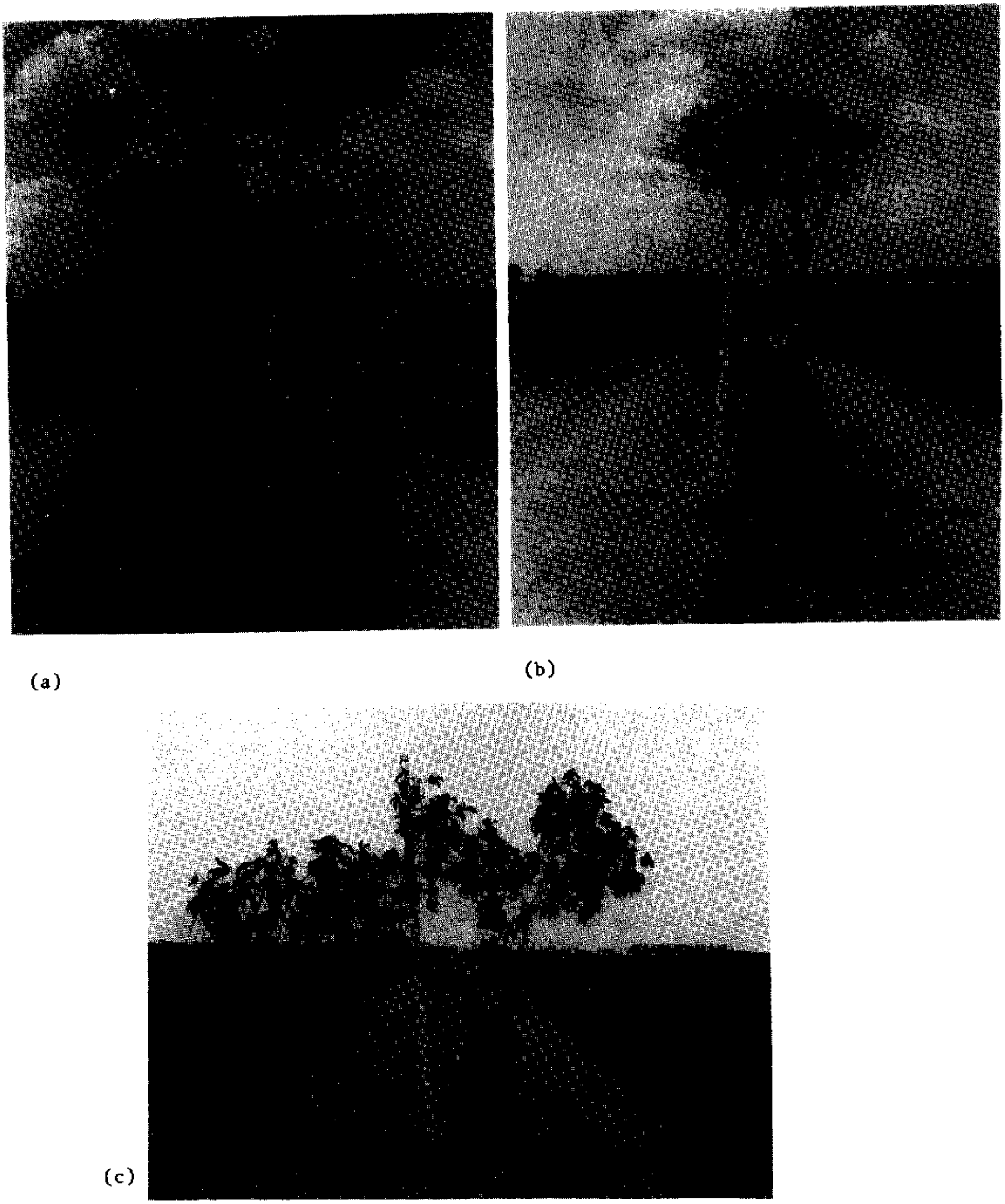

Fig. 2 Plants of clones MCol 1684 (a), MPtr 26 (b) and MMex 59 (c).

high average temperature (approx. 28°C), moderate rainfall (700-1000 mm per year) and a long (3-4 months) dry season. CIAT is doing research on cassava in this region, at Caribia and Media Luna (for location see Fig. 1) (Kawano et al., 1978; Toro, 1979). MMex 59 (Fig. 2c) originates from Chiapas, Mexico (average temperature approximately 25°C) (Irikura et al., 1979). Finally, both MVen 77, a very tall clone, and MCol 638 are well adapted to the high stress conditions prevailing in the Carimagua experimental station in the Llanos Orientales of Colombia (see Fig. 1) (Toro, 1979).

3.3 CULTURAL PRACTICES

In each experiment, cuttings approximately 20 cm long (diameter circa 2 cm), were used.

The selected cuttings were treated by immersing them for 10 minutes in a mixture of Dithane M-45 (222 g) and Manzate 80 (125 g) per 100 l water (according to Lozano et al., 1977) plus zinc sulphate, 2 kg/100 l water (as recommended by Howeler, 1978).

The cuttings were planted at a slant (45°), about 15-18 cm deep and spaced 1 m × 1 m on ridges. Just after planting 100 $kg.ha^{-1}$ of N, P_2O_5 and K_2O in the form of NPK 15-15-15 composite fertilizer was applied in bands. Weeds were controlled chemically 2-4 days after planting by spraying with a mixture of Karmex (diuron 80% a.i.) and Lasso (alachlor 43% a.i.) in water, at a rate of 1.0 kg and 2.5 l commercial product, respectively, per hectare, as recommended by Doll and Piedrahita (1976). During most experiments two or three complementary hand weedings were usually performed for good weed control. Irrigation by gravity was applied if necessary during dry periods.

After sprouting only one shoot was allowed to develop from each planted cutting, to standardize the basic plant form. Extra shoots were removed as they appeared. Failed cuttings were replaced 3-4 weeks after planting with plants of the same age that had been planted in polyethylene bags. It has been shown that this replacement technique does not affect the storage root yield (CIAT, 1980).

The total growth period of cassava in these experiments varied from 6 to 12 months, depending on the purpose of the specific experiment.

3.4 EXPERIMENTAL DESIGN, NUMBER OF BORDER ROWS AND SAMPLE PLANTS

All field experiments were laid out as a randomized complete block design, replicated four times. In all cases sample plants were surrounded on all sides by two border rows of plants of the same clone. A design with two border rows was chosen, because it had been shown (CIAT, 1974), (though for only one clone) that storage root yield of sample plants surrounded by two border rows did not differ from the yield of sample plants surrounded by three border rows and that, in contrast the yield of sample plants from plots with only one border row differed markedly from the yield of those with two border rows (CIAT, 1974). From a study with different clones with different plant types and planted at different sites (CIAT, 1980) it was concluded that for ascertaining yield, it is sufficient to have only one border row. Thus in the present study is wat decided that two border rows would be sufficient to give a realistic estimate of the storage root yield.

The sample size was six plants per plot in the plots harvested early in the growth period, but was otherwise 9 or 12 plants per plot.

3.5 MEASUREMENTS OF THE GROWTH PROCESS

A number of measurements were carried out on the plants in the plots that had been earmarked (by being roped off) for the last harvest.

3.5.1 Plant height, leaf formation rate, branching pattern

Plant height, number of new-formed leaves on one apex, number of nodes and time taken to produce branching points (Fig. 3), number of active apices and number of fallen leaves on one apex were measured and/or calculated at regular intervals, depending on the particular experiment. The number of fallen leaves was obtained by counting the number of bare nodes on one apex. Plant height was measured from soil surface to the general height of the canopy. All these measurements were carried out on all sample plants.

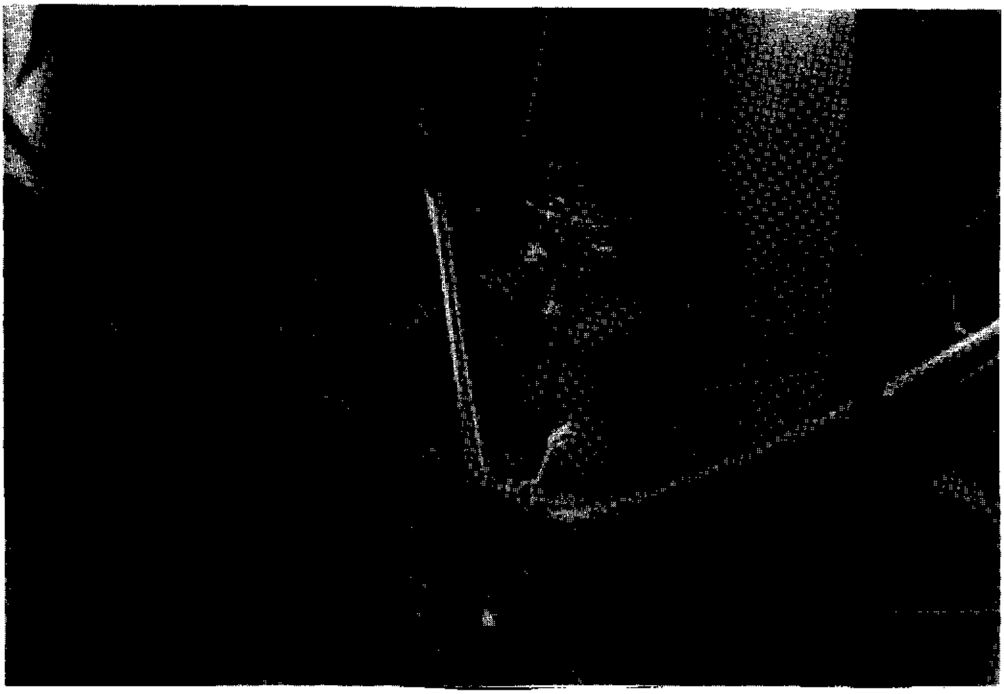

Fig. 3 Inflorescence of cassava with three branches at the branch level.

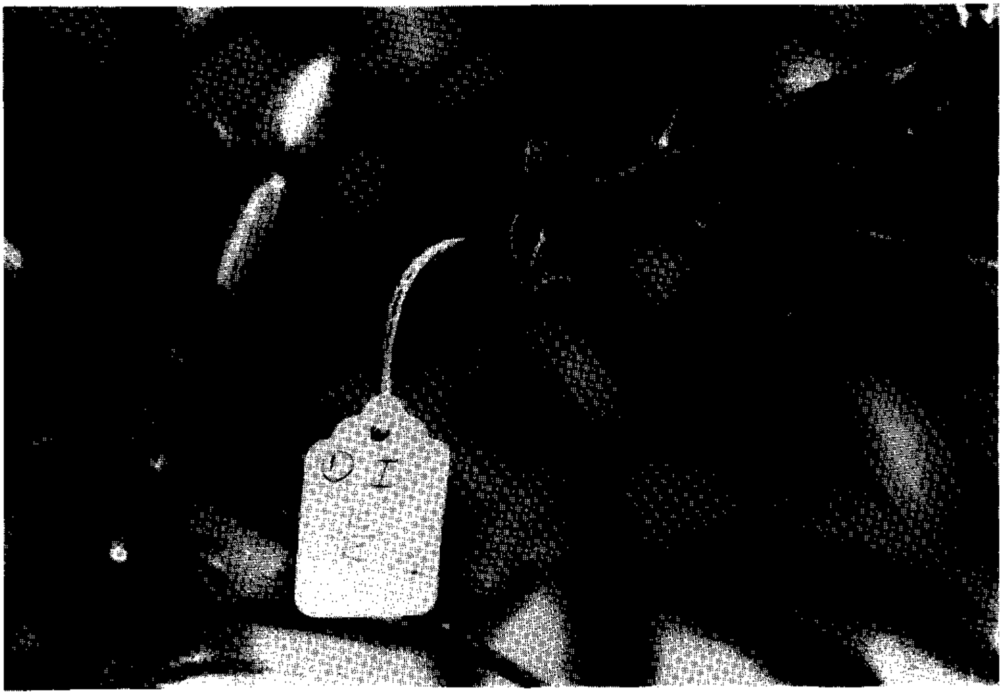

Fig. 4 A cassava leaf labelled for study of its growth and longevity.

3.5.2 Leaf life

Regularly (generally once monthly) one of the youngest leaves (not unfolded, length approximately 1 cm) per plant of all sample plants was tagged with a label on which the clone, plant number, date of labelling and replication number were coded (Fig. 4). The tagged leaves that had fallen were collected every week, enabling the life of individual leaves formed at different plant ages to be calculated.

3.5.3 Leaf size

For two experiments (experiments 1 and 2) the average leaf size was calculated from data on total leaf area per plant and total number of leaves per plant.

In experiment 3 individual leaf sizes were estimated by regression equations giving the relationship between the length of the central lobe and the individual leaf area. This relationship was introduced by Chew and Tan (1969), who compared several non-destructive methods, all based on linear measurements, for rapidly estimating the area of individual leaves of cassava. Of the methods they studied, the measurement of the length of the central lobe, which correlated well with the leaf area, was the most convenient. Hammer (1980) also concluded that the length of the central lobe is a good parameter for estimating the individual leaf area.

The general regression equation is:

$$y = a \cdot x^{b} \quad \text{or} \quad \ln y = a_1 + b_1 \ln x$$

where

y = leaf area (cm^2)

x = length of the central lobe (cm)

a and b = constants, dependent on the clone.

The constants a and b were calculated for each clone. To do this, 112 leaves were collected per clone, to represent the range of central lobe lengths of fully expanded leaves present in the sample plants. The areas of these individual leaves were measured with an automatic Hayashi Denko AM 400 leaf area meter. The relationships between the length of the central lobe and the area per leaf for the four clones studied are shown in Table 4.

For the study of the changes in the individual leaf area during the growth period of tagged leaves the length of the central lobe was measured at 2 and 4 weeks after tagging. Leaf size was then estimated using the previously mentioned equations as shown in Table 4.

Table 4 Relationship between the area of individual leaves (Y, cm^2) and the length of the central lobe (X, cm) for four cultivars of cassava ($n = 112$).
Coefficients for the relationship of the form $\ln Y = a_1 + b_1 \ln X$

clone	a_1	b_1	r^2	range of X (cm)
MCol 1684	0.84	1.59	0.907	4.1 - 28.6
MMex 59	-0.29	2.07	0.962	4.2 - 28.7
MCol 638	-0.83	2.11	0.938	6.4 - 32.5
MPtr 26	0.10	1.90	0.944	7.6 - 27.0

3.5.4 Light interception by the foliage

Data on the total global radiation during the period of the experiments are presented in Table 2. In all field experiments, measurements of global radiation were carried out regularly (once monthly) above and beneath the canopy, the latter circa 20 cm above the soil surface. These measurements were done using a Licor quantum meter Model LI-170 from Lambda Instruments Corporation with a one-metre-long line-sensing length. In each plot, one measurement was taken above the canopy and four were taken at different sites beneath the canopy and were than averaged per plot. From these data the percentage of light intercepted by the foliage was calculated.

3.5.5 Diagnosis of nutritional status of the crop during the growth period

To ascertain the nutritional status during the growth period, leaf samples were taken once per experiment to be analysed for their concentrations of the main elements. As recommended by Howeler (1980) the youngest fully expanded leaf blade of each sample plant was harvested for this analysis. The harvested leaves were bulked per plot. Samples were dried at 70-80°C until constant weight and then ground to pass through a 40 µ screen in a Wiley laboratory mill. The analyses were carried out at the CIAT Chemical Laboratory; samples were analysed for N, P, K, Ca and Mg.

3.5.6 Fallen leaves

At weekly intervals all the leaves that had fallen in the plots marked by cord were collected and dried in a forced-draught oven at 70-80°C until constant weight and then weighed. These data, together with data from the standing crop were used for calculating of the total dry matter production and the real pattern of distribution of the assimilates over the different plant parts. Fallen leaves were collected in all field experiments.

3.5.7 Fresh and dry weights

In the different experiments sample plants (6 to 12 per plot) were harvested periodically. These plants were separated into leaves, stems, original stem cuttings, storage roots and roots, and bulked per plot. The fresh weight of the storage roots was measured. The different plant parts (stems, cuttings and storage roots) were chopped into small pieces and then dried in a forced-draught oven at 70-80°C until constant weight before dry weight was determined.

3.5.8 Total leaf area

At each harvest a subsample of three leaves per plant was taken for leaf area measurements. To obtain a sample as representative as possible, the leaf column was arbitrarily stratified into three parts, top, middle and base, and one leaf was taken from each section. The leaves were bulked per plot and then divided into leaf blades and petioles. The leaf blade area was measured with an automatic Hayashi Denko AM 400 leaf area meter, after which the leaves (leaf blades plus petioles) were dried and weighed. Using these data and the total leaf dry weight of the standing crop per plot, the leaf area in m^2 per m^2 ground area, i.e. the leaf area index (LAI), was calculated.

The estimated leaf area indices showed a very good correlation with the real leaf area indices. In an associated study the results of these two methods for determination of LAI were compared. To ascertain the real leaf area index for 52 plants (4 clones, 13 plants each, plant age 4 months) the total leaf area per plant was measured. This was very laborious. To ascertain the accuracy of the estimated LAI, sampling was carried out as described before, based on the area and the dry weight of three leaves per plant and total leaf dry weight per plant. The relationship between real and calculated LAI (Fig. 5) did not differ significantly ($p = 0.05$) from $y = x$. Therefore, in all harvests, the short-cut method for ascertaining the leaf area was used, without any correction.

3.5.9 Number of storage roots

In one experiment (experiment 1) the number of storage roots per plant was measured from 4 months after planting onwards. A root was considered to be a storage root if it was at least 1 cm thick.

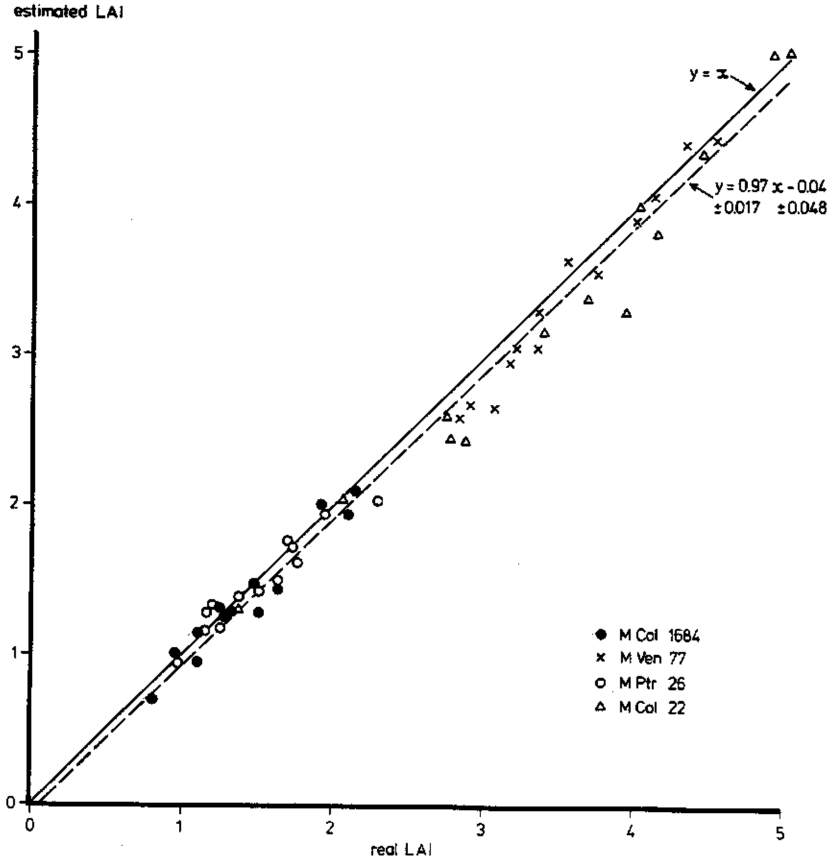

Fig. 5 Relationship between real and estimated LAI of cassava.

4 PHOTOSYNTHESIS, TRANSPIRATION, WATER USE EFFICIENCY AND LEAF AND MESOPHYLL RESISTANCE OF CASSAVA AS INFLUENCED BY LIGHT INTENSITY

4.1 INTRODUCTION

One of the main physiological determinants of the yield of a crop is the rate of photosynthesis per unit leaf area. Several authors (Moss and Musgrave, 1971; Loomis et al., 1971) have suggested improving the photosynthetic efficiency by seeking genetic variation in photosynthetic rates among species and cultivars, and by using genotypes with superior photosynthetic capacity in breeding programmes - when heritability of photosynthetic rates is sufficiently large. Considerable differences between cultivars in photosynthetic rate per unit leaf area have been reported for a number of plant species (e.g. Zelitch, 1971).

Until recently no data were available on the photosynthesis of cassava and most other tropical root crops. Only for sweet potato had studies on the CO_2 exchange rate been carried out (Tsuno and Fujise, 1965).

In their publication on the productivity of root crops Loomis and Rapoport (1977) stated that 'it would be helpful if more information on the photosynthetic capabilities of the root crop species were available. Response functions to temperature, light and CO_2 concentration and their variations are needed'. Research on this was already in progress when they wrote those words. In 1976 research on the photosynthetic rates of some clones of cassava at different light intensities was started at CIAT by Cock (CIAT, 1977). Moreover, a group of researchers at the University of Guelph, Canada, started similar research on cassava. The first data on the photosynthesis of attached leaves of cassava were published by Mahon et al. (1976). Using plants grown under controlled environmental conditions, Mahon et al. (1977a,b) studied the variation in the rate of photosynthesis of cassava clones and related species of *Manihot*, and the effects of the environment on photosynthesis, transpiration, and leaf resistance and residual resistance.

The purpose of the research reported in this chapter was to study leaf photosynthesis, transpiration, water use efficiency and resistance to water vapour and CO_2 diffusion of four cassava clones, grown outdoors at CIAT, Cali, Colombia, as part of a larger study to ascertain the basic differences between these clones. As mentioned in the preceding chapter, one of the clones used was MCol 1684, which is considered to be the best accessions in the CIAT cassava germ plasm bank (Kawano et al., 1978; CIAT, 1980).

4.2 MATERIAL AND METHODS

4.2.1 Plant material and growth conditions

Stem cuttings approximately 20 cm long, of four clones (MCol 1684, MVen 77, MPtr 26 and MCol 22) were planted vertically on July 17, 1979, in polythene pots (diameter 25 cm, height 26 cm) filled with a mixture of peat and sand (1:1 v/v). Two cuttings were planted per pot and there were ten pots per clone. After sprouting, i.e.2-3 weeks after planting, in each pot the weaker of the two plants was removed and all shoots but one were removed from the remaining cuttings. Then 6 g of NPK 14-14-14 composite fertilizer was added per pot. The plants were sprayed against thrips and spider mite regularly. Pots were watered daily. Fertilizing was repeated at 4 weeks after planting. The plants were grown in the open at natural daylength at CIAT near Cali, Colombia. Data on photosynthesis and other parameters were recorded in the period 20-30 August 1979 (35-45 days after planting). Meteorological data for the growing period have been presented in Table 2. For the measurements the experimental plants were moved to a temperature-controlled (25°C) laboratory room.

4.2.2 Gas exchange measurements

Photosynthesis by attached leaf parts was measured by a series 225 MK 11 open circuit infrared gas analyser of the Analytical Development Company, calibrated with standard bottled gas. It was measured in the differential mode and at ambient CO_2 concentration (340 vppm or 0.622×10^{-3} kgm^{-3}). For this measurement the central lobe of the first fully grown leaf (age 14 days from the moment that the non-expanded leaf measured approximately 1 cm long along the central lobe) was always used. This lobe was sealed into a clear acrylic assimilation chamber that covered the bottom surface of the leaf (surface area was normally 8 cm^2; for small lobes a chamber with a surface area of 5 cm^2 was used). The air flow in the chamber was 1.0 $lmin^{-1}$. The photon flux density, measured with a Li-cor quantum sensor Model LI-185 of Lambda Instruments Corp., varied from 1500 to 100 $\mu Em^{-2}s^{-1}$, 400-700 nm photosynthetically active radiation (PAR) (equivalent to irradiances of 327 to 22 Wm^{-2}, 400-700 nm) at the leaf surface. Net photosynthesis was measured at five light levels. In addition, respiration measurements were carried out in the dark. Lower photon flux densities were obtained by changing the distance between the lamp (400 W HPLR-N lamp of Philips Ltd.), which served to illuminate the sealed leaf part, and the leaf surface. A water filter of 3 cm was placed between the lamp and the leaf part for cooling.

At the same time that the rate of photosynthesis was being measured leaf temperature was measured with a thermocouple pressed to the lower leaf surface and recorded by a Model Bat 8 instrument of Baily Instruments. The temperature of the outgoing air and the dewpoint of the air streams were measured with a Model 880 dewpoint hygrometer of EG and G International Inc. The inlet air stream had a dewpoint of ca 15°C (variation 14.6°C - 15.2°C). Average leaf temperature was 24.7°C (variation 25.4°C - 23.9°C depending on photon flux density level). The system was equilibrated for about 1 h before results were recorded. All measurements were taken between 9.00 h and 15.00 h and the results presented are means of eight similarly sized plants per clone selected before measurement from the ten original plants.

4.2.3 Calculations

Transpiration (T) was calculated from the data on the concentration of water vapour in the air at saturation level, derived from the measured dewpoint temperatures of the outgoing and the ingoing air, the air flow and the sealed area of the leaf (Gaastra, 1959). Dewpoint of the air within the leaf was assumed to be the same as the leaf temperature. Total leaf resistance to diffusion of water vapour ($r_a + r_\ell$) was also calculated according to a method described by Gaastra (1959) from the rate of transpiration and the difference in concentration of the water vapour at the two ends of the diffusion path:

$$r_\ell + r_a = \frac{[H_2O]_i - [H_2O]_a}{T} \qquad (1)$$

where:
r_ℓ = leaf resistance to water vapour diffusion
r_a = water vapour diffusion resistance in the laminar air layer
T = transpiration
$[H_2O]_i$ and $[H_2O]_a$ = concentrations of water vapour inside the leaf (i) and in the laminar air layer (a).

The water vapour diffusion resistance in the laminar air layer (r_a) was determined by measuring the evaporation from strips of blotting paper exposed to the same conditions as the leaves. The calculated value of r_a was 67 sm^{-1}. From (1) and the value of r_a the leaf resistance to diffusion of water vapour (r_ℓ) was calculated.

As the diffusion coefficients of CO_2 and water vapour in air differ, the relationships mentioned by Milthrope and Moorby (1974) were used to convert the water vapour diffusion resistance in water (r_a) and the leaf resistance to water vapour diffusion (r_ℓ) to the corresponding resistances to CO_2 (r'_a and r'_ℓ): $r'_a = 1.37\ r_a$ and $r'_\ell = 1.54\ r_\ell$.

The total leaf conductivity for CO_2 was derived from the reciprocal of the total leaf resistance to CO_2 diffusion: $\frac{1}{r'_a + r'_\ell}$

The CO_2 concentration in the intercellular spaces (C_i) was calculated from the relationship between the net photosynthesis and the total leaf conductivity for CO_2 as proposed by Goudriaan and Van Laar (1978a):

$$C_i = C_a - 1/S \qquad (2)$$

where S = slope of the relation between P_n and $\frac{1}{r'_a + r'_\ell}$,
and C_a = ambient CO_2 concentration (340 vppm).

Gross photosynthesis (P_g) was calculated by summing the P_n and dark respiration of the leaf (R):

$$P_g = P_n + R \qquad (3)$$

The relationship between photon flux density (H) and gross photosynthesis was described according to Goudriaan and Van Laar (1978b), i.e. with an asymptotic exponential equation:

$$P_g = P_{g,max} (1 - e^{-\frac{1}{HH} \times H}) \qquad (4)$$

H = photon flux density incoming visible light
$P_{g,max}$ = maximum rate of photosynthesis at light saturation
HH = level of H required to reach half the light saturation level.

The efficiency of the use of light at low light intensity (α) is represented by the ratio $\frac{P_{g,max}}{\text{absorbed HH}}$. It is assumed that 80% of the incoming visible light is absorbed.

The mesophyll resistance (r_m) was calculated from:

$$P_n = (C_i - C_{chl})/r_m \qquad (5)$$

C_{chl} = CO_2 concentration at the chloroplast level (CO_2 compensation point). Mahon et al. (1977a) reported a CO_2 compensation point of 68 vppm for cassava. This value was used in (5) to calculate r_m. Water use efficiency was ascertained from the ratio of net leaf photosynthesis (P_n) to transpiration (T). The greater the ratio the more efficient a clone is in water use.

4.3 RESULTS

4.3.1 Effect of light intensity on photosynthesis

The effect of different light levels on the gross photosynthesis of leaves of the four cassava clones is shown in Fig. 6. The different lines represent the best fits using the equation $P_g = P_{g,max}(1 - e^{H/HH})$. R^2 values for the fit of the equations were 0.98 - 0.99. Clonal differences for net photosynthesis at the highest light level are shown in Table 5. MCol 22 had the highest net photosynthetic rate at that light level (0.81×10^{-6} kg CO_2 $m^{-2}s^{-1}$ or 29.2 mg CO_2 $dm^{-2}h^{-1}$), being 9% more than that of MVen 77, which showed the lowest photosynthetic rate of the four cultivars studied. However, the observed differences between the four clones were not statistically ($p = 0.05$) significant.

The dark respiration of the leaves of the four clones ranged from 0.047×10^{-6} to 0.056×10^{-6} kg CO_2 $m^{-2}s^{-1}$ (1.7 - 2.0 mg CO_2 $dm^{-2}h^{-1}$).

The photosynthetic efficiency (α) of the four clones varied from 9.0×10^{-9} for MCol 1684 to 12.4×10^{-9} kg CO_2 J^{-1} for MVen 77, with an average of 10.7×10^{-9} kg CO_2 J^{-1} for all four clones (Table 5).

Table 5 Mean net photosynthesis (P_n) at 1500 $\mu Em^{-2}s^{-1}$ (PAR) and maximum efficiency of light energy conversion (α) of four clones of cassava (n = 8 plants per clone)

Clone	$P_n(10^{-6}$ kg CO_2 $m^{-2}s^{-1})$	$\alpha(10^{-9}$ kg CO_2 $J^{-1})$
MCol 1684	0.76	9.0
MVen 77	0.74	12.4
MPtr 26	0.78	10.2
MCol 22	0.81	11.5
average	0.77	10.7

4.3.2 Transpiration and leaf resistance to water vapour diffusion

Mean values of the transpiration (T) as influenced by the light intensity are shown in Fig. 7. Maximum transpiration varied little (1.7 - 1.8 g H_2O $dm^{-2}h^{-1}$) at the highest light level. No significant differences in transpiration rate were observed between the

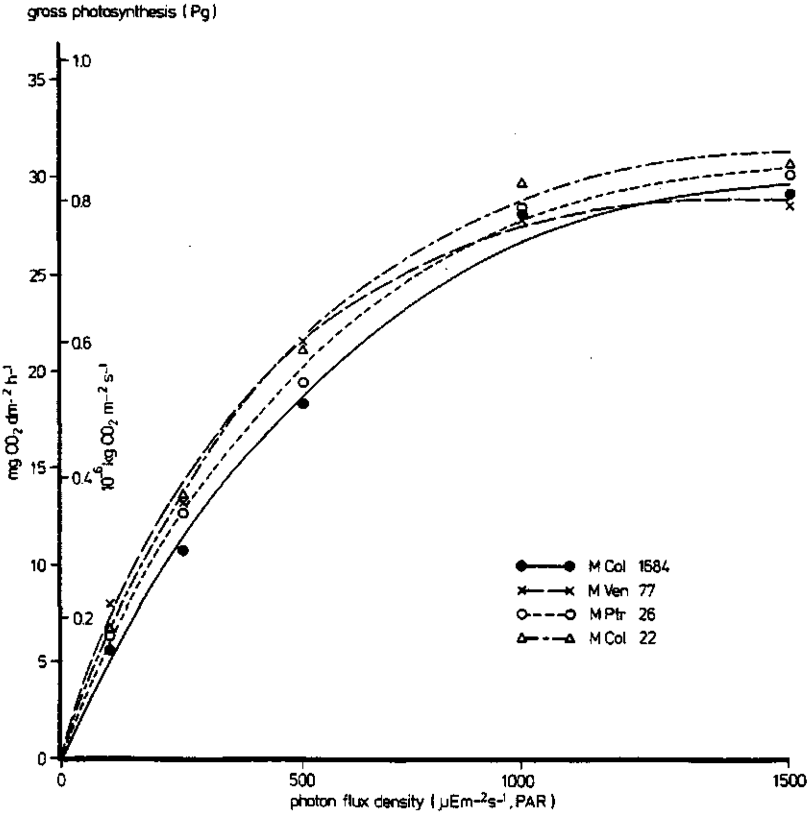

Fig. 6 Rates of gross photosynthesis of leaves of four cassava clones at different photon flux densities (0 to 1500 $\mu Em^{-2}sec^{-1}$) at 340 $\mu l.l^{-1}$ CO_2.

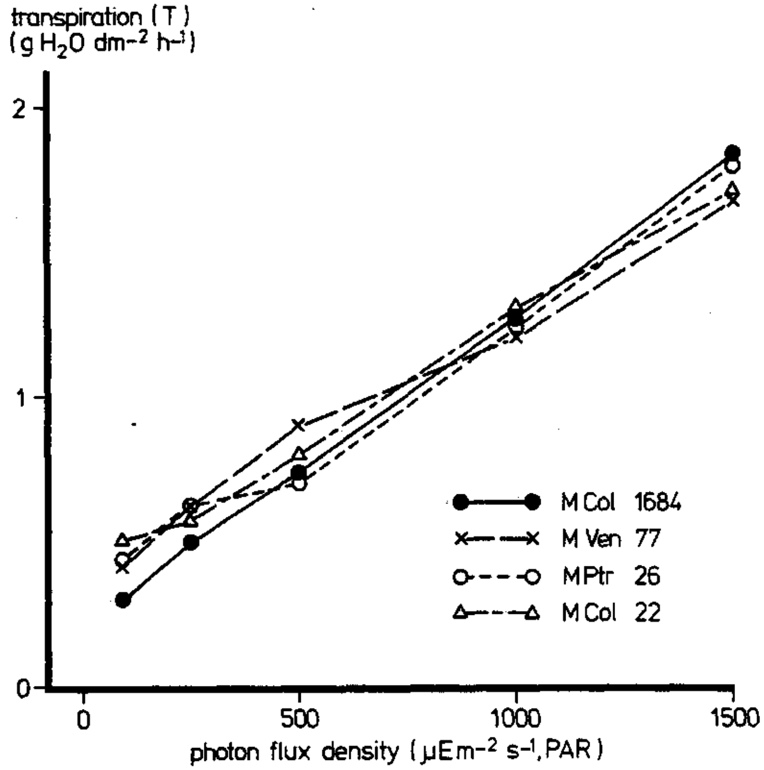

Fig. 7 Transpiration rates of leaves of four cassava clones at different photon flux densities at $340\ \mu l.l^{-1}\ CO_2$.

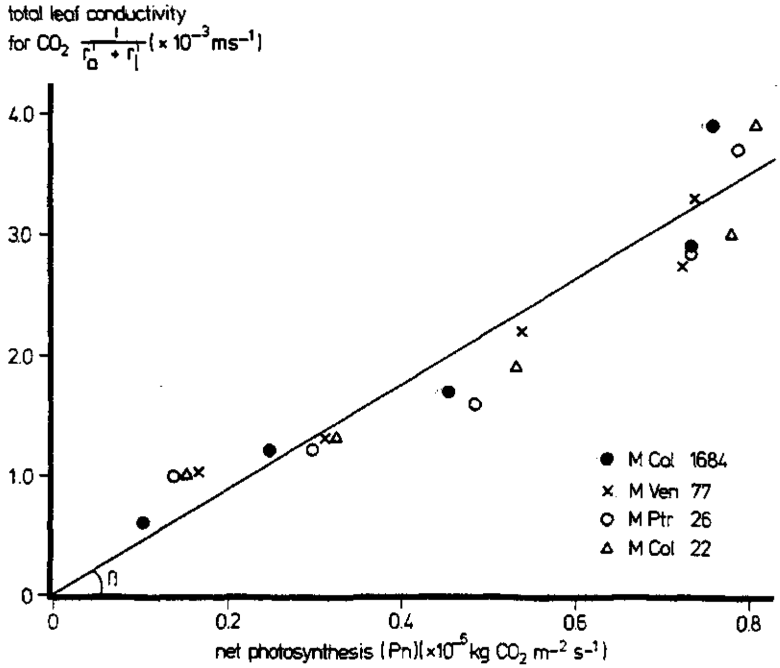

Fig. 8 Relationship between total leaf conductivity for CO_2 and the rate of net photosynthesis.

four clones.

Leaf resistance to water vapour diffusion varied from 110 - 140 sm^{-1} at a photon flux density of 1500 $\mu Em^{-2}s^{-1}$ (PAR) for the different clones.

4.3.3 Total leaf conductivity for CO_2, leaf resistance to CO_2 diffusion, mesophyll resistance and water use efficiency

The relation between the total leaf conductivity $(1/r'_a + r'_\ell)$ and the net photosynthesis is presented in Fig. 8: it is a linear relation ($R^2 = 0.98$), indicating that the CO_2 concentration in the intercellular spaces remained approximately constant. The average internal CO_2 concentration (C_i) was 212 vppm (0.387×10^{-3} kgm^{-3}).

The mesophyll resistance did not vary much for the four clones at a photon flux density of 1500 $\mu Em^{-2}s^{-1}$ (PAR) (Table 6). In Table 6 the values of leaf resistance to CO_2 diffusion (r'_ℓ) are also shown. For all four clones the mesophyll resistance was higher than the leaf resistance to CO_2. Differences in water use efficiency of the four clones were small. MCol 22 was the most efficient in water use (Table 6).

Table 6 Leaf resistance to CO_2 diffusion (r'_ℓ), mesophyll resistance (r_m) and water use efficiency (WUE) at a photon flux density of 1500 $\mu Em^{-2}s^{-1}$ (PAR) for four clones of cassava (n = 8 plants per clone)

Clone	r'_ℓ (sm^{-1})	r_m (sm^{-1})	WUE (mg CO_2/g H_2O)
MCol 1684	170	340	15.1
MVen 77	220	350	15.6
MPtr 26	180	330	15.7
MCol 22	170	320	17.1

4.4 DISCUSSION AND CONCLUSIONS

A relatively low photon flux density was required for light saturation of the photosynthetic rate (Fig. 6). Furthermore, Mahon et al. (1977a) reported a CO_2 compensation point of 68 vppm for cassava. Both of these characteristics are typical of a plant species that has a C_3 type of photosynthesis.

Because at a certain site under optimal growing conditions the maximum leaf photosynthesis ($P_{n,max}$) and the light efficiency at low intensities (α) are very important variables affecting dry matter production (De Wit, 1965; Goudriaan and Van Laar, 1978b) clones must be compared for these two characteristics at least. No significant clonal differences in maximum rate of leaf photosynthesis were observed between the four clones used in this study (Table 5). Mahon et al. (1977b), however, when testing a large number of clones and species belonging to the genus *Manihot*, observed large differences. In the present experiment, the measured maximum values of the rate of net leaf photosynthesis (27.7 to 29.2 mg CO_2 $dm^{-2}h^{-1}$) were in the range as reported by Mahon et al. (1977a), and are normal values for C_3 plants (De Wit et al., 1979). Recently, Palta (1982) reported similar net photosynthetic rates at high light levels. As in the present study, MCol 22 showed the highest rate among the clones used at a light level of 1500 $\mu Em^{-2}s^{-1}$. Also the calculated values for the initial light use efficiency (α) (CO_2 absorption per unit intercepted, absorbed radiation) found in the present study (9.0×10^{-9} to 12.4×10^{-9} kg CO_2 J^{-1}) are similar to values reported for several other C_3 crops, e.g. cotton (Constable and Rawson, 1980), although in other crops (e.g. tomato (Peat, 1970) and wheat (Planchon, 1979)) somewhat lower efficiencies have been found. Acock et al. (1971) reported a range for α of $7.4 - 20.3 \times 10^{-9}$ kg CO_2 J^{-1} for large number of plant species.

At a high light level (1500 $\mu Em^{-2}s^{-1}$) the values of the mesophyll resistance to CO_2 diffusion (r_m) were larger than those of the leaf resistance to CO_2 diffusion (r_ℓ'), indicating that r_m is the dominant resistance to CO_2 diffusion into the leaf, as has also been found for a number of other C_3 crops (Aslam et al., 1977).

A constant CO_2 concentration of approximately 212 vppm was found in the intercellular spaces of cassava leaves, independent of the light level. For other crops, too, a stabilization of the internal CO_2 concentration has been reported, as e.g. for cotton (Constable and Rawson, 1980), beans and maize (Goudriaan and Van Laar, 1978b).

In the cases where a stable CO_2 concentration in the cavity of the stomata has been reported, this was about 210 vppm for C_3 crops and 120 vppm for C_4 crops (De Wit et al., 1979), signifying that for a C_3 crop like cassava the transpiration coefficient (mg H_2O transpired per mg CO_2 assimilated) will be about double that of a C_4 crop, both at low and high irradiances (De Wit et al., 1978). Under conditions in which water is limited, stabilization of the internal CO_2 concentration is a desirable property. De Wit et al. (1978) showed that such a stabilization leads to a reduction of up to 50% in potential transpiration, compared with a situation where stomata remain open and the internal and ambient CO_2 concentration are more or less equal. In this study, and also in the study reported by Palta (1982), MCol 22 had the most efficient water use of the clones studied. An efficient water use is crucial for a crop such as cassava, which is quite often cultivated under stress conditions such as water stress (Cock, 1979; Hahn et al., 1979). However, in a field study a large negative effect on dry matter yield was found for MCol 22 plants when submitted to water stress during part of the growing season (Connor et al., 1981). When screening cassava cultivars for efficient water use, laboratory research has to be complemented by field testing of clones under water-stress conditions.

5 *INTERRELATIONSHIPS BETWEEN LAI, LIGHT INTERCEPTION AND TOTAL DRY MATTER YIELD OF CASSAVA*

5.1 INTRODUCTION

For many years, the analysis of the growth and yield of crops was based on the magnitude of the leaf area per unit ground area - the leaf area index (LAI) - and the net assimilation rate - the rate of dry matter production per unit leaf area (Watson, 1952).

For cassava, several authors have suggested that variations in yield were possibly caused by differences in leaf area or leaf area duration (Doku, 1965; Sinha and Nair, 1971; Enyi, 1972b,c; Cock, 1976; Cock et al., 1979).

More recently, attention has been focussed on the relationships between the amount of incoming radiation intercepted by the canopy of a crop and the dry matter production (Monteith, 1977).

In this chapter, first the results of a study on the relation between the LAI and the percentage of light interception by the crop canopy are reported; this is followed by a report of an investigation on the relationships between the cumulative intercepted radiation and the total dry matter yield for different clones of cassava.

5.2 MATERIALS AND METHODS

For meteorological data and some general experimental procedures that were used in this study, see Chapter 3, in which the harvest procedure, yield determination, procedure for calculating the LAI and the light interception by the canopy were also described.

Three experiments were conducted. The clones MCol 1684 and MPtr 26 were used in all three experiments, MVen 77 and MCol 22 in experiment 1 and 2, while MMex 59 and MCol 638 were planted in experiment 3.

Experiment 1 Planting was done on 15 December 1978. First harvest took place on 15 February 1979 (62 days after planting (DAP)). Successive harvests followed on 17 April 1979 (123 DAP), 18 June (185 DAP), 13 August (241 DAP), 15 October (304 DAP) and finally on 12 December 1979 (362 DAP). Light measurements were carried out at 62, 90, 123, 151, 185, 213, 241, 279, 304, 335 and 360 DAP. LAI of the plants was calculated at 62, 123, 185, 241, 304 and 362 DAP.

The energy content of whole plants was ascertained from plants harvested on 17 April 1979 (123 DAP) and 15 October 1979 (304 DAP). Dried material from all four clones was used for the analysis of the four-month-old plants, whereas for the analysis of the energy content of 10-month-old plants samples of dried matter from MCol 1684 and MPtr 26 only were used.

On each harvest date twelve plants were sampled per plot.

Experiment 2 Cuttings of the same four clones were planted on 13 July 1979. During the growth period, which was 178 days, sample plants were harvested on five occasions. Twelve plants were sampled per plot per harvest. Harvests took place on 30 August 1979 (48 DAP), 24 September (73 DAP), 9 October (88 DAP), 7 November 1979 (117 DAP) and finally on 7 January 1980. LAI was calculated on the harvest dates.

Light measurements were carried out at 48, 73, 88, 115, 125, 144 and 178 DAP.

Experiment 3 The cuttings of MCol 1684, MMex 59, MCol 638 and MPtr 26 were planted on 29 January 1980. These clones were the control treatments of a study on sink-source relationships of cassava. The complete results have been reported elsewhere (Veltkamp, 1985). Sample plants were harvested on 13 June 1980 (138 DAP), 30 July (185 DAP), 29 September (246 DAP) and 25 November 1980 (303 DAP). For these dates the LAI was also calculated.

Six plants were harvested per plot for the harvests at 138 and 185 DAP, and nine on the other dates.
At 73, 96, 125, 152, 171, 194, 229, 246, 275 and 303 DAP, measurements on light interception by the canopy were taken.

The efficiency (E) with which a cassava crop utilized the intercepted light for the production of dry matter was calculated for all three experiments according to the method of Hayashi (1966):

$$E\ (\%) = \frac{a \times \text{produced dry weight}}{\text{intercepted PAR}} \times 100$$

a = energy content of the dry matter produced by cassava plants.
PAR = photosynthetically active radiation

It was assumed that the photosynthetically active radiation (PAR) is 50% of the total incoming radiation (Cooper, 1976).

The energy content of the dry matter produced by cassava plants was ascertained as follows: subsamples of dried entire plants were ground in a Wiley mill to pass through a 40 μ screen. The ground samples were compressed into pellets, to facilitate the combustion of the material. The energy content of the dry matter was then determined in a Parr adiabatic calorimeter from Parr Instrument Company (Moline, Illinois, USA).

The relation between the percentage of light interception and the LAI was calculated using the equation proposed by Monsi and Saeki (1953): $\ln (I/I_0) = -K \cdot LAI$, where I = light received at about 20 cm above the soil surface, I_0 = incoming light just above the crop canopy, K = extinction coefficient, which gives an indication of the arrangement of the leaves in a canopy (Cooper, 1976).

5.3 RESULTS

5.3.1 Total dry matter yield

In experiment 1, total dry matter yield - including the dry weight of the fallen leaves - continued to increase until the last sampling at 362 DAP (Fig. 9a). Clonal differences in total dry weight were not significant on any of the six sampling dates.

Fig. 9b shows the pattern of total dry matter yields at different times after planting for experiment 2. At 178 DAP, MCol 1684, MVen 77 and MPtr 26 had produced significantly more dry matter than MCol 22. Total dry matter yields at 178 DAP were considerably lower, however, than in these clones at about the same age in experiment 1.

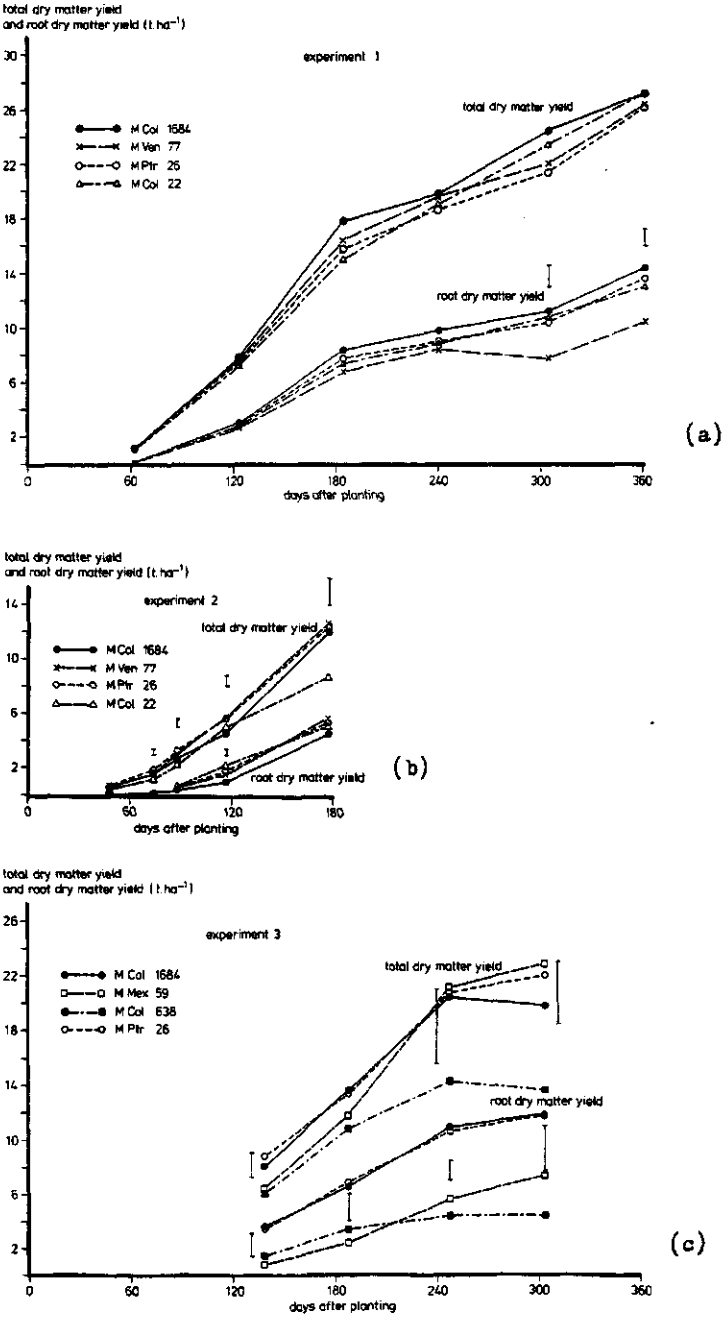

Fig. 9 Total and root dry matter yield of several cassava clones at different times after planting. In this and other graphs vertical lines indicate least significant difference (p = 0,05).

In experiment 3, MPtr 26, MCol 1684 and MMex 59 produced the highest amounts of dry matter at 303 DAP (Fig. 9c). Differences between these clones were not significant. But these three clones all yielded significantly more than MCol 638. At all four harvests MCol 638 gave the lowest total dry matter yield. Total dry matter yields of MCol 1684 and MPtr 26 at an age of six months were intermediate between those of experiments 1 and 3.

5.3.2 Light interception by the canopy

Experiment 1 Patterns of percentage light interception by the canopies of the four clones are shown in Fig. 10a. On the first two dates on which light measurements were carried out MCol 22 intercepted a lower percentage of the incoming PAR than MCol 1684, MVen 77 and MPtr 26. At 90 DAP the light interception by the canopy of MCol 22 was 11% to 16% lower than for the other clones. At that moment MCol 1684 and MPtr 26 had already reached a light interception level of at least 90%. High light interception levels were maintained until about 185 DAP. In a dry period from 190 to 210 DAP the percentages of light interception decreased considerably because of considerable leaf fall in all clones except MCol 22. At 185 DAP, clonal differences in total intercepted PAR were negligible (Table 7). The fraction of the incoming PAR intercepted by the canopies was 0.66 for the period up to 185 DAP, with only small differences between clones (Table 7).

Experiment 2 Intercepted PAR at 178 DAP varied from 740 MJm^{-2} for MCol 22 to 940 MJm^{-2} for MCol 1684 and MPtr 26. Differences between MCol 1684, MVen 77 and MPtr 26 were only small. The intercepted PAR was 56% of the total incoming PAR on average, and ranged from 47%-61% (Table 7).

Experiment 3 Percentages of light interception at different times in the growth period of 303 days are shown in Fig. 10b. MCol 638 showed very low percentages of light interception during the first three months; this could be attributed to the low sprouting percentage, which made replacement of some cuttings necessary, and to slugs that attacked cuttings and young plants, damaging bark and buds in

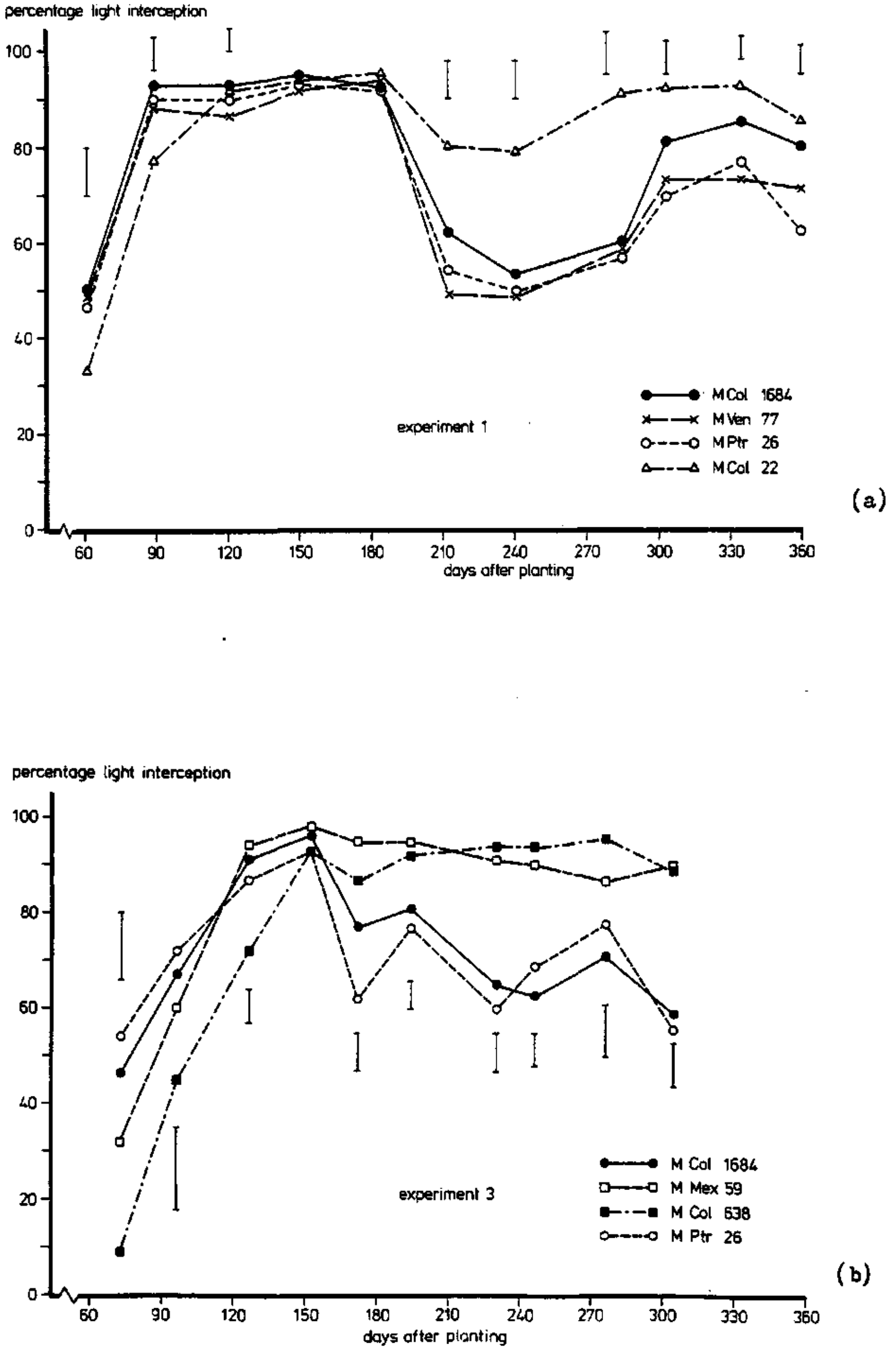

Fig. 10 Percentage light interception by the canopy of several cassava clones at different times after planting. Experiments 1 and 3.

particular (see also CIAT (1980)). At 152 DAP the light interception was 90% or more for all four clones. At 125 DAP, MCol 1684, MMex 59 and MPtr 26 had already reached the 90% light interception level. MCol 638 and MMex 59 maintained high percentages of light interception until the last harvest at 303 DAP. For MCol 1684 and MPtr 26, on the other hand, a high percentage of light interception was maintained for a short period only. The cumulative intercepted PAR at 185 DAP is shown in Table 7. At that time MCol 638 had intercepted only 800 MJm^{-2}, compared with 1040 to 1080 MJm^{-2} for the clones MCol 1684, MMex 59 and MPtr 26.

5.3.3 Relationship between percentage of light interception and LAI

LAI data on the clones studied are presented in Chapter 6.

Fig. 11 shows the relationships between the percentage of light interception and the LAI of the clones in experiment 1. The relationships were calculated according to Monsi and Saeki (1953), who suggested that the penetration of light down the canopy approximately followed the law of Lambert-Beer. With this formula good fits were obtained between the LAI and percentage light interception. The K values in the formula, being the extinction coefficient, are also shown in Fig. 11. The high values of K support the observations that all clones had a canopy with dominantly horizontally-orientated leaves.

A light interception of 90% was reached at LAI values ranging from 2.6 (MCol 22) to 3.2 (MVen 77) (Fig. 11).

In experiment 2 the values of K found from the relationships between LAI and percentage light interception were similar to those reported for experiment 1.

In experiment 3 the K values for MCol 1684 and MPtr 26 lay in the range reported for these clones in experiment 1, but the K value of MMex 59 was 0.68 ± 0.09 and that of MCol 638 was 0.61 ± 0.12. The leaves of MCol 638 were less horizontal than those of the other clones.

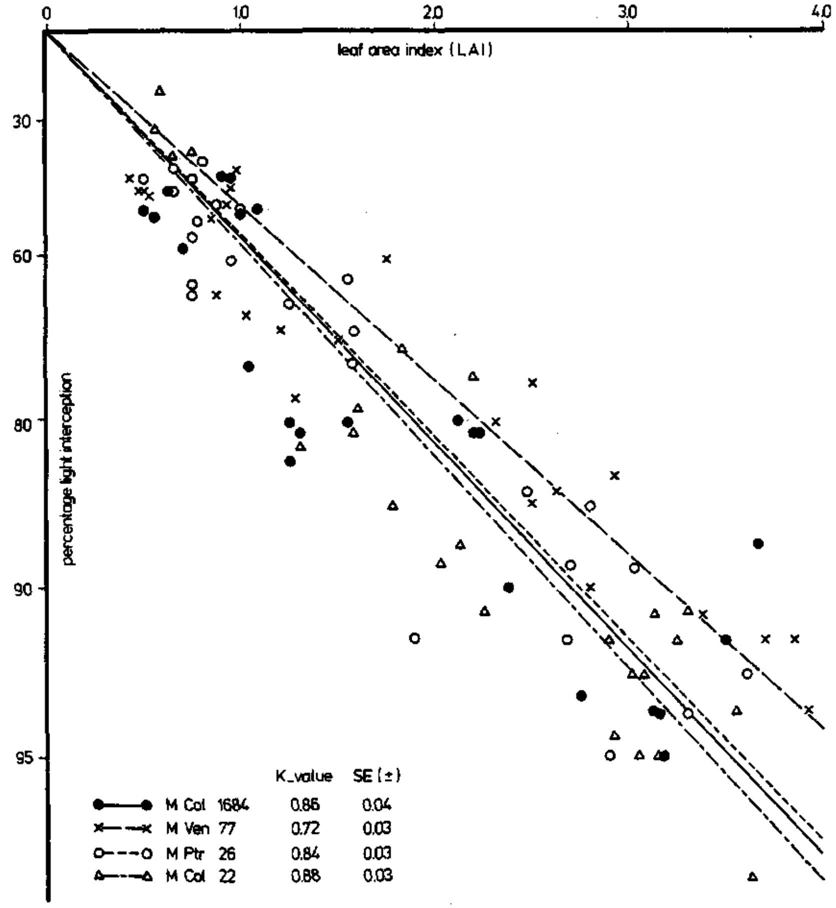

Fig. 11 Relationship between LAI and percentage light interception for four cassava clones. Experiment 1.

5.3.4 Relationship between total dry matter yield and intercepted PAR

In Fig. 12 data on total dry matter yield have been plotted against the cumulative intercepted PAR, using all data from experiment 1. The relationships shown in Fig. 12 are linear for all clones until approximately six months after planting. There is a close correlation between the total dry matter yield and the intercepted PAR. During the first six months of the growth period dry matter was produced at a rate of 1.34-1.40 g per MJ intercepted PAR. Multiplying these values by 16.7, which is the average energy content ($kJ \cdot g^{-1}$) (Table 8), gives the efficiency of the photosynthetic system (E), expressed as a percentage (Table 7). These data are shown in Table 7 for the first six months of the growth period of all three experiments.

The photosynthetic efficiency of MCol 1684, MVen 77, MPtr 26 and MCol 22 showed only a small variation between the clones in experiment 1, and varied from 2.3% to 2.5% (average 2.4%), based on PAR. In experiments 2 and 3 average photosynthetic efficiency was lower, as was the overall efficiency (which is the product of the fraction of the incoming PAR intercepted by the canopy (f) and the photosynthetic efficiency (E): see Table 7).

Photosynthetic efficiency was also lower for plants older than 185 days (Fig. 12).

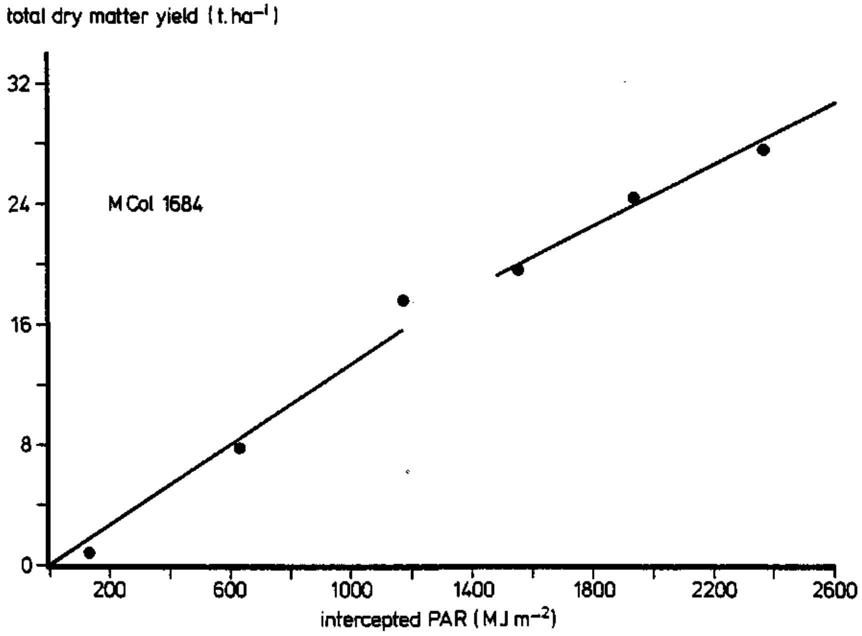

Fig. 12 Relationship between total dry matter yield and total intercepted PAR for cassava clone MCol 1684. Experiment 1.

Table 7 Fraction of incoming PAR intercepted (f) and efficiency (E) of use of intercepted PAR for about six months from planting of the cuttings

clone	crop age (days)	incoming PAR (MJcm^{-2})		total dry weight (t·ha^{-1})	f	E (%)	overall efficiency (%)
		total	intercepted				
Experiment 1							
MCol 1684	185	1716	1180	17.7	0.69	2.5	1.7
MVen 77	185	1716	1136	16.4	0.66	2.4	1.6
MPtr 26	185	1716	1140	15.7	0.66	2.3	1.5
MCol 22	185	1716	1066	15.1	0.62	2.4	1.5
Experiment 2							
MCol 1684	178	1550	943	12.0	0.61	2.1	1.3
MVen 77	178	1550	870	12.6	0.56	2.4	1.4
MPtr 26	178	1550	936	12.4	0.60	2.2	1.3
MCol 22	178	1550	736	8.9	0.47	2.0	0.9
Experiment 3							
MCol 1684	185	1864	1042	13.6	0.56	2.2	1.2
MMex 59	185	1864	1069	11.9	0.57	1.9	1.1
MCol 638	185	1864	794	10.8	0.43	2.3	1.0
MPtr 26	185	1864	1079	13.4	0.58	2.1	1.2

Table 8 Energy content of dry matter of four cassava clones

clone	energy content (kJ/g)*
123-day-old plants	
MCol 1684	16.7
MVen 77	16.5
MPtr 26	16.8
MCol 22	17.0
304-day-old plants	
MCol 1684	16.7
MPtr 26	16.2
average	16.7

* each value is the average of four determinations

5.4 DISCUSSION AND CONCLUSIONS

For approximately the first six months of the growth period the total dry matter increase of a cassava crop was proportional to the intercepted PAR (Fig. 12). The same phenomenon has also been reported for several other crops, e.g. soybean (Shibles and Weber, 1966), wheat (Gallagher and Biscoe, 1978), barley (Monteith, 1977; Gallagher and Biscoe, 1978), potato (Monteith, 1977, Allen & Scott, 1980), sugarbeet (Monteith, 1977; Scott and Jaggard, 1978), lettuce (Bierhuizen et al., 1973) and apple (Monteith, 1977).

The highest dry matter production rate was 1.40 g per MJ intercepted PAR, equivalent to a photosynthetic efficiency (E) of 2.5% (Table 7). Boerboom (1978b) also reported a photosynthetic efficiency for a cassava crop of 2.5%, based on PAR, between 17 and 41 weeks after planting. However, such efficiencies are low compared with those measured for other crops (potato, sugarbeet) grown under conditions of adequate fertilizer and water in experimental plots in England for which Monteith (1977) reported an increase of dry matter of about 2.8 g per MJ intercepted PAR, equivalent to a 4.8% efficiency, based on PAR.

It remains to be seen which factors can be held responsible for this much lower photosynthetic efficiency. This also holds for the lower photosynthetic efficiency found from six months after planting (Fig. 12). For barley it has also been reported that later in the growth cycle the leaf surface was less responsive to intercepted radiation (Biscoe and Gallagher, 1977). For cassava there may be a relation with drought stress later in the growth period. In order to prevent the storage roots from rotting the experimental plots were not irrigated during dry periods when plants were about 6.5-9 months old (experiment 1). Palta (CIAT, 1981) observed that rates of leaf photosynthesis in pot-grown cassava plants fell to about 20% of those of non-stressed plants within one week after the stress was induced. Connor et al. (1981) also reported a decrease in the total dry matter yield for plants grown under waterstress for several weeks. Other reasons for the lower photosynthetic efficiency may be an increase in the crop respiration (Veltkamp et al., 1985) or a limitation of the growth of the storage root sink (Veltkamp, 1985) resulting in a decrease in the photosynthesis, as suggested by Williams (1972). Cock et al. (1979) and Tan and Cock (1979a), however, suggested that root sink activity does not normally limit photosynthetis in cassava. Another possible explanation of the lower photosynthetic efficiency of cassava may be a decrease in the crop photosynthesis, resulting from a mobilization of nitrogen from the leaves in high-yielding crops, (see Evans, 1975). For several crops, a linear relationship between the nitrogen content of a leaf and its photosynthetic rate has been suggested (Natr, 1972). For cassava it has been found that from the moment leaves reached their final size the nutrient contents decreased again (Howeler et al., 1983; Veltkamp, unpublished results), while the nutrient contents of the first fully expanded leaves decreased with time (CIAT, 1981). However, there are no data available for cassava on the relation between the nutrient contents in the leaves and the photosynthetic rates of those leaves.

The calculated values of the extinction coefficients (K) (0.72-0.88 in experiment 1) correspond with a canopy with a planophile leaf distribution and are of the same order as reported for white clover, cotton and potato (Cooper, 1976; De Wit, 1965). In only one clone (MCol 638) was a lower K value (0.61) found. Williams and Ghazali (1969) suggested that a more vertical orientation of the upper foliage, permitting a better light penetration to the lower leaf layers, would result in a greater crop photosynthesis and increased storage root yield of cassava. Models for simulation of crop photosynthesis (De Wit, 1965; Duncan et al., 1967), however, showed that only in crops with high LAI values (6 and more) dominantly vertical leaves do show a clear advantage.

The energy content of cassava dry matter varied from 16.2 to 17.0 kJg^{-1}. These values lay in the range from 15.1 to 18.1 kJg^{-1} reported for whole herbaceous plants (Loomis et al., 1971).

6 *CANOPY CHARACTERISTICS OF DIFFERENT CASSAVA CULTIVARS*

6.1 INTRODUCTION

Selection of morphological characteristics that have physiological significance has been shown to be highly successful in the process of breeding for yield in several crops, e.g. rice and wheat (Austin et al., 1980; Jennings, 1964).

The leaf area is one such characteristic. For wheat a number of authors have reported a linear relationship between the leaf area duration (LAD) after ear emergence and the grain yield (Evans et al., 1975).

A positive correlation between the leaf area or LAD and the yield of storage roots of cassava has also been suggested (Doku, 1965; Sinha & Nair, 1971; Enyi, 1972b,c; Cock, 1976; Cock et al., 1979). These findings imply that the supply of assimilates e.g. the rate of leaf photosynthesis, plus the development of leaf area are important in determining storage root yield of cassava. The results of the study reported in Chapter 5, on the relationships between the LAI and the percentage of light intercepted by the canopy on the one hand, and the cumulative intercepted light and the total dry matter yield on the other hand, support this hypothesis.

For cassava the leaf area per plant depends on the number of active apices, that is the branching pattern, the number of leaves formed per apex, the leaf size and the leaf life.

The objective of this study was to characterize several cassava cultivars according to the development of leaf area and its components.

6.2 MATERIALS AND METHODS

General experimental procedures and data on meteorological conditions were described in Chapter 3 and also in Chapter 5. The clones MCol 1684, MVen 77, MPtr 26 and MCol 22 were planted in experiments 1 and 2, whereas MCol 1684, MMex 59, MCol 638 and MPtr 26 were used in experiment 3.

Experiment 1 Planting was done on 15 December 1978. Measurements of plant height and leaf area development (number of leaves formed per apex, number of active apices, number of branches per branching point and number of nodes up to different branch levels) were carried out at 62, 90, 123, 151, 185, 213, 241, 279, 304, 335 and 360 DAP. These measurements were done on twelve plants in the plots harvested at the last harvest, i.e. on 12 December 1979 (362 DAP). Average leaf size was calculated from the total leaf area per plant and the number of leaves on the plants. Data on average leaf size are only available for the moments at which plants were harvested, namely at 62, 123, 185, 241, 304 and 362 DAP. For those dates the LAI of the different clones was also calculated. At 59, 91, 123, 153, 189, 213, 241, 277 and 305 DAP the youngest leaf per plant was tagged with a ticket. The fallen tagged leaves were collected weekly.

Experiment 2 Cuttings of the same four clones as used in experiment 1 were planted on 13 July 1979. The total growth period was 178 days. The same measurements as mentioned for experiment 1 were conducted in this experiment, on nine plants per clone per replication. Plants were measured at 48, 73, 88, 117, 144 and 175 DAP. Average leaf size and LAI were calculated as described for experiment 1, on the harvest dates (48, 73, 88, 117 and 178 DAP). The procedure followed for calculating of the leaf life was the same as mentioned for experiment 1. Youngest leaves were tagged at 48, 73, 88, 117 and 144 DAP.

Leaf blade samples for diagnosis of the nutritional status of the crops were taken at 118 DAP, according to a procedure described by Howeler (1980) (see also Chapter 3), and analysed for N, P, K, Ca and Mg. Plants were sprayed once to control an attack by thrips.

Experiment 3 The cuttings were planted on 29 January 1980. Nine plants per replication per cultivar were measured for the same parameters as reported for experiments 1 and 2, at 54, 89, 131, 159, 194, 227, 264 and 294 DAP. Individual leaf size at different times after planting was determined according to a method described in Chapter 3. To ascertain leaf life leaves were tagged at 54, 89, 103, 117, 131, 145, 157, 194 and 262 DAP. LAI was calculated at the harvest dates (138, 185, 246 and 303 DAP). The last harvest was on 25 November 1980 (303 DAP). Leaf samples for nutritional diagnosis were taken on 150 DAP and analysed for N, P, K, Ca and Mg.

6.3 RESULTS

6.3.1 General observations on sprouting and growth

In experiments 1 and 2, sprouting of the cuttings was good for all clones. Sprouting of MCol 22 was about one week later than that of MCol 1684, MVen 77 and MPtr 26. In experiment 3 sprouting of MCol 638 was variable; this was also a result of the activities of slugs (identified as *Vaginulus* (*Sarasinula*) *plebeius* (*Veronicellidae*) (CIAT, 1980)), which consumed parts of the bark of the cuttings and sprouting buds and leaves of the young plants.

Results of the leaf blade analysis revealed that in experiment 2 the N, P and K contents of MCol 22 were somewhat below the critical levels proposed by Howeler (1980) (Table 9). In the other clones the N and P contents were slightly below the critical levels. In experiment 3 the nutrient concentrations (N, P, K, Ca and Mg) in the youngest fully expanded leaves were above the critical levels at 150 DAP, in all four clones.

Table 9 Nutrient concentration in youngest fully expanded leaves of four clones of cassava at 118 DAP (Experiment 2)

Clone	Concentration (% of dry weight)				
	N	P	K	Ca	Mg
MCol 1684	4.9	0.36	1.6	0.9	0.45
MVen 77	4.9	0.37	1.4	0.8	0.38
MPtr 26	4.6	0.35	1.4	0.7	0.33
MCol 22	4.3	0.29	1.1	0.7	0.45
Critical level (Howeler, 1980)	5.0	0.4	1.2	0.7	0.3

6.3.2 Plant height

Fig. 13a,b shows the plant heights of the clones studied in experiment 1 (Fig. 13a) and experiment 3 (Fig. 13b) at different times after planting. The heights of the plants in experiment 2 were similar to those in experiment 1. Considerable differences in plant height were observed between the clones under study. MVen 77 was an exceptionally tall clone, being more than 3.5 m at 362 DAP (experiment 1) (Fig. 13a). MCol 22 and MCol 638 were shorter, with MCol 22 being 1.9 m at 362 DAP in experiment 1 and MCol 638 being 1.8 m at 294 DAP in experiment 3.

6.3.3 Leaf area index

Experiment 1 MCol 1684, MPtr 26 and MVen 77 reached an LAI of 1.0 by approximately 62 DAP (Fig. 14a). The leaf area development of MCol 22 was somewhat slower, possibly because it took longer to sprout: (nearly three weeks, whereas for MCol 1684, MVen 77 and MPtr 26 it took two weeks).

In the period from 62 to 123 DAP LAI increased greatly, reaching an average value of 2.8 at 123 DAP. At that date there was no significant clonal difference in LAI. From 123 to 185 DAP, LAI values continued to increase, peaking on average at 3.4. Just after the sampling at 185 DAP a dry period occurred. In the period from about 190 to 220 DAP a tremendous leaf fall was observed, resulting in very low LAI's at 241 DAP for all clones except MCol 22. The decrease in LAI in that clone was much less. At 241 DAP, MCol 22 had an LAI of 1.9, which was significantly higher than that for the other clones, which had an average LAI value of 0.6. Until the last sampling at 362 DAP, MCol 22 maintained a higher LAI than the other clones.

In the rainy season from October to November 1979, LAI values increased again for all clones, but especially in MCol 1684 and MVen 77.

Experiment 2 Leaf area development, expressed as LAI, during the growth period of 178 days is shown in Fig. 14b. At 48 DAP, LAI values ranged from 0.21 for MCol 22 to 0.34 for MPtr 26. At 73 DAP MCol 1684 and MPtr 26 had already passed the LAI=1 level, while

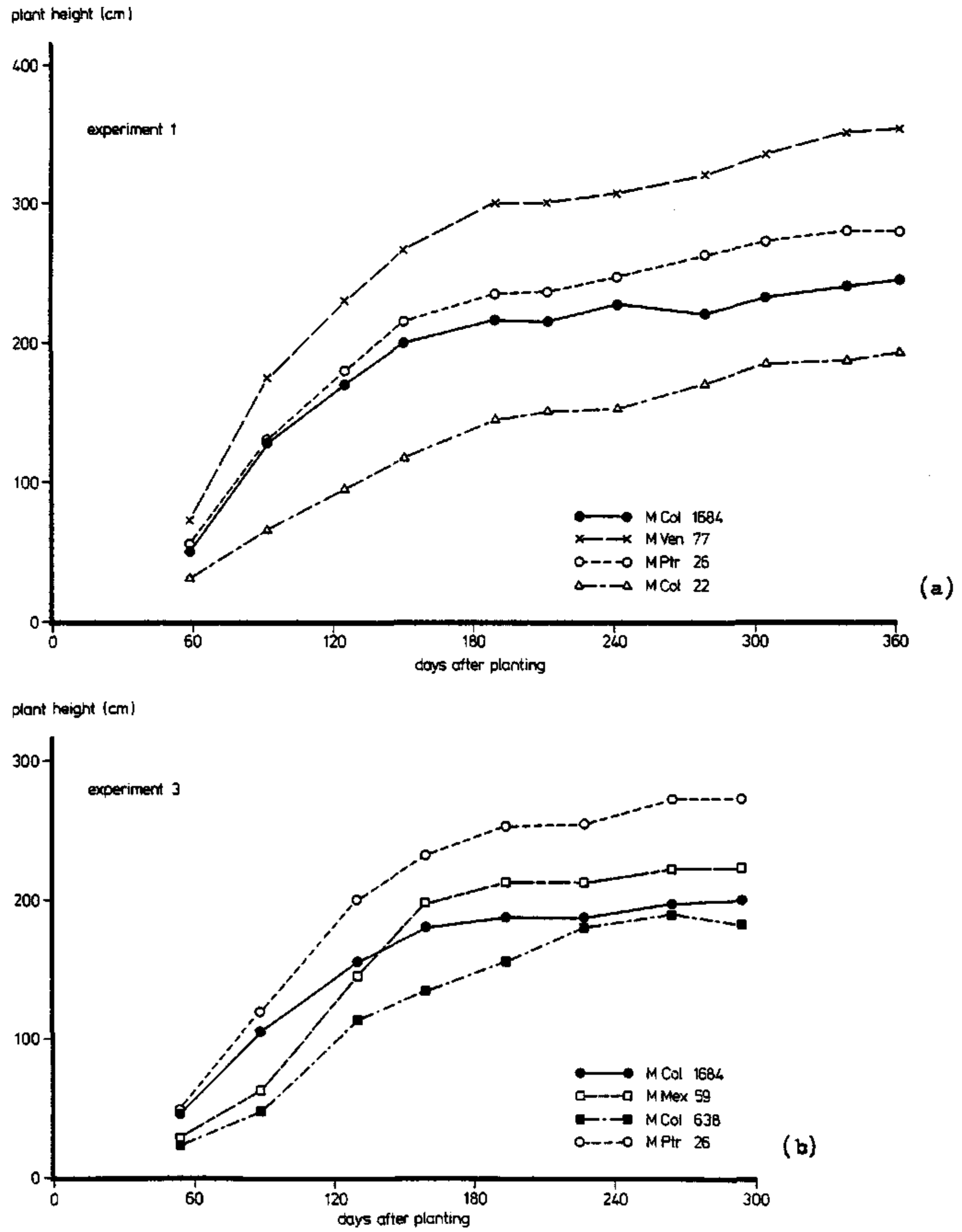

Fig. 13 Plant height as a function of plant age, in six cassava clones.

MVen 77 and MCol 22 were approaching it. Great increases in LAI were observed from 73 to 88 DAP. Maximum LAI values reached in this experiment were relatively low (2.0-2.4). Until 117 DAP, MCol 22 had significantly lower LAI values than MPtr 26, with MCol 1684 and MVen 77 being intermediate. At 178 DAP clonal differences in LAI values were not statistically significant.

Experiment 3 Significant clonal differences in LAI values were found for all sampling dates. Although initial leaf area development of MCol 638 was very slow, at 138 DAP this clone had already reached a LAI of 3.7 and did not differ significantly from MMex 59, which had already peaked (4.7) at that time (Fig. 14c). On the other sample dates MMex 59 and MCol 638 had statistically significant higher LAI values than MCol 1684 and MPtr 26, although the differences between both groups decreased gradually.

6.3.4 Cumulative number of leaves formed per apex

The number of leaves formed per apex for the four clones in experiment 1 is shown in Fig. 15a. New leaves were formed continuously. As plants grew older, the number of new-formed leaves per apex decreased. At 59 DAP no clonal differences in leaves formed per apex were observed. From 91 DAP, MPtr 26 had a significantly higher number of leaves formed per apex than the other clones, whereas MVen 77 formed more leaves per apex than either MCol 1684 or MCol 22.

In experiment 2 the leaf production showed the same patterns as in experiment 1 (Fig. 15b). At 175 DAP, MPtr 26 had produced significantly more leaves per apex than the other clones (Table 10).

In experiment 3 the cumulative number of leaves formed per apex for MPtr 26 was significantly higher than that for the other clones from 89 DAP (Fig. 15c). The number of leaves formed per apex at 194 and 294 DAP are shown in Table 12.

6.3.5 Number of active apices per m^2

The number of active apices can be studied in terms of three aspects: the duration of the period from planting until the first branch level is reached; duration of the periods until subsequent

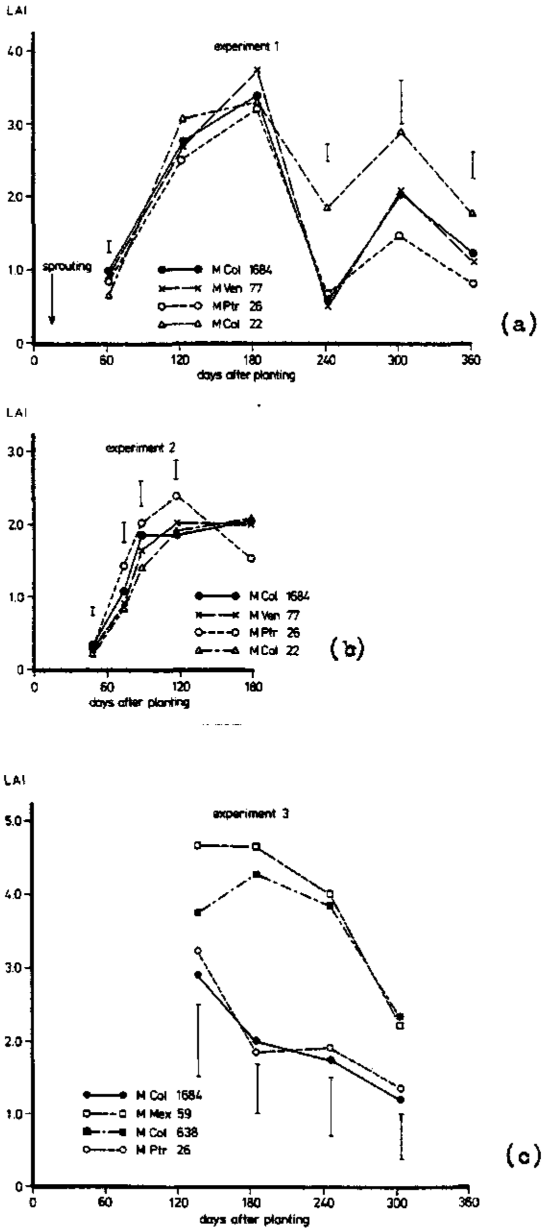

Fig. 14 LAI at different times after planting, in six cassava clones.

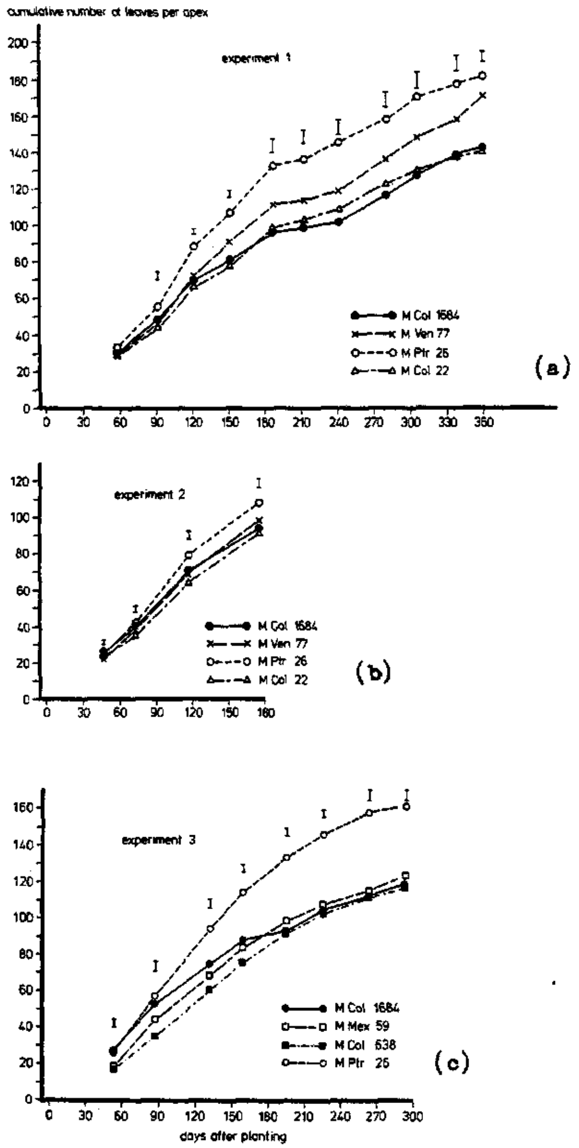

Fig. 15 Cumulative number of leaves per apex, in clones at different times after planting.

Table 10 Branching patterns, cumulative number of leaves produced per apex and number of active apices per m^2 of four cassava cultivars. Experiment 2

	MCol 1684	MVen 77	MPtr 26	MCol 22	F-test	LSD
No. of nodes from:						
. planting to first branch level	18	56	59	56	**[1]	7.7[2]
. first to second branch level	27	-[3]	-	-		
. second to third branch level	25	-	-	-		
No. of days from:						
. planting to first branch level	33	93	94	100	**	13
. first to second branch level	46	-	-	-		
. second to third branch level	40	-	-	-		
No. of branches per branching point at:						
. first branch level	2.1	3.0	3.2	2.8	**	0.11
. second branch level	3.1	-	-	-		
. third branch level	2.7	-	-	-		
No. of leaves produced per apex at 175 DAP	93	98	108	91	**	5.6
Number of active apices per m^2 at 175 DAP	25.4	8.1	6.2	4.4	**	5.5

[1] confidence limits: ** = $p < 0.01$

[2] $p = 0.05$

[3] no data, because the plants had not all reached that branch level at 175 DAP

Table 11 Branching patterns of four cassava cultivars. Experiment 1

	MCol 1684	MVen 77	MPtr 26	MCol 22	F-test	LSD[2]
No. of nodes from:						
. planting to first branch level	14	56	86	19	**[1]	4.5
. first to second branch level	26	33	41	41	**	6.0
. second to third branch level	26	19	29	31	**	3.5
No. of branches per branching point at:						
. first branch level	2.2	3.1	3.0	2.2	**	0.11
. second branch level	3.0	2.7	2.6	2.7	**	0.14

[1] confidence limits: ** = $p < 0.01$

[2] least significant difference at $p = 0.05$

branch levels; and, finally, the number of branches formed per branching point.

Experiment 1 The number of active apices as a function of time has been presented in Fig. 16a. From 185 to 241 DAP the number of active apices decreased considerably for MCol 1684, because the branches at the highest branch levels partially died back. Fig. 17 presents the time taken from planting until the first and subsequent branch levels were produced. The period from planting to the first branch level varied from 38 days for MCol 1684 to 121 days for MPtr 26. MCol 22 also branched early. The differences between the four clones in number of days to first branching were very significant (Fig. 17). The length of the periods from the first to the second and the second to the third branch level did not differ much among the clones (Fig. 17).

The number of nodes (leaves) formed until the first branching occurred varied from 14 for MCol 1684 to 86 for MPtr 26 (Table 11). Branching occurred in distinct phases (Fig. 17) The number of branches formed per branch at the first and second branch levels are also shown in Table 11. Generally, MCol 1684 formed two branches at the first branch level, although some plants had three branches. At the second branch level the average number of branches per branching point was 3.0 for MCol 1684. In the other clones differences were also found for the number of branches per branching point at the first and second branch levels.

Experiment 2 The number of days from planting to first branching was 33, 93, 94 and 100 for MCol 1684, MVen 77, MPtr 26 and MCol 22, respectively. Only MCol 1684 plants branched for a second and third time in the growth period of 178 days (Table 10).

The number of nodes formed until the moment of first branching, the number of branches growing from the first branch level and the number of active apices at 175 DAP are also shown in Table 10. The number of active apices as a function of time has been presented in Fig. 16b.

Experiment 3 MCol 1684 branched earliest, at 49 DAP, followed by MMex 59 at 66 DAP and MCol 638 at 71 DAP. MPtr 26 branched late, at 134 DAP (Table 12). The mean number of branches at the first branch level was 2.3, 2.3, 2.8 and 3.0 for MCol 1684, MVen 77,

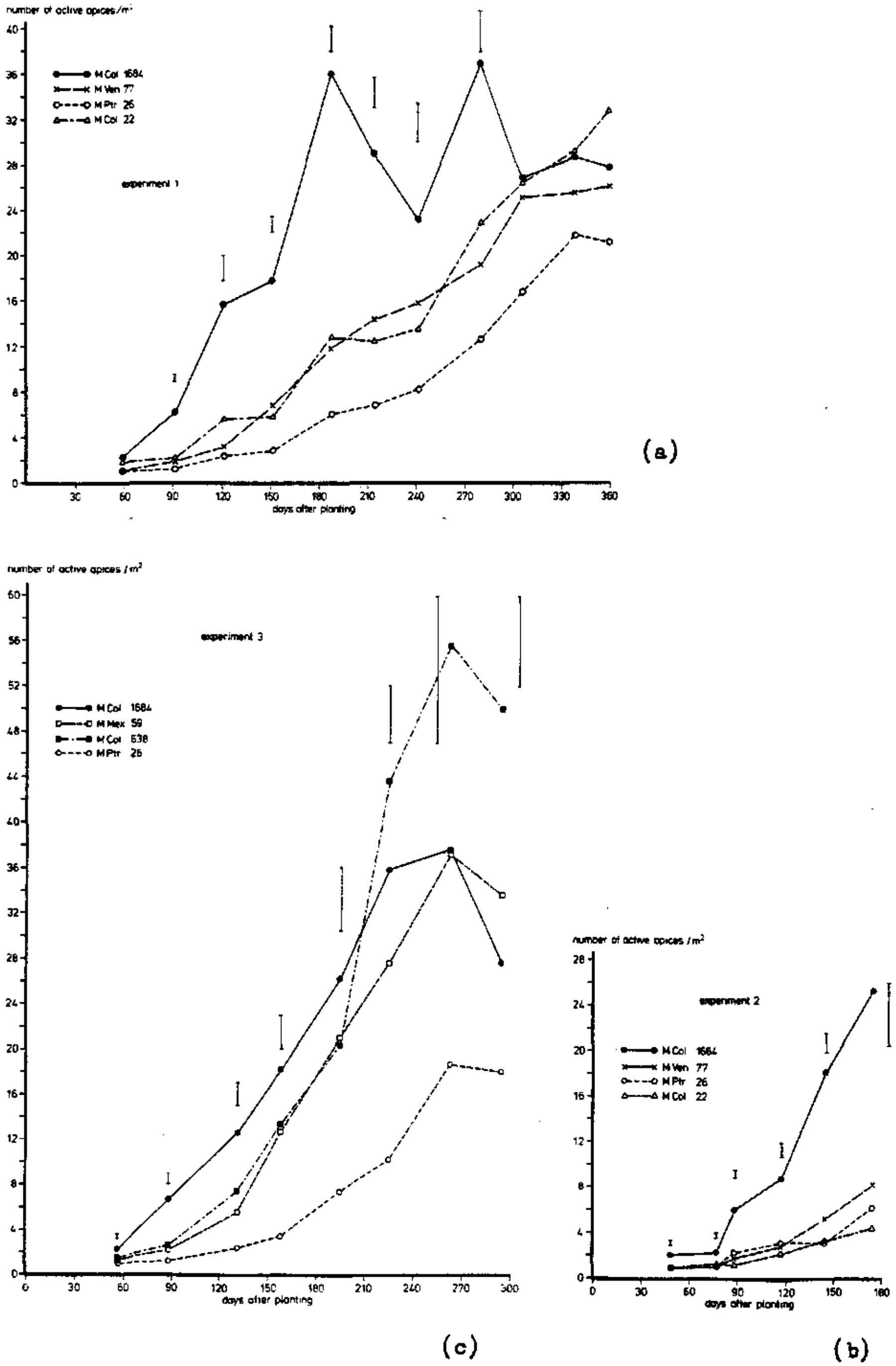

Fig. 16 Number of active apices per m² at different times after planting for several cassava clones.

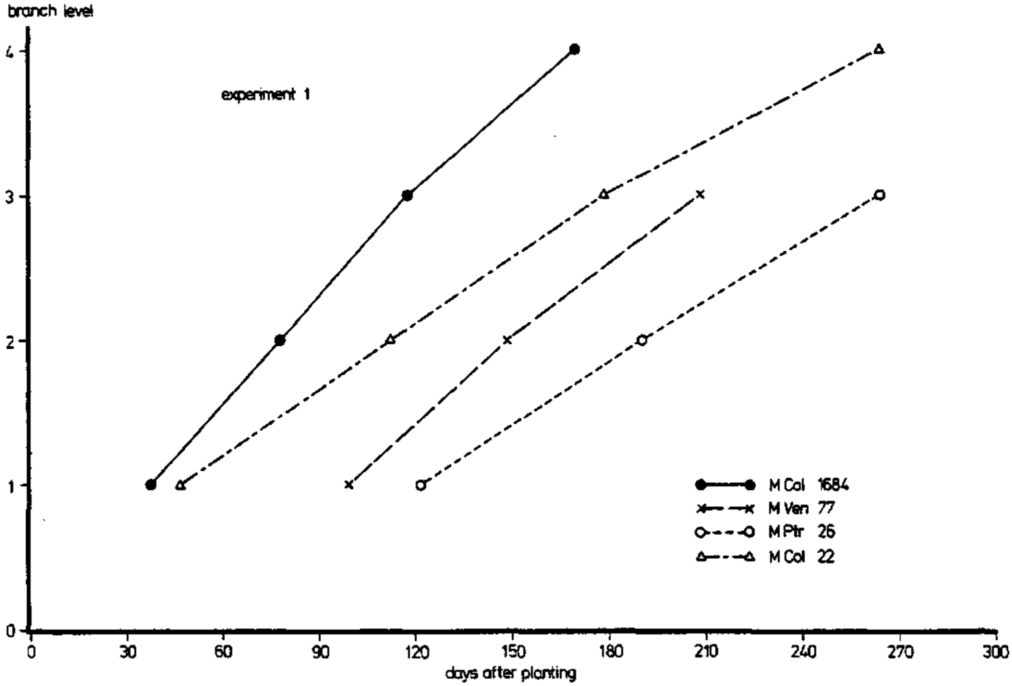

Fig. 17 Time to branching for four cassava clones. Experiment 1.

Table 12 Cumulative number of leaves formed per apex and branching patterns of four cassava cultivars. Experiment 3

	MCol 1684	MMex 59	MCol 638	MPtr 26	F-test[1]	LSD[2]
Cumulative number of leaves formed per apex at:						
. 194 DAP	92	98	91	133	**	4.2
. 294 DAP	118	124	117	162	**	4.7
No. of nodes from:						
. planting to first branch level	22	27	26	96	**	4.2
. first to second branch level	28	30	28	38	**	3.9
. second to third branch level	27	26	25	-[3]		
No. of days from:						
. planting to first branch level	49	66	71	134	**	9.1
. first to second branch level	36	45	49	61	**	4.2
No. of branches per branching point at:						
. first branch level	2.3	2.3	2.8	3.0	**	0.24
. second branch level	2.9	2.7	3.1	3.0	ns	

[1] confidence limits: ** = $p < 0.01$; ns = non-significant

[2] $p = 0.05$

[3] no data, because the plants had not all reached that branch level at 294 DAP

MPtr 26 and MCol 22, respectively. Data on number of nodes from planting to first, second and third branching (only MPtr 26 did not reach the third branch level), number of days from first to table 12 second branch level and number of branches at the second branch level are presented in Table 12.

The patterns of number of active apices as a function of time after planting are shown in Fig. 16c.

6.3.6 *Leaf life*

Experiment 1 Considerable differences between clones were observed regarding the life-span of the leaves (Fig. 18a). No clonal difference was observed in leaf life for the first leaves formed after sprouting. Clonal differences in life-span of leaves tagged at 59 and at 91 DAP were already very significant, however. At both times the life-span of MCol 1684 leaves was much shorter than that of the other clones. Leaves tagged in the period from 123 to 153 DAP all fell at about 190 to 210 DAP, in a very dry period.

Leaves of clone MCol 22 tagged in the period from 189 to 241 DAP lived longer than those of the other clones. The longest average leaf life - nearly 120 days - was recorded for MCol 22 leaves tagged at 185 DAP.

No data can be presented on the life-span of leaves tagged later than 240 DAP, as those leaves had not always fallen at the time the experiment was terminated at 362 DAP.

Experiment 3 Life-span of leaves was recorded for leaves tagged in the period from 54 to 194 DAP (Fig. 18b). Leaves tagged when plants were older had not all fallen, so that the life-span of those leaves could not be calculated.

Clonal differences in the life-span of the leaves were recorded for leaves tagged at plant ages from 54 to 134 days. Leaves of MPtr 26 and MCol 638 formed during that period had a longer life-span than those of MMex 59 and MCol 1684 (Fig. 18b).

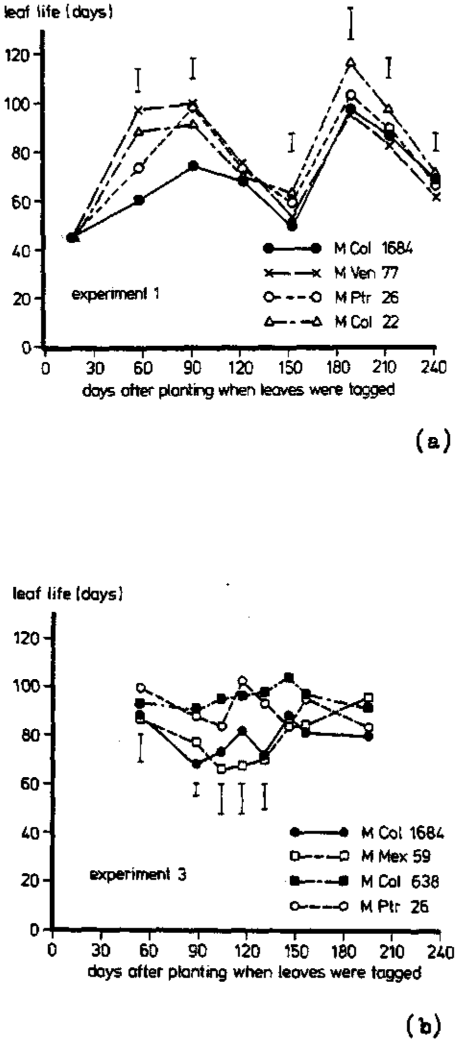

Fig. 18 Leaf life of six cassava clones at different times after planting.

6.3.7 Leaf size

For experiments 1 and 2 the average leaf size was calculated from the total leaf area per plant and the total number of leaves per plant. In experiment 3 the individual leaf size was derived from the calculated relationships between the length of the central lobe and the leaf size (see Chapter 3).

Experiment 1 Large clonal differences in average leaf size were observed (Fig. 19a). At 62 DAP, MVen 77 had the biggest average leaf blade size. By then, MCol 1684 and MVen 77 had already reached their maximum average leaf size. The maximum size for both MCol 22 and MPtr 26 was found at 123 DAP. The average leaf size decreased tremendously in the period from 123 to 185 DAP. At 185 DAP, MPtr 26 had the biggest leaves. The average leaf size declined further from 185 DAP onwards. In the period from 241 to 362 DAP the average leaf size was less than 100 cm^2 for all four clones. For that period clonal differences in leaf size were not statistically significant.

Experiment 2 Already at 48 DAP significant clonal differences in average leaf size were observed (Fig. 19b). The maximum average leaf size for MCol 1684 and MPtr 26 was reached at 73 DAP. Leaf sizes of MCol 22 and MVen 77 declined after 88 DAP. At all sampling dates MCol 1684 had the smallest leaves.

Experiment 3 The leaf sizes mentioned for this experiment refer to the size of individual leaves. Fig. 19c gives the patterns of leaf size during the growth period. MMex 59 and MPtr 26 had the biggest leaves during the whole growth period. The size of the leaves tagged at 54 DAP and measured at 68 DAP already showed much variation between the clones studied. Leaves of MCol 1684 had their maximum size at 54 DAP. From 157 to 262 DAP changes in individual leaf size were only small.

6.4 DISCUSSION AND CONCLUSIONS

Several authors (Doku, 1965; Sinha and Nair, 1971; Enyi, 1972b,c; Cock, 1976; Cock et al., 1979) have suggested that the leaf area is

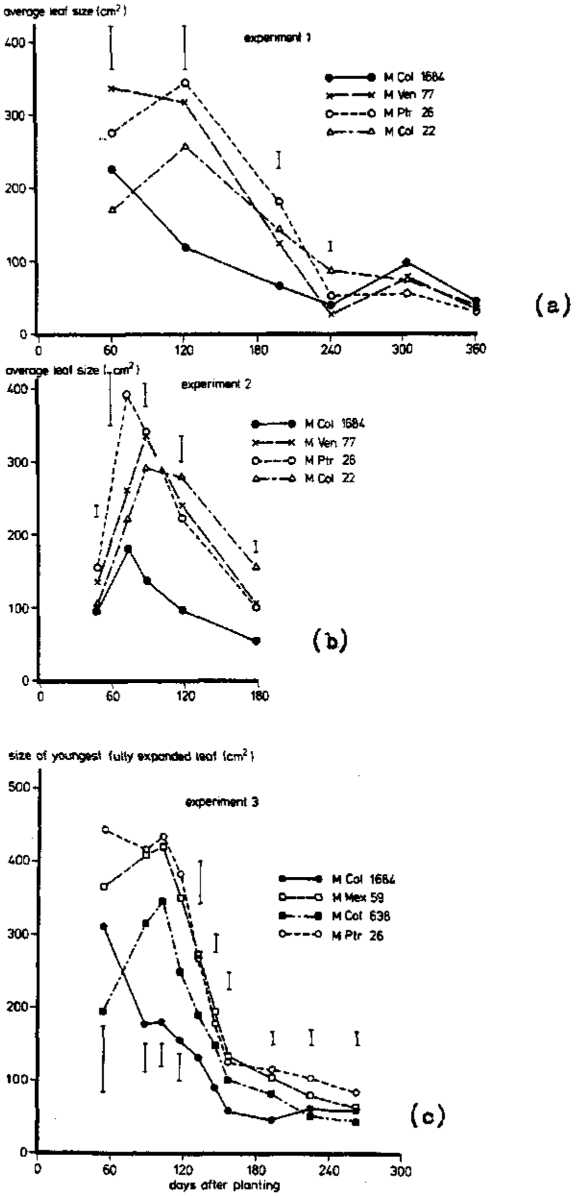

Fig. 19 Average leaf size of four cassava clones at different times after planting (experiments 1 and 2) and size of youngest fully expanded leaves of four cassava clones at different times after planting (experiment 3).

crucial in determining the crop growth rate and the storage root bulking rate of cassava. Cock et al. (1979) found the optimal LAI for storage root bulking rate to be 3 to 3.5. Irikura et al. (1979) suggested that this optimum LAI existed over a wide range of temperatures. In order to obtain a high storage root yield it seems to be necessary for a cassava crop to reach an LAI of 3 to 3.5 as quickly as possible and to maintain that LAI for as long as possible.

In this study it was found that initial leaf area development was slow, taking 60-80 days from planting before an LAI of 1.0 was reached (Fig. 6a,b). An LAI = 3, which coincides with a light interception by the canopy of approximately 90%, was reached between 120 to 150 DAP (Fig. 14a,c), i.e. approximately 40% of the crop growth period elapsed before the reported optimal LAI was reached. For one experiment (experiment 2) an LAI = 3 was never reached (Fig. 14b). Genotypes with very different canopy characteristics took approximately the same time to attain an LAI = 3.

The development of LAI depends on several factors, such as leaf formation rate, leaf longevity, branching pattern and leaf size. For all these factors significant genotypic variations were found in this study, but environmental conditions, too, were of influence.

An important interaction between genotype and planting date was found for the period from planting until the first branch level was produced (Fig. 17 and Tables 10 and 11), even though temperature and daylength variation during the year are relatively small at the experimental site (Table 2). Data from Irikura et al. (1979) suggest that differences in temperature may be responsible for the variation observed in the period from planting until first branching, but the temperature range in their study was much larger (20-28°C) than that at the CIAT experimental farm area. In Chapter 8 it is shown that under long days (16 hours) the final branch number was greater, but no general reaction to daylength was found in the period from planting until the first branch level was produced (Chapter 8). Miège (1957) found that cuttings taken from the main stem branched later than cuttings taken from the first to the third branch levels. In the present study, all the cuttings were taken from the middle part of the plants, including the main stem and the first and sometimes also second branch levels, so the variation in period from planting until the first branching observed in this study cannot be explained in this way. Cassava clones grafted onto different stocks branched at similar times, suggesting that the period from planting till first branching is scion determined (Veltkamp, 1985).

Large clonal differences were found in leaf longevity (Fig. 18). Rosas et al. (1976) reported that shading of the leaf blade and the presence of an active apex strongly shortened the leaf life. However, the storage root bulking rate did not influence the leaf life, making selection possible for a high root bulking rate on the one hand and for a long leaf life on the other. Leaf life was influenced strongly by a drought stress that occurred during the growth period of the plants in the experiment 1 from 190 to 210 DAP.

At first, leaf size increased with plant age, but later it decreased. Genotypic variation was found in the plant age at which maximum leaf size was obtained (Fig. 19). Maximum leaf size varied by clone and by planting date (Fig. 19). Leaf size was influenced by changing the branching pattern; larger leaves were produced when the number of active apices was reduced (Tan and Cock, 1979a).

To date, little variation has been found in leaf formation rate per apex (Cock et al., 1979; Tan and Cock, 1979a,b; Irikura et al., 1979). Of the cultivars tested in this study, however, MPtr 26 showed a significantly higher leaf formation rate in all three experiments (Fig. 15; Tables 10 and 12).

The results of this study show that even small variations in environmental conditions (Table 2) can lead to significant differences in canopy characteristics. For successful modelling of leaf area development of a cassava crop, detailed studies under controlled conditions of the effects of temperature and light on the canopy characteristics of diverse cassava genotypes are also necessary, with emphasis on interactions between the different components that contribute to the development of the leaf area.

7 PARTITIONING OF DRY MATTER IN CASSAVA

7.1 INTRODUCTION

It has been shown (Chapter 5) that in cassava there is a close correlation between the total dry matter yield and the intercepted PAR. Because in cassava the storage root yield is more relevant than the total dry matter yield, it is important to study the distribution of produced dry matter among the different plant parts, particularly in the storage roots.

Indira and Sinha (1970) and Cours (1951) reported that secondary growth of the roots had already started by three weeks after the cuttings were planted, with starch deposition in the secondary xylem of the roots following approximately one week later. The capacity for initiating storage roots of cassava is an inherent characteristic of the genotype of the roots (Cours, 1951).

Boerboom (1978a) suggested that during the storage root filling period the distribution of dry matter over the different plant parts can be described by a linear regression equation with an intercept. However, in this equation the intercept with the axis of root dry matter production is only a calculated point. Therefore Flach (1982) preferred the term 'apparent initial start of starch accumulation' (AISS). The slope of the linear equation represents the efficiency of storage root production (ESRP). Boerboom's ESRP does not represent the true distribution of produced dry matter, because the weight of fallen leaves has not been included in the model.

The partitioning process of dry matter over the different plant parts with emphasis on storage roots is reported in this chapter for different cultivars.

7.2 MATERIALS AND METHODS

The experimental designs, site and meteorological conditions have been described in Chapter 3 and supplemented in Chapters 5 and 6.

MCol 1684, MVen 77, MPtr 26 and MCol 22 were the clones used in experiments 1 and 2. In experiment 3, MCol 1684, MMex 59, MCol 638 and MPtr 26 were used.

'Measured' harvest index was calculated as the fraction of the dry matter yield of the standing crop that had been allocated to the storage roots. For calculating the 'real' harvest index the dry weight of the fallen leaves, which were collected weekly, was included in the total dry matter yield.

To study the partitioning of the produced dry matter two models were tested. Two equations relating the dry storage root weight to the total dry matter weight were fitted separately to the harvest data per plot of experiment 1. The first relationship was a non-linear regression equation: $\ln y = A + b . \ln (x - x_0)$, where y = dry storage root yield, x_0 = the total dry matter yield at which the storage roots were apparently initiated, x = the total dry matter yield, A = intercept with the y-axis and b = slope of the regression line. In the second relationship a linear regression with an intercept was tested: $\ln y = a + \ln (x - X_0)$. For each plot the values for A, b and x_0 in the first equation and a and X_0 in the second equation were calculated. Also, the variance, being $s^2 =$

$$= \sum_{1}^{N} \{\ln y - (\widehat{\ln y})^2\}(N - k),$$

was estimated for each plot, to fit the regression equations. N = the number of harvests and k = the number of parameters, being 3 for the first model tested and 2 in the case where b is assumed to have a value of 1.0.

For experiments 2 and 3 only the second model $\ln y = a + \ln (x - X_0)$, was fitted to the harvest data.

7.3 RESULTS

7.3.1 Yields of total dry matter and root dry matter

Changes in the total dry matter yield are shown for all three experiments in Chapter 5.

In experiment 1 no storage roots (roots with a diameter of more than 1.0 cm) were found at 62 DAP. At 123 DAP all sample plants had storage roots. None of the four clones showed significant changes in the number of storage roots per m² during the growth period from 123 to 362 DAP. On all sampling dates the number of storage roots of MCol 22 was significantly higher ($p = 0.05$) than that of MCol 1684 (Fig. 20). Until 241 DAP no significant clonal differences in yield of dry storage roots were observed (Fig. 9). Maximum root growth rate was found for the period from 123 to 185 DAP, being 77 (range 71-89) kg root dry matter$\cdot$ha$^{-1}\cdot$day^{-1}. From 185 to 304 DAP the yield of dry storage roots changed more gradually. MVen 77 had a significantly lower yield of dry storage roots at 304 and 362 DAP than the other clones. Yield of dry storage roots yield at 185 DAP is shown in Table 13.

Dry storage root yield at 178 DAP is also shown in Table 13 for the clones used in experiment 2. On that date there were no significant clonal differences in yield of dry storage roots yield. Yield of dry storage roots was, however, considerably lower than for the same clones found in experiment 1.

In experiment 3, MCol 1684 and MPtr 26 yielded significantly more than MMex 59 and MCol 638 (Fig. 9). Yield of dry storage roots at 185 DAP is shown in Table 13.

Table 13 Yield of dry storage roots (t.ha^{-1}) of different cassava clones circa six months after planting

clone	experiment 1 (185 DAP)	experiment 2 (178 DAP)	experiment 3 (185 DAP)
MCol 1684	8.3	4.7	6.5
MVen 77	6.8	5.7	
MPtr 26	7.7	5.6	6.6
MCol 22	7.4	4.9	
MMex 59			2.2
MCol 638			3.5
F-test	n.s.	n.s.	**
LSD (p=0.05)			2.0

7.3.2 Partitioning of dry matter

Fig. 21 shows the distribution of dry matter among the plant parts as a percentage of the total dry matter produced, for the clones in experiment 1. The dry matter production shown in the figure includes the dry weight of leaves that fell during the growth period. Later in the growth period, at 362 DAP, the dry weight of the fallen leaves

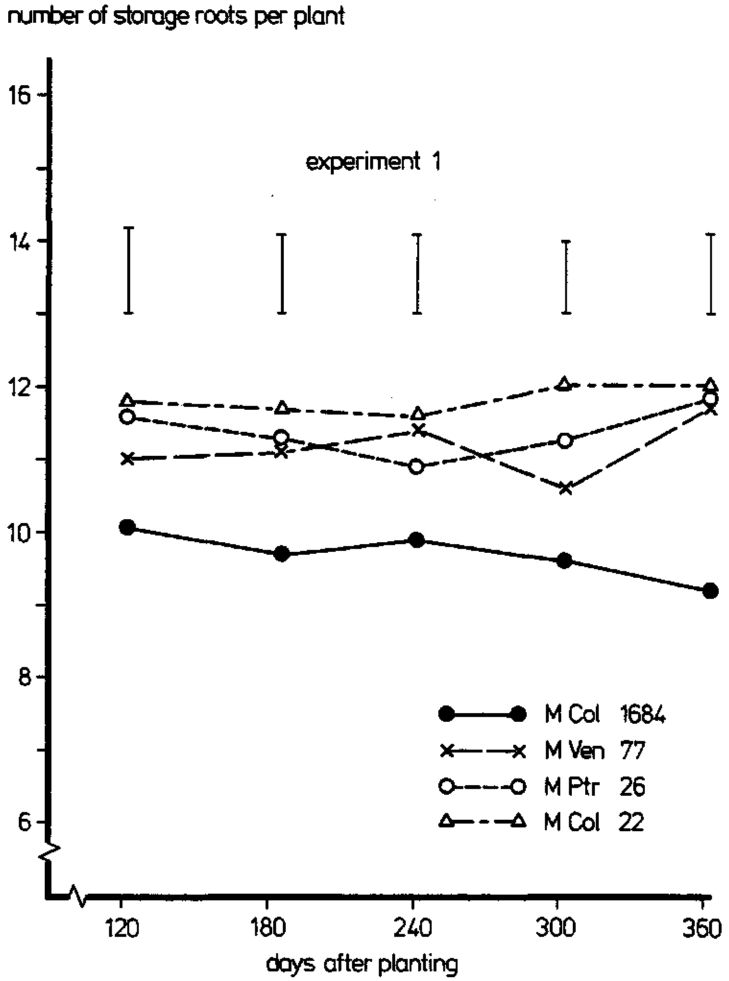

Fig. 20 Number of storage roots per cassava plant at different times after planting. Experiment 1.

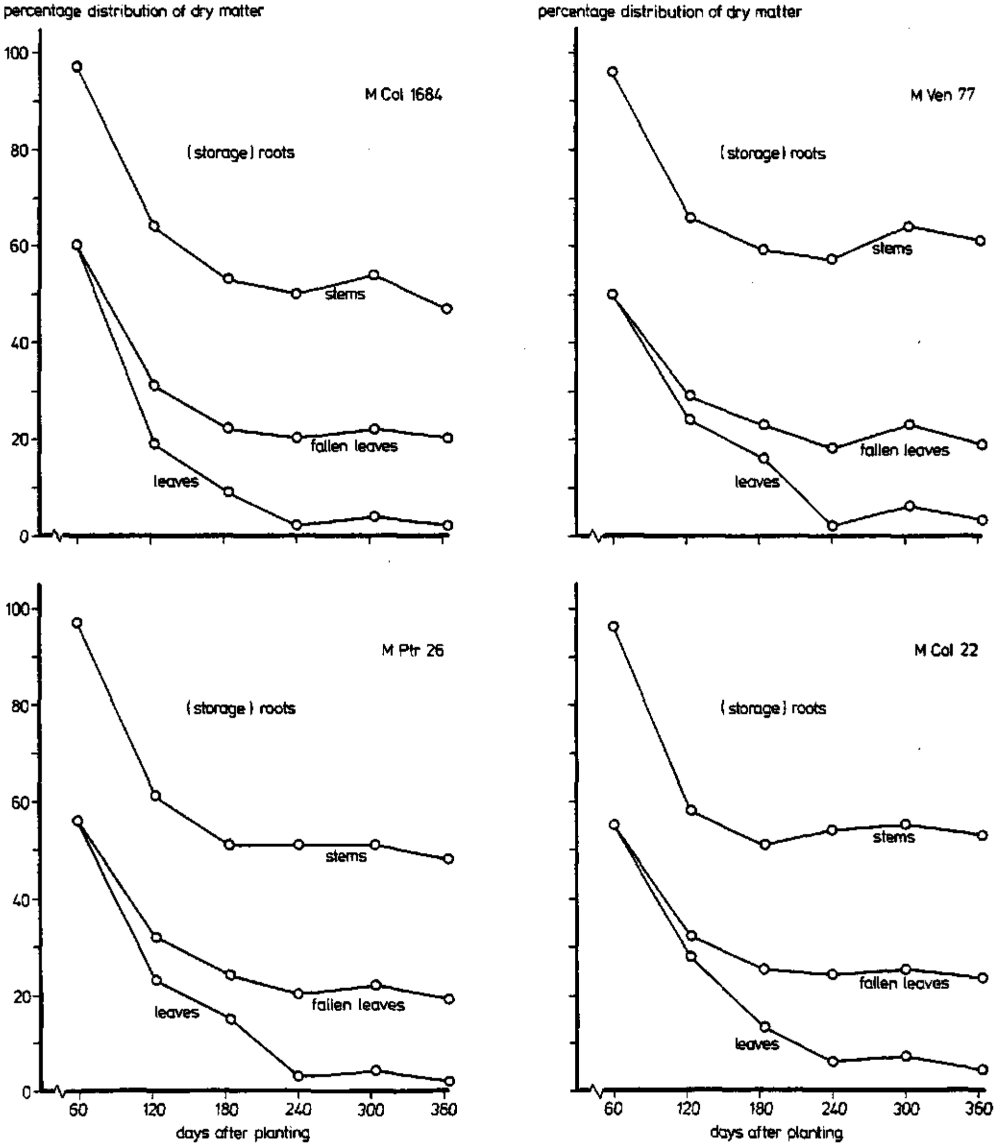

Fig. 21 Percentage distribution of dry matter over storage roots, stems and leaves (including fallen leaves) for four cassava clones. Experiment 1.

made up an appreciable percentage of the total dry matter yield, varying from 15.5% to 18.6%, depending on the clone. Plots of the 'real' harvest index against the 'measured' harvest index are shown in Fig. 22: the difference between these indices is substantial, particularly in the older plants (i.e. more than 8 months). The 'measured' harvest index overestimates the 'real' part of the total dry matter production that has been stored in the storage roots. At 362 DAP the differences between 'real' and 'measured' harvest index were on average, 0.10, with a range of 0.07 to 0.11.

In Table 14, the values for A, b and x_0 in the non-linear regression equation $\ln y = A + b \ln (x - x_0)$ and the values a and X_0 in the equation $\ln y = a + \ln (x - X_0)$ are shown for each plot of experiment 1, together with the estimates of the variance (s^2). The standard errors for a and X_0 were much smaller in the model where b was assumed to have a value of 1.0, whereas the estimates of the variance for the different plots were not substantially or systematically higher for the model $\ln y = a + \ln (x - X_0)$. Therefore, the regression equation $\ln y = a + \ln (x - X_0)$ is more suitable for testing differences in cultivars for the efficiency of storage root production and for the plant weight at which the storage root production apparently started. If this logarithmic equation is transformed to a linear equation, the e^a values (the efficiency of storage root production (ESRP)) are obtained. The ESRP values are presented in Table 15 for the plots of experiment 1, together with the values of X_0, the crop weight at which storage root production apparently started (AISS values). Analysis of variance of ESRP and AISS values shows that MCol 1684 and MPtr 26 had the highest ESRP values; they were significantly higher than the value of 0.43 found for MVen 77. Also in this experiment significant clonal differences for AISS were found; they were lowest for MCol 22 (1.0 $t \cdot ha^{-1}$). In experiment 2, MCol 22 also had the lowest AISS value (Table 16). In experiment 3, MMex 59 had the highest AISS value and the lowest ESRP. The ESRP values of MMex 59 and MCol 638 were 0.32 and 0.37 respectively. Relatively large differences in ESPR and AISS values were found for the same clones in different experiments (Tables 15 and 16).

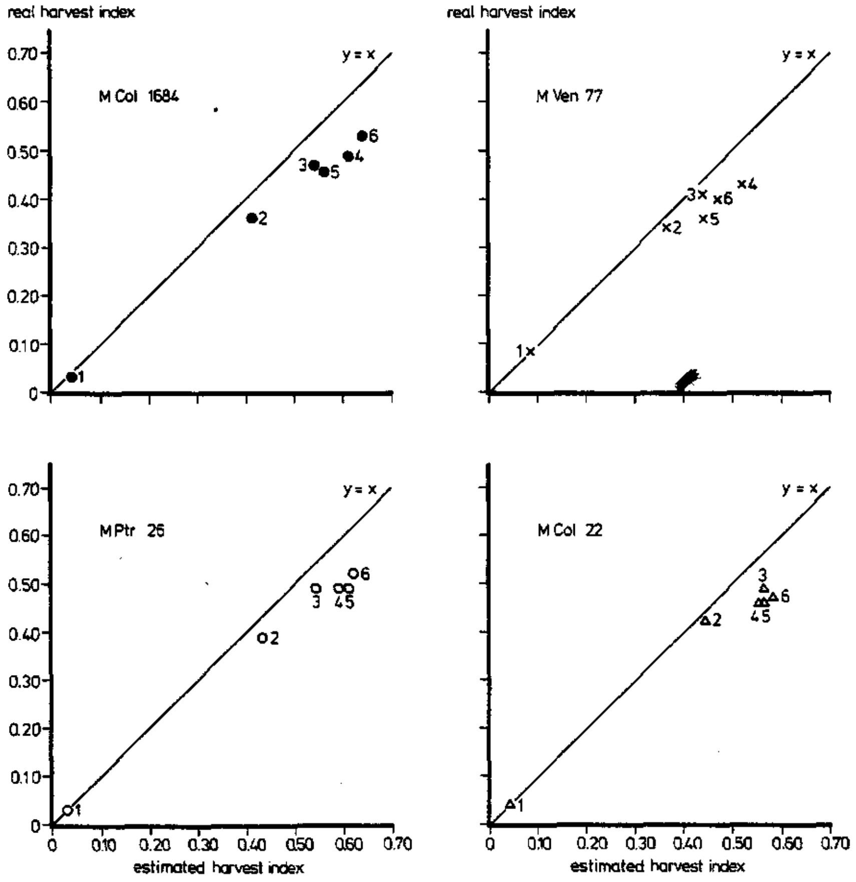

Fig. 22 Relationships between 'measured' and 'real' harvest indices for four cassava clones. Experiment 1.

Table 14 Parameters for two equations describing the relationship between the yield of dry storage roots and the total dry matter yield of cassava. Experiment 1. Number of harvests = 5.[1]

plot		equation											
cultivar	replication	$\ln y = A + b \ln (x - x_0)$							$\ln y = a + \ln (x - X_0)$				
		A	±S.E.	b	±S.E.	x_0	±S.E.	s^2	a	±S.E.	X_0	±S.E.	s^2
MCol 1684	1	-0.149	1.10	0.86	0.34	3.67	2.73	0.006927	-0.60	0.05	2.55	0.46	0.004916
	2	-0.178	0.96	0.90	0.28	4.23	2.85	0.004621	-0.54	0.05	3.17	0.51	0.003251
	3	-1.155	1.25	1.17	0.34	0.92	3.60	0.002498	-0.53	0.03	2.69	0.35	0.001908
	4	-1.029	1.36	1.11	0.38	1.86	3.71	0.007107	-0.65	0.05	2.85	0.49	0.004921
MVen 77	1	-0.908	1.70	1.01	0.50	2.08	4.33	0.010324	-0.89	0.06	2.13	0.57	0.006883
	2	0.560	1.33	0.56	0.43	5.41	4.60	0.022549	-0.96	0.14	-0.11	2.04	0.016970
	3	0.289	0.52	0.71	0.16	5.21	1.52	0.002120	-0.69	0.05	2.28	0.53	0.002904
	4	1.092	0.41	0.39	0.14	6.85	0.82	0.007915	-0.88	0.10	1.17	1.15	0.012282
MPtr 26	1	0.535	0.41	0.67	0.14	5.84	0.79	0.004107	-0.48	0.05	3.70	0.35	0.004661
	2	-3.842	1.46	1.80	0.35	-8.50	4.38	0.001482	-0.75	0.05	0.87	0.60	0.003279
	3	-1.029	0.46	1.16	0.13	0.72	1.27	0.000519	-0.49	0.02	2.21	0.21	0.000662
	4	-0.163	0.84	0.88	0.25	3.47	2.46	0.002736	-0.60	0.04	2.20	0.41	0.002014
MCol 22	1	0.108	0.59	0.77	0.18	3.73	1.71	0.002455	-0.69	0.04	1.42	0.46	0.002564
	2	0.674	0.27	0.60	0.09	4.99	0.71	0.001251	-0.66	0.06	1.12	0.69	0.005472
	3	-0.058	0.89	0.79	0.26	2.81	2.96	0.006654	-0.79	0.07	0.34	0.82	0.005392
	4	-0.755	0.80	1.01	0.22	0.77	2.56	0.001665	-0.71	0.03	0.92	0.34	0.001112

[1] for explanation of the different models: see text

Table 15 Efficiency of storage root production (e^a = ESRP values) and crop weight at which storage root production apparently started (X_0 = AISS-values) of four cassava clones. Experiment 1.
Model: $y = e^a (x - X_0)$

cultivar	replication				
	I	II	III	IV	average
ESRP					
MCol 1684	0.55	0.58	0.59	0.52	0.56
MVen 77	0.41	0.38	0.50	0.41	0.43
MPtr 26	0.62	0.47	0.61	0.55	0.56
MCol 22	0.50	0.52	0.45	0.49	0.49
F-test					**
LSD (p= 0.05)					0.078
AISS ($t \cdot ha^{-1}$)					
MCol 1684	2.6	3.2	2.7	2.9	2.8
MVen 77	2.1	-0.1	2.3	1.2	1.4
MPtr 26	3.7	0.9	2.2	2.2	2.2
MCol 22	1.4	1.1	0.3	0.9	1.0
F-test					*
LSD (p=0.05)					1.27

Table 16 Efficiency of storage root production (ESRP (= e^a)) and the apparent crop weight at which storage roots were initiated (AISS (= X_0)) in six cassava clones. Experiments 2 and 3.

clone	AISS ($t \cdot ha^{-1}$)		ESRP	
	experiment 2	experiment 3	experiment 2	experiment 3
MCol 1684	2.3	2.7	0.49	0.64
MVen 77	2.5		0.53	
MPtr 26	2.5	3.3	0.56	0.63
MCol 22	1.5		0.66	
MMex 59		3.6		0.32
MCol 638		1.9		0.37
F-test	**	**	**	**
LSD (p=0.05)	0.33	0.77	0.081	0.062

The relationships between the total dry matter yield and the leaf yield and the stem yield respectively of the clones used in experiment 2 were also studied. Fig. 23abcd shows the partitioning of dry

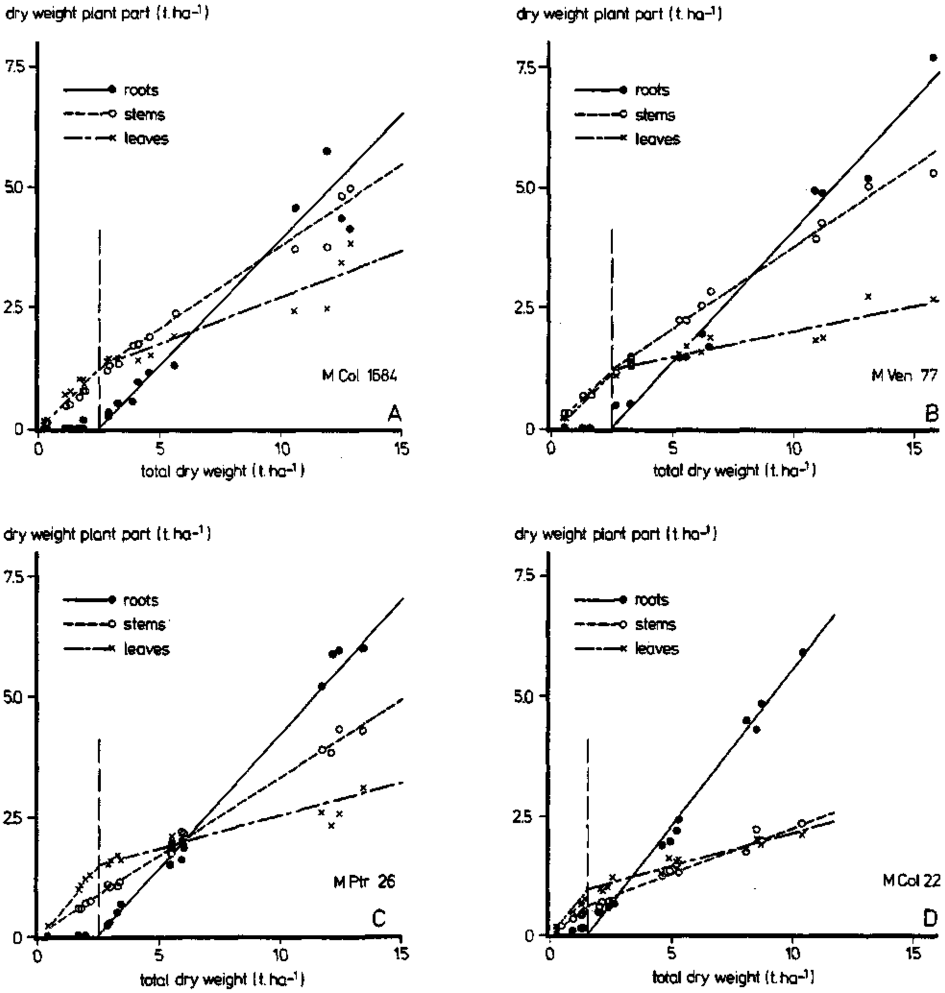

Fig. 23 Relationships between total dry weight and dry weight of plant parts of four cassava clones during the period from planting until apparent storage root initiation, and during the storage root filling period. Experiment 2.

matter over the leaves, stems and roots from the moment that the storage roots were apparently initiated. Therefore in all cases the general regression equation ln y = a + ln $(x - X_0)$ was fitted to the data.

Fig. 23abcd also shows the partitioning of dry matter during the period before the initiation of the storage roots. The lines were fitted by eye. From the moment that the storage roots were apparently initiated a lower percentage of produced dry matter was allocated to the leaves and the stem or stems.

7.4 DISCUSSION AND CONCLUSIONS

Phase until the apparent initiation of storage roots

The formation of storage roots began some time between 73 and 88 DAP for the clones used in experiment 2 and between 62 and 123 DAP for these same clones in experiment 1. (A storage root was defined as a root with a diameter of at least 1.0 cm). Wholey and Cock (1974) reported that several clones of the CIAT germ plasm bank already had storage roots two months after planting. In that study, however, the definition of a storage root was not specified. The factors causing storage root initation in cassava are not yet well understood. The factors that cause tuber initiation in other plants e.g. potato are not understood either (Lovell and Booth, 1967). In cassava no clear changes in plant growth habit occur in the above-ground parts during the period when storage roots are apparently initiated (Chapter 6). Significant clonal differences in plant weight existed at the apparent start of storage root formation (Tables 15 and 16). De Bruijn (1982) reported significant differences in the plant weight at which storage root formation apparently started for cassava cultivated under widely differing environmental conditions. The scion as well as the stock of different cassava clones appears to influence the plant weight at which storage root formation apparently starts (Veltkamp, 1985). Krochmal and Samuels (1970) found that high nitrogen levels promoted top growth and prevented storage root formation. In Chapter 8 the effects of daylength on phenomena such as the initiation of storage roots and the partitioning of dry matter are discussed.

During the period from planting the cuttings until the apparent initiation of storage roots it seems the pattern of partitioning of dry matter over the plant parts remains constant (Fig. 23abcd). A similar dry matter distribution pattern has also been reported for potato (Wittenrood, 1958) and sugarbeet (Van der Sande Bakhuysen, 1950).

Number of storage roots per plant

In experiment 1 it was shown that by 123 DAP the storage roots had reached their final number (Fig. 20). These results are similar to those obtained by other authors (Hunt et al., 1977). On the other hand, in a few clones, Wholey and Cock (1974) observed an increase of the number of storage roots up to seven months after planting. They did not mention, however, whether the increase was statistically significant. This also holds for data presented by Soetono et al. (1982), who observed an increase until the last harvest at 60 weeks after planting. De Bruijn (1982) observed that the number of storage roots increased slightly but significantly with time, the most important increase taking place between 12 and 15 months. Cours (1951) also reported an increase in the number of storage roots for one-year-old plants after a cold, dry season with low growth activity, at the onset of a second period of root filling.

The factors influencing the number of storage roots of cassava are not well understood. Orioli et al. (1967) observed a positive effect of fertilization on the number of storage roots. Environmental conditions significantly influenced the number of storage roots in a study by De Bruijn (1982). Comparing Mukibat cassava (*Manihot glaziovii* grafted onto ordinary cassava) with ordinary cassava, Soetono et al. (1982) found that, in general, Mukibat cassava had slightly more storage roots than ordinary cassava. In dense populations, plants have fewer storage roots per plant than at lower plant densities (Enyi, 1972a; Cock et al., 1977; Soetono et al., 1982). The number of shoots per plant was found to influence the number of storage roots per plant, there being more storage roots when plants had more than one shoot (Enyi, 1972ac).

Harvest index

Data on harvest index are shown in Fig. 21 for experiment 1. Boerboom (1978a) stated that with increasing total dry weight the values of the relation between the total dry weight and the harvest index approach the values of the efficiency of storage root production, as also recently shown by De Bruijn (1982), who concluded that this is mathematically evident because of the decreasing relative importance of the AISS.

Usually, researchers presenting data on harvest index record the ratio of weight of storage roots to the weight of the standing crop (e.g. Kawano et al., 1978; Cock, 1976; De Bruijn, 1982), and ignore the weight of the leaves shed during the growth period. As mentioned, for experiment 1 the weight of the fallen leaves at 362 DAP amounted to 15.5% to 18.6%, of the total dry matter yield, depending on the clone.

The difference between the 'real' and the 'measured' harvest indices increased with plant age (Fig. 22), because the amount of fallen leaves increased. The relationship between the 'real' and 'measured' harvest index is not consistent and there is not a systematic bias between the two, at least not for plants of approximately 10 to 12 months old, as reported by CIAT (1978). Therefore, for realistic estimations of the harvest index or the efficiency of storage root production, it is necessary to include the weight of the fallen leaves too. This implies that the harvest index will be based on a dry weight basis. The 'measured' harvest indices reported in the literature are usually calculated from fresh weight (e.g. Kawano et al., 1978), and therefore are again removed from reality, because of the differences in dry matter content of the different plant parts.

Partitioning of dry matter after the initiation of storage roots

The partitioning of dry matter during the storage root filling period for the experiments reported in this study could be adequately described by the linear model $\ln y = a + \ln (x - X_0)$ or equivalently $y = e^a (x - X_0)$. For each field the efficiency of storage root production (e^a)(ESRP) and the plant weight at which storage roots were apparently initiated (X_0) could be calculated, enabling a clonal selection to be made for ESRP for each statistical design chosen. Significant clonal differences in ESRP were found (Tables 15 and 16). The ESRP value is largely stock-determined, but a significant scion effect was also found. When used as a scion, cultivars such as MMex 59 and MCol 638, which have LAI values of 4 and more for much of the growth period (Fig. 14) induced lower ESRP values than the less leafy cultivar MCol 1684 (Veltkamp, 1985).

There are several suggestions in the literature that the translocation of assimilates in plants is controlled hormonally: The greater part of the discussion relates to hormones released from sinks (Moorby, 1968). Gifford and Evans (1981) concluded, however, that hormonal influences have not yet been sufficiently defined for generalizations in relation to assimilate partitioning to be made.

8 GROWTH, TOTAL DRY MATTER YIELD AND ITS PARTITIONING IN CASSAVA AT DIFFERENT DAYLENGTHS

8.1 INTRODUCTION

Cassava is cultivated between latitudes 30°N and 30°S. The most northerly regions where cassava is cultivated are the coastal area of the southern states of the USA (Tan and Bertrand, 1972) and the southernmost provinces of China (Anonymous, 1979). In the southern hemisphere the most southerly regions where cassava is still of importance are in South America in the provinces of Missiones and, to a lesser extent, Corrientes, in northern Argentina (Henain and Cenoz, 1968), in Africa in the northern part of Natal province in South Africa (Daphne, 1980), while in Australia cassava is cultivated on a limited scale in Queensland, at least as far as 26°S (Hammer, 1980). Most of the area planted with cassava, however, lies between 15°N and 15°S (Cock and Rosas, 1975). Jones (1959) suggested that this limited distribution was related to negative effects of daylength on the growth and storage root yield of cassava.

Literature on the effects of daylength on growth and storage root yield of cassava is limited (Bolhuis, 1966; Lowe et al., 1976; Indira and Ramanujam, 1979; Keating, 1982).

At the Centro Internacional de Agricultura Tropical (CIAT) in Cali, Colombia, preliminary research under field conditions on the effects of daylength on storage root yield and harvest index of cassava was started in 1972. An extensive study of the effects of daylength on growth and on total and storage root dry matter yields was conducted in 1980-1981. Two similar experiments were carried out in a greenhouse at the Department of Tropical Crops of the Agricultural University in Wageningen, The Netherlands. The results of these investigations are reported in this chapter.

8.2 MATERIALS AND METHODS

Three experiments were conducted. The first one (experiment 4) was a field experiment and was carried out on the CIAT experimental farm in Palmira, near Cali (Colombia). Meteorological data and some general experimental procedures have been described in Chapter 3. The other two experiments (experiments 5 and 6) were conducted in a greenhouse at the Department of Tropical Crops, Agricultural University in Wageningen, The Netherlands.

Experiment 4 Three clones, MCol 1684, MPtr 26 and MCol 22, were grown under two daylengths, the natural daylength at CIAT and a daylength of 16 h that was held constant during the whole growth period. Data on the natural daylength at CIAT were calculated from data presented by Francis (1972) and are shown in Fig. 24.

For this experiment an area was divided into two blocks, each 30 m × 38 m, and separated by a 15 m-wide strip. Fig. 25 shows a general view of a part of the experimental area. In one block an installation was constructed to prolong the natural daylength. Two rows of concrete poles with a height of 5-6 m above the soil level were placed 38 m apart. Each row contained 7 poles, spaced 5 m apart. Wires were strung across the field from pole to pole. On the wires 300 W incandescent bulbs were hung at 5 m intervals in a triangular pattern. In all, there were 53 light bulbs on this part of the experimental area. The distance between the light bulbs and the soil level at planting was about 2 m. With this distance between the bulbs and the soil level a minimum light intensity of 25 lux (measured with a Toshiba SPI-7 photocell illuminometer) was reached over the whole block. This is substantially more than the minimum light intensity of 10 lux required for a daylength effect on cassava (Cock, unpublished results). During the first six months of the growth period a distance of about 2 m was maintained between the light bulbs and the tops of the plants, by raising the wires on which the bulbs were strung. Because of large clonal differences in plant height this distance could not be fully maintained above the taller clones in the last part of the growth period.

The illuminated block and the control block were 15 m apart: at that distance the light intensity was practically zero at soil level in the first row of the control block. For added protection six rows of cassava and a 2 m-wide strip of tall maize were planted between the experimental blocks at the same time as the cassava, to prevent the artificial light from influencing the plants of the control block

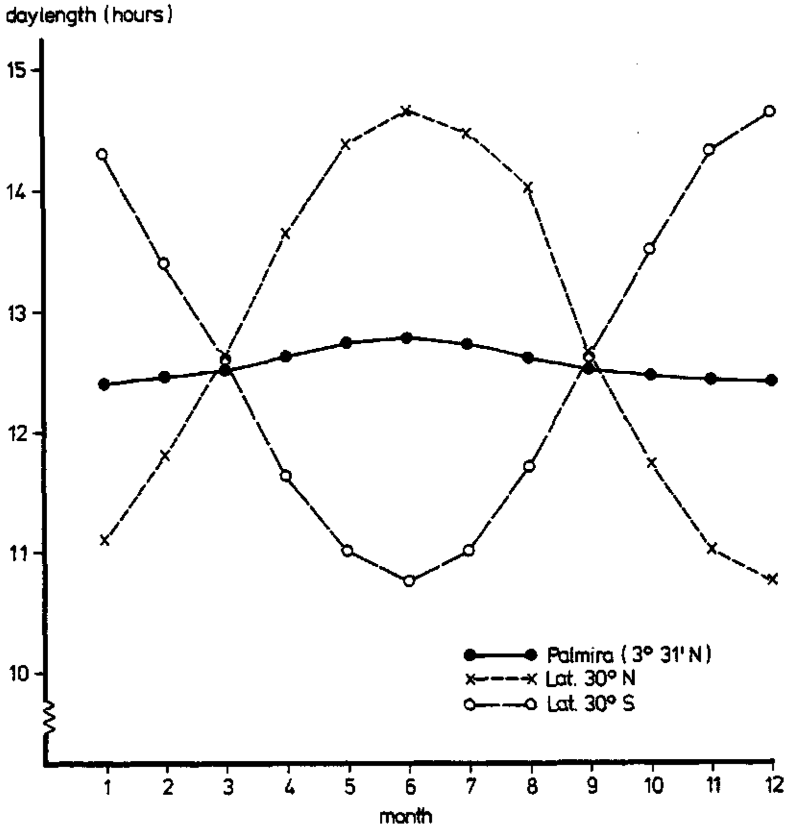

Fig. 24 Daylength at CIAT experimental station in Palmira, near Cali, Colombia (Lat. 3°31'N), and at Lat. 30°N and 30°S, with a minimum intensity of 21.5 lux (in hours) (according to Francis, 1972). Daylengths on the 22nd of each month 1,........,12 = months, January to December.

Fig. 25 General view of the experimental area, with plants grown at natural daylength on the left.

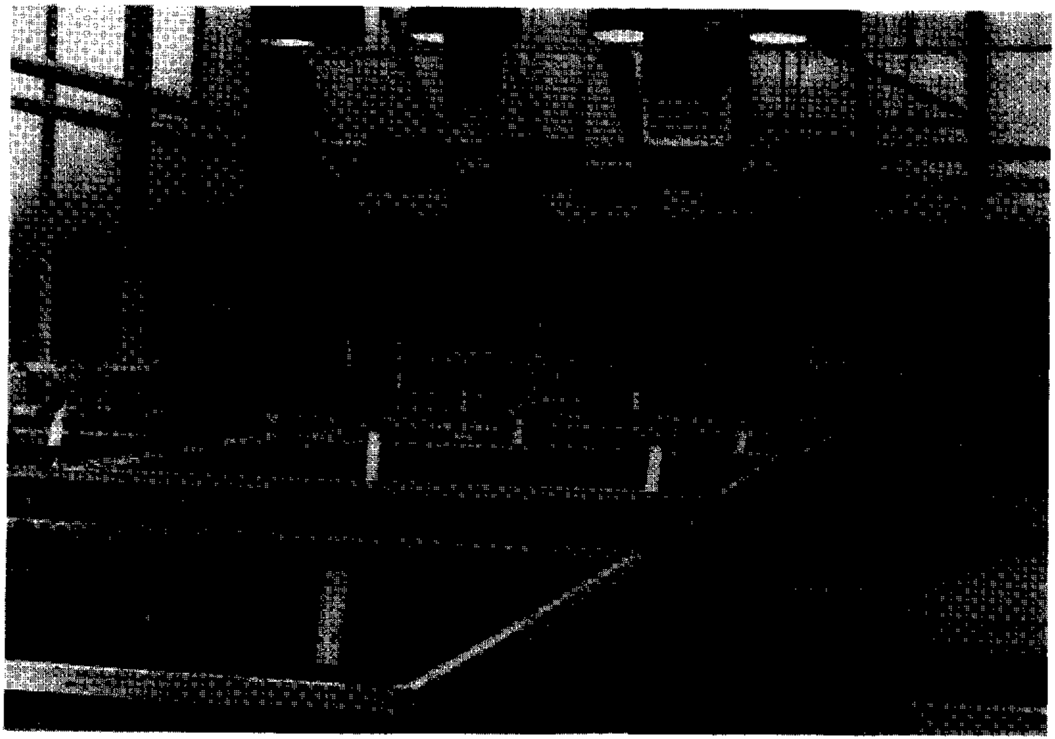

Fig. 26 A view of part of the experimental site in the greenhouse.

with the natural daylength.

Planting was on 24 June 1980. Plot size per clone per daylength and per replication within each block was 7 m × 15 m. Clones were replicated three times per plot. There were three harvests. Six plants per plot were sampled on the harvests at 86 and 177 DAP and nine on the last harvest at 272 DAP. A preliminary harvest consisting of three plants per clone and three replications was done at 51 DAP.

At 78 and 123 DAP, leaf blades that had just expanded fully were collected (one per sample plant) for diagnosis of the nutritional status of the crop. Samples were analysed for N, P, K, Ca and Mg.

At 52, 83, 108, 133, 159, 176, 205, 238 and 265 DAP, plant height, number of newly formed nodes per apex, number of nodes to different branch levels, and the number of active apices were measured. These measurements were only carried out on the sample plants that had been earmarked for the final harvest. Individual leaf size of the youngest fully expanded leaves was calculated at regular intervals (approximately once a fortnight), according to a method described in Chapter 3. To ascertain individual leaf life during the growth period, young leaves about 1 cm long (one per sample plant) were tagged with a label also approximately once every 14 days. Fallen tagged leaves were collected weekly for calculating the leaf life. Light measurements were carried out at 83, 105, 127, 157, 176, 204, 237 and 272 DAP. LAI was calculated on the harvest dates (51, 86, 177 and 272 DAP). On harvesting plants were divided into leaves, stems and roots (including storage roots), and bulked per plot. Dry weights of all plant parts were determined. Weekly, fallen leaves were collected, dried and weighed.

To study the distribution of dry matter the regression equation $\ln y = a + \ln (x - X_0)$ $[y = e^a (x - X_0)]$ was used (see Chapter 7). In this equation e^a represents the efficiency of storage root production (ESRP) and X_0 the crop weight at which the storage root production apparently started (AISS).

*Experiment 5** First greenhouse experiment. In this experiment the effects of a daylength of 11 h or 14 h on the growth and production of four cassava clones, MCol 1684, MPtr 26, MCol 22 and Llanera, were studied. Plants were grown in a greenhouse, in trucks on rails, so they could be transferred into and out of dark sheds. At both daylengths, plants were grown under natural light conditions for 9 hours per day, supplemented with 2 or 5 hours of low intensity light from luminous tubes and incandescent bulbs in the dark sheds. The equipment for supplementary light was operated by electric time switches. Each truck (1.8 m x 1.6 m) was divided into four by wooden partitions, and one cutting was planted per compartment in a mixture of sand and humus. A view of a part of the experimental site is shown in Fig. 26.

Cuttings were planted on 25 October 1980. Because of the low light intensity in the winter season the daily 9 h period of natural daylight was boosted with 'daylight' lamps. Harvesting took place on 2 March 1981, 127 DAP, because the plants of some clones had then grown so high that the daily transfer to and from the dark sheds caused insuperable problems. Average weekly temperature varied from 24° to 26°C during the day and from 21° to 23°C during the night.

Observations and measurements of plant height, number of living leaves per apex, number of fallen leaves per apex, occurrence of branching and number of apices were carried out. At harvest the plants were divided into leaves, stems and roots including storage roots. Total leaf area per plant was determined by a Licor automatic leaf area meter. To ascertain the dry weights of the different plant parts the whole root fraction was dried, as well as subsamples of the other parts, at 105°C in a forced-draught oven.

Experiment 6 Second greenhouse experiment. This experiment was carried out in the same trucks as described for experiment 5. The experimental design and procedure were the same as in experiment 5, except that Llanera was replaced by Betawi, a clone that had been used by Bolhuis (1966) in daylength studies. Four cuttings from each clone were planted on 23 March 1981. They were harvested in

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* This experiment was carried out by Mr. F. van den Bosch, as partial fulfilment for a 'doctoral' (M.Sc.) study on tropical crop husbandry

the period 27-30 July 1981, i.e. at circa 127 DAP; thus the duration of growth of these plants was the same as that of plants in experiment 5. During daytime the plants were not supplemented with additional light, because this experiment was conducted in the summer season at a much higher radiation level. Average weekly temperature varied from 25° to 29°C during the day period and from 21° to 24°C during the dark period.

Measurements on plant height, leaf formation rate per apex, number of fallen leaves per apex, number of apices, branching pattern and leaf size were carried out. Leaf size was measured using the technique described in Chapter 3. Young leaves (about 1 cm long) were tagged and the central lobe length was measured 14 days after tagging. At final harvest dry plants were divided into leaves, stems, cuttings and storage roots, and then dried before being weighed.

8.3 RESULTS

Experiment 4 Plants germinated well and showed uniform initial growth. No visible differences were observed in the initial growth of the plants in the two main blocks under natural daylength and under 16 h daylength. By 52 days after planting the plants experiencing 16 h days were taller than those experiencing the natural days. These differences continued to increase until final harvest (Fig. 27). LAI was similar in natural and 16 h treatments at 51 DAP and 86 DAP but thereafter was greater in the plants grown under 16 h days (Fig. 28). The increased LAI under 16 h days could not have resulted from changes in leaf size because this parameter was not significantly different between light treatments at any harvest.

For all clones the number of leaves formed per apex was similar in natural and 16 h days up to about 150 days after planting. Thereafter the number of leaves per apex was greater under 16 h days in MPtr 26 and MCol 1684, but hardly any effect of 16 h daylength was found in MCol 22 (Fig. 29). The total number of leaves formed per plant depends not only on leaf formation rate per apex, but also on apex number per plant, i.e. on branching pattern. MCol 22 and MPtr 26 branched earlier under 16 h days (Table 17), but the number of branches was the same in natural and 16 h days at the first branch level (Table 17). The interval between first and second

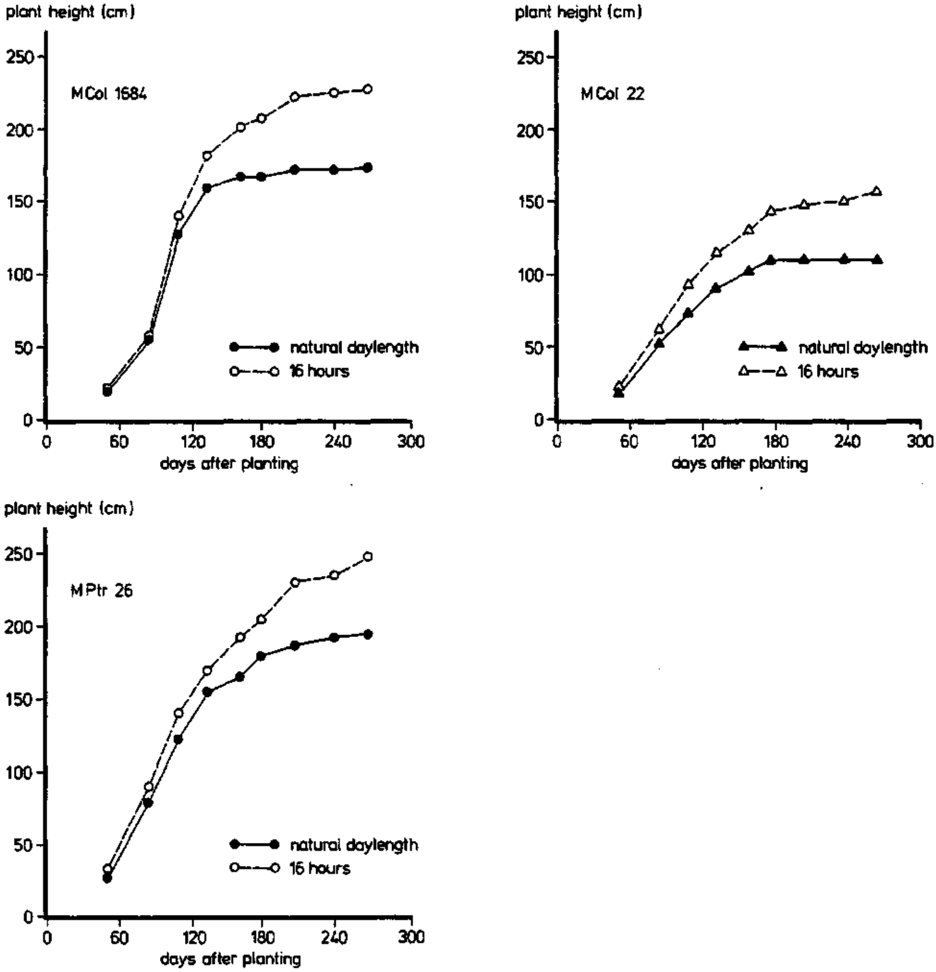

Fig. 27 Effect of daylength on plant height of three cassava clones at different times after planting.

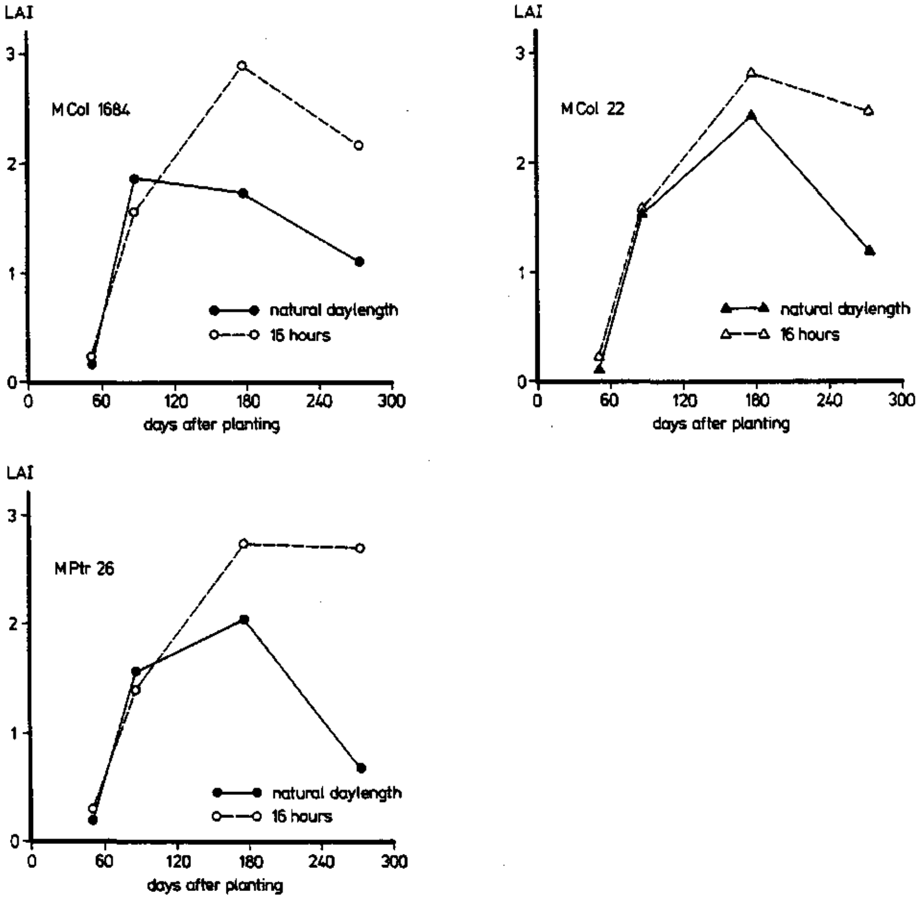

Fig. 28 Effect of daylength on LAI of three cassava clones at different times after planting.

branching was greater under natural than under 16 h days, both in terms of days and of nodes (Table 17). At the final harvest, total apex number was much greater in all clones under 16 h days (Fig. 29).

There was a tendency for leaf life to be longer under short days. The difference was smallest in MCol 22 (Fig. 29), and most marked in MCol 1684.

The percentage interception of PAR reflected the differences in LAI, plants grown under 16 h days having a greater interception of PAR (Fig. 30). At 272 DAP there was a slight positive effect of long days on total dry weight. The total dry weight was closely related to the PAR intercepted (Fig. 32).

No storage roots were found at 51 DAP, but all clones in both treatments had storage roots at 86 DAP. Fig. 31 shows the patterns of total dry matter yield and root dry matter yield at different times after planting at natural and 16 h daylength. The yield of dry storage roots was greater at final harvest (272 DAP) under natural days in all clones (Table 18). The percentage decrease in yield under long days was greatest in MCol 1684 (47%) and least in MCol 22 (13%). The yield differences must have mainly resulted from a decreased efficiency of storage root production (ESRP) under 16 h days, because total dry matter was greater under 16 h days and no daylength effect was found for the crop weight at which the starch accumulation in the roots apparently started (AISS values) (Table 18).

Table 17 Effects of daylength on the branching patterns of three cassava clones

	MCol 1684		MCol 22		MPtr 26	
	ND*	16 h	ND	16 h	ND	16 h
Days from planting to first branch level	40	39	62	48	121	104
Days from first to second branch level	40	36	69	44	76	71
Nodes from planting to first branch level	16.0	16.3	27.8	19.0	85.6	70.0
Nodes from first to second branch level	24.9	22.8	37.7	28.4	34.5	48.5
Branches per branching point at first branch level	2.1	2.2	2.4	2.2	2.9	3.0
Branches per branching point at second branch level	2.6	2.7	2.3	2.7	2.6	2.8

* ND = natural daylength; 16 h = daylength of 16 hours

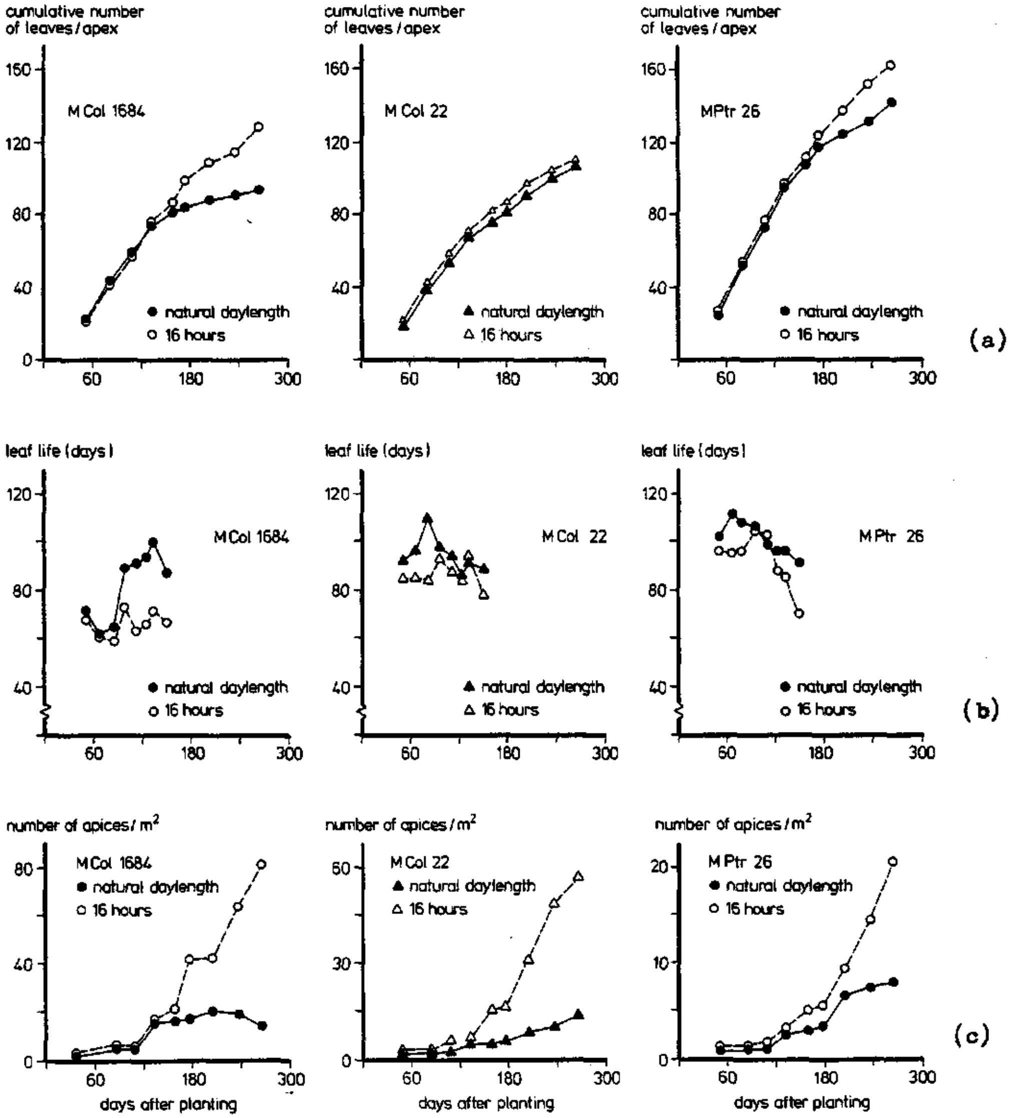

Fig. 29 Effect of daylength on cumulative number of leaves formed per apex (a), leaf life (b) and number of apices per m^2 (c) of three cassava clones at different times after planting.

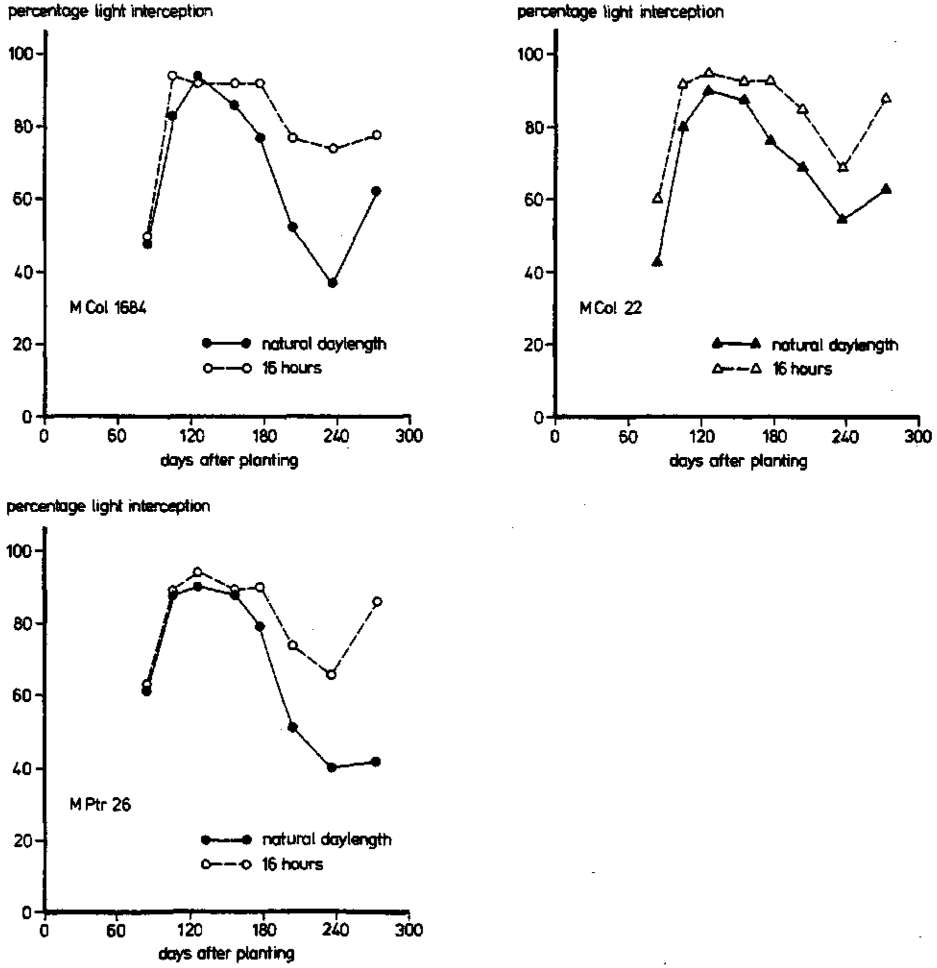

Fig. 30 Percentage of light interception by the foliage of three cassava clones, grown at two daylengths.

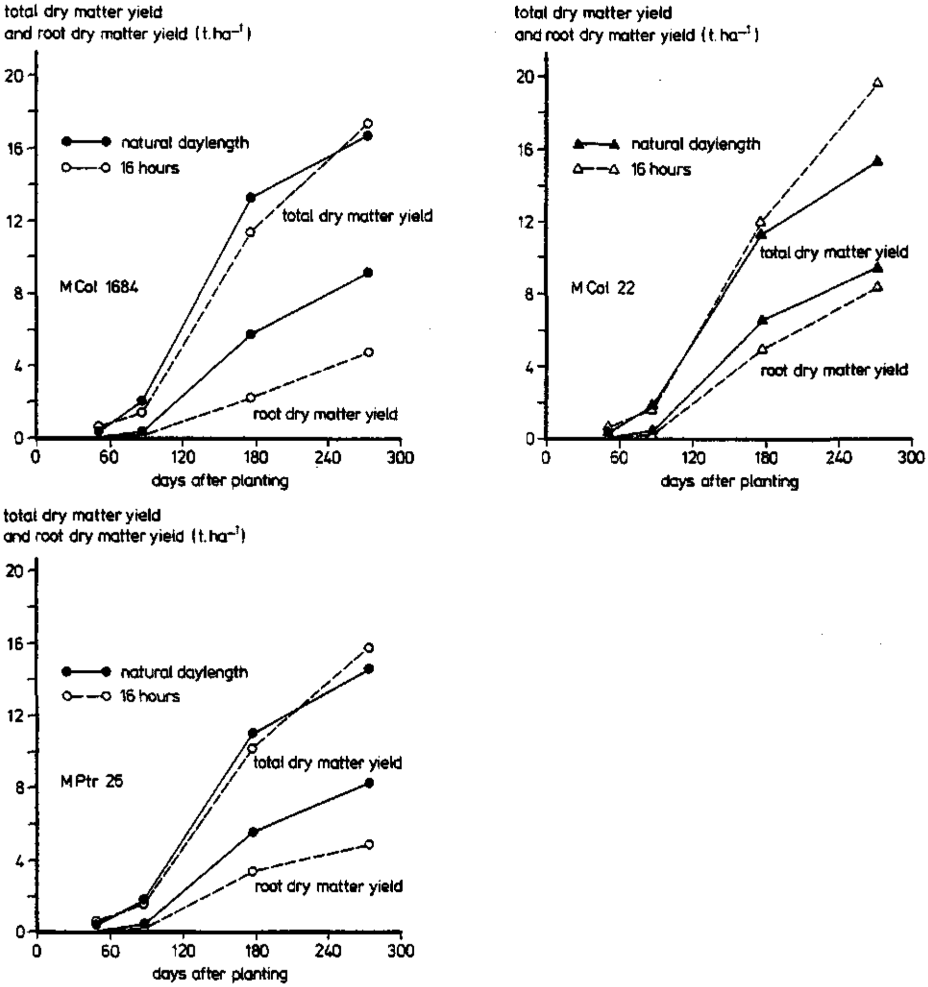

Fig. 31 Total dry matter yield and root dry matter yield of three cassava clones grown at two daylengths, at different times after planting.

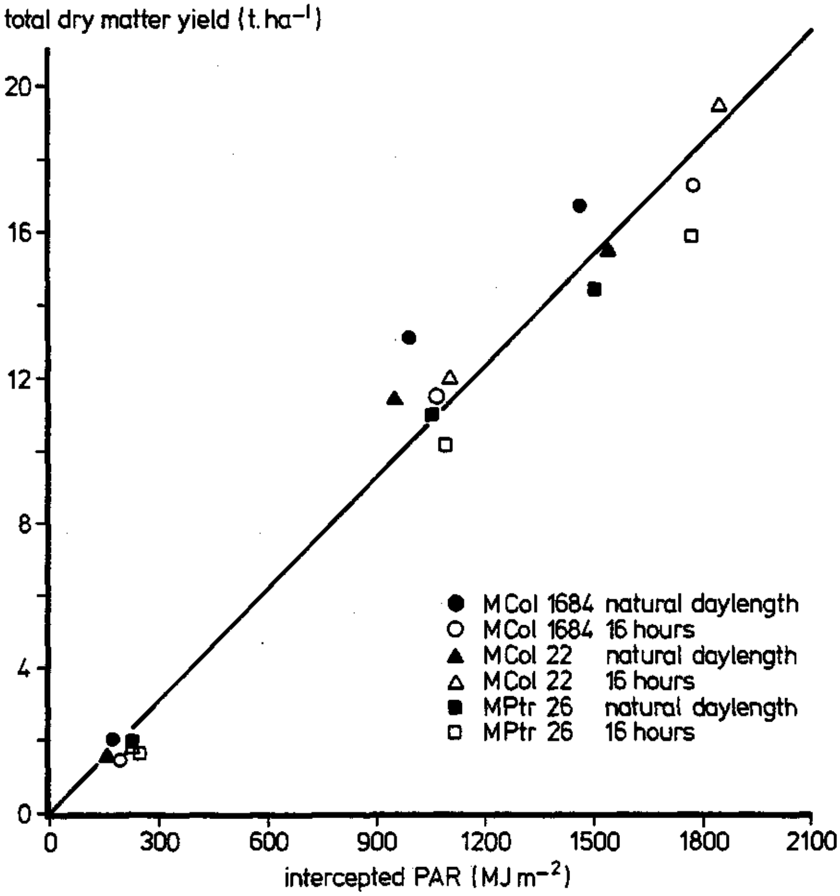

Fig. 32 Relationship between total dry matter yield of three cassava clones, grown at two daylengths, and cumulative intercepted PAR.

Table 18 Dry matter production and distribution 272 days after planting under 16 h and natural daylength

Clone	Daylength	Total dry matter yield ($t \cdot ha^{-1}$)*	Dry weight of storage roots ($t \cdot ha^{-1}$)	ESRP	AISS ($t \cdot ha^{-1}$)
MCol 1684	Natural	16.7	9.1	0.55	1.5
	16 h	17.3	4.6	0.25	1.2
MCol 22	Natural	15.5	9.5	0.65	1.2
	16 h	19.6	8.3	0.45	1.1
MPtr 26	Natural	14.5	8.1	0.60	1.5
	16 h	15.9	4.9	0.36	1.3

* includes the weight of the fallen leaves

Experiment 5 Sprouting was not uniform in this experiment and this resulted in unequal number of plants per treatment. Llanera did not grow well and produced no storage roots in any treatment.

Plants under 14 h days were taller and had greater leaf area per plant than those under 11 h days. MPtr 26 did not branch in this experiment, but the other clones produced more branches under the 14 h treatment (Table 19). There was no significant difference in fallen leaves per apex, thus there were more living leaves per apex under 14 h days.

The total dry weight per plant was consistently greater under 14 h days, whereas storage root weight was greater under 11 h days (Table 19).

Experiment 6 Sprouting and growth were more uniform than in experiment 5. Results of this experiment were similar to those in experiment 5 (Table 20); in this case, however, the total dry weight per plant did not always increase under 14 h days. Storage root yield was again higher for plants grown under a daylength of 11 hours.

Clone Betawi branched significantly earlier under 14 h days. For MCol 1684 and MCol 22 daylength had no significant effect on time to first branching.

Table 19 Plant height, leaf area per plant and its components and total and root dry matter yield under the influence of daylength for four cassava clones at 127 DAP. Experiment 5.

	MCol 1684		MPtr 26		MCol 22		Llanera		CL	D	Cl×D*
	11 h	14 h	11 h	14 h	11 h	14 h	11 h	14 h			
Plant height (cm)	76	171	141	291	106	168	38	105	xxx	xxx	x**
Leaf area per plant (m^2)	0.81	1.95	0.84	2.06	0.64	1.50	0.23	0.56	xxx	xxx	xx
Apices per plant	2.0	3.5	1.0	1.0	1.3	2.7	1.3	3.0	xx	x	n.s.
Living leaves per apex	35.3	40.1	49.0	74.3	36.4	56.8	29.8	31.2	xxx	xxx	x
Fallen leaves per apex	7.5	10.5	5.7	7.0	10.0	8.7	6.0	13.5	n.s.	n.s.	n.s.
Dry weight (g/plant) of											
. Storage roots	20	1	39	15	37	15	-	-	n.s.	x	n.s.
. Unthickened roots	3	8	3	12	3	9	3	5	n.s.	xxx	n.s.
Total dry plant weight (g/plant)	118	167	188	336	166	207	49	71	xxx	xx	n.s.

* Cl = clone; D = daylength

** x = $0.01 < p < 0.05$; xx = $0.001 < p < 0.01$; xxx = $p < 0.001$; n.s. = $p > 0.05$

Table 20 Plant height, leaf area per plant and its components and total and dry storage root weight of four cassava clones at two daylengths. Date of measurement: 127 DAP. Experiment 6.

	MCol 1684		MPtr 26		MCol 22		Betawi		CL	D	Cl×D*
	11 h	14 h	11 h	14 h	11 h	14 h	11 h	14 h			
Plant height (cm)	220	260	239	254	146	210	210	208	xxx	n.s.	n.s.**
Leaf area per plant (m^2)	4.0	5.2	2.2	3.1	1.8	2.5	2.2	3.0	xxx	xx	n.s.
Apices per plant	10.8	15.3	1.0	1.0	2.0	3.5	1.3	5.8	xxx	x	n.s.
Leaves per apex	66	71	84	94	56	70	72	68	xxx	x	x
Fallen leaves per apex	17	17	13	12	8	13	13	16	xxx	n.s.	n.s.
Days to first branch level	50	42	-	-	43	69	>107	43	xxx	n.s.	xx
Total dry weight (g/plant)	578	577	512	459	277	376	293	367	xxx	n.s.	n.s.
Storage root dry weight (g/plant)	179	41	188	45	89	65	57	44	xx	xx	xx

* Cl = clone; D = daylength

** x = $0.01 < p < 0.05$; xx = $0.001 < p < 0.01$; xxx = $p < 0.001$; n.s. = $p > 0.05$

8.4 DISCUSSION AND CONCLUSIONS

With one exception, the results of the experiments reported here support previous reports that yields of cassava storage roots are reduced by long days (Bolhuis, 1966; Mogilner et al., 1967; Lowe et al., 1976; Cock and Rosas, 1975 and Keating, 1982). The exception was MCol 22, in which very little storage roots yield reduction was observed. Therefore the storage root production of this clone can be considered as being largely insensitive to effects of day length.

The yield reduction does not appear to be related to a delay in storage root initiation, but rather to a change in the distribution patterns of dry matter. Keating (1982) suggests that shoot development is affected by photoperiod, whereas root development (as opposed to growth) is not, thus implying that the photoperiod primarily affects shoots, and a secondary response occurs in the roots. Cock et al. (1979) and Tan and Cock (1979a) suggest that top growth has preference over root growth and that root growth occurs after the tops' requirements have been fulfilled. Tan and Cock (1979a) also found that by artifically reducing the number of branches the yield of roots could be increased because dry matter distribution changed within the plant.

In the experiments reported here a major effect of long days was the increase of branching. In all experiments where branching occurred the final number of apices per plant was greater under long days than under short days. Keating (1982) also reports an increase in the number of growing points per plant with daylengths greater than 12 h. This suggests that long photoperiods may increase the growth requirements of the tops and hence reduce the excess carbohydrate available for root growth. Keating (1982), however, reported effects of changes in plant height and leaf area per plant before branching occurred, indicating that not all the difference in assimilate distribution results from changes in branching pattern. In experiments 5 and 6 MPtr 26 did not branch before harvesting at 127 DAP and yet the harvest index was reduced from 0.21 under 11 h days to 0.04 under 14 h days in experiment 5 and, correspondenly, from 0.37 to 0.10 in experiment 6. Leaf area per plant was also greatly increased under long-day conditions. These data clearly demonstrate that daylength as well as having an effect on branching also affects dry matter distribution.

It may also be that changes in the distribution pattern of the dry matter produced by plants grown at different daylengths are hormonally controlled. Spraying cassava plants with gibberellic acid resulted in less of the of produced dry matter being allocated to the storage roots (Boerboom, 1978b). Menzel (1980) and Lovell and Booth (1967) obtained similar results for potato. Menzel (1980) suggested that gibberellins and inhibitors play a role in the process of distribution of dry matter. Lovell and Booth (1967) reported that the change in the distribution pattern preceded any large morphological change in the shoot. Menzel (1980) confirmed this, working with single-node cuttings that grew only at the axillary bud, thus largely eliminating possible competition between shoots and tubers.

Long days had no effect on leaf size (experiment 4), but did increase the number of leaves formed per apex in all experiments where this parameter was measured (experiments 4, 5 and 6), except in the clone Betawi and only to a limited degree in MCol 22. Thus long days may promote top growth not only through increased branching, but also by boosting the number of leaves formed per apex. The increase in number of leaves formed per apex and in branching under long days led to a large leaf area, which resulted in more light being intercepted. The larger total dry matter yield under long days in experiment 4 was probably caused by a higher amount of intercepted light, because the total dry matter production per unit intercepted light was not influenced by daylength (Fig. 32). In MCol 22 the dry weight increase was sufficient to substantially offset the decreased percentage distribution of dry weight to the roots. Thus the percentage reduction in storage root yield in MCol 22 was less than in MCol 1684 and MPtr 26. This clone, however, is not less sensitive to photoperiod in terms of effects of long days on final number of branches.

De Bruijn (1977) suggested that cassava is a quantitative long-day plant in terms of flowering (branching). Whilst it is true that branching is normally stimulated by long days, this is not always so. The time to the first branch level was not affected by daylength in MCol 1684, was decreased in MPtr 26 and Betawi, and increased (experiment 6) or decreased (experiment 4) in MCol 22 under long days. Nevertheless, in all experiments where branching occurred, the final branch number was greater under long days. This finding is in agreement with data obtained by Keating (1982).

Because the number of apices per m^2 increased under long days, with no important increase in the number of branches per branching point, the *potential* number of inflorescences per plant increased: it is known (Van der Stok, 1910; Hunt et al., 1977) that branching occurs at the apex of the stem when the apical meristem changes to the reproductive state. This could be of considerable importance in a cassava breeding programme. In practice, however, clonal reactions to flower initiation and flowering are more complicated. Generally, the clones that branch frequently are the flowering ones, but there are exceptions, i.e. because of the early abortion of the whole inflorescence (Van der Stok, 1910).

9 GENERAL DISCUSSION AND CONCLUSIONS

Donald (1968) proposed an approach to plant breeding, known as breeding a crop ideotype (a plant with model characteristics known to influence positively photosynthesis, growth and yield). Donald's approach has also been adopted for cassava, by CIAT in 1972 (CIAT, 1974; Cock et al., 1979). It remains to be seen whether, given the results of the present study, development of a cassava ideotype is useful. Ecological conditions greatly influence cassava plant habitus (Chapter 8), and there are large genotype x site interactions on storage root yield (e.g. Irikura et al., 1979; CIAT, 1981). The research reported in this thesis increases our knowledge of the plant properties that <u>can</u> positively influence the yield of storage roots. When the existing variation for each property in the available genotypes is also known, the breeding of improved cultivars of cassava will be facilitated.

Useful characteristics of a cassava cultivar for a high yield of storage roots

As early as 1951 Cours published a list of useful characteristics for a cassava cultivar with a high-yielding ability when grown in a fertile soil. A number of plant properties that could be useful for a higher yield of storage roots will be discussed below:

- ESRP (efficiency of storage root production), AISS (apparent initial start of starch accumulation), and harvest index
- LAI, leaf canopy characteristics and light interception by the canopy
- leaf photosynthetic rate
- sink potential

ESRP, AISS and harvest index

Cours (1951) mentioned a high storage root fraction as a useful characteristic of a cassava cultivar. Kawano et al. (1978) at CIAT used the harvest index as a selection criterion as early as 1973, when the evaluation of CIAT cassava germ plasm bank started. However, the ESRP and AISS have to be preferred as selection criteria over the harvest index, because these properties give an insight into the growth of a cassava plant in the two most important growth phases that can be distinguished, namely before and after the start of storage root filling (Chapter 7). Moreover, the ESRP as a selection criterion appears to be constant for any length of the growth period and is therefore more useful than the time-dependent harvest index. In practice, the length of the growth period is very variable (e.g. Purseglove, 1968), particularly because no ripening phase can be distinguished. Measurements of ESRP and AISS are more laborious, because they require that plants be harvested at least three times.

For a proper comparison of the ESRP and AISS values of different genotypes the dry weight of the plant or the plant parts must be used - contrary to practice at CIAT (Kawano et al., 1978) - and the weight of the already fallen leaves must be included because this forms a substantial part of the total dry weight (16-19% in experiment 1 of this study: Chapter 7). The results of this study show that the systematic relation reported by CIAT (1978) between the 'measured' harvest index (ignoring the weight of the fallen leaves) and the 'real' harvest index (Fig. 22) does not, in fact, exist.

Stem weight forms a substantial part of the total plant weight. Several authors have drawn attention to cassava clones and Manihot species that have a much lower stem weight fraction than normal. Rogers (1972) mentioned *M. anomala* and *M. stipularia*, both short-stemmed with a dense leaf canopy. Jennings (1959) considered that hybrids between cassava and *M. melanobasis* (a herbaceous species with a long leaf life and now also considered to belong to the species *M. esculenta*) have a great yield potential.

Assuming that the stem weight of the clones used in experiment 1 would have been only 50% of the values actually observed at one year after planting the cuttings and that there was no change in total dry matter weight and AISS value, then the yield of dry storage roots would have been 36% higher (Table 21).

Table 21 Effects of halving stem weight, with unchanged total dry matter production, on increase of dry yield of storage roots

clone	'real' dry weight ($t.ha^{-1}$)			dry weight ($t.ha^{-1}$) with halved dry stem weight			increase in dry storage root yield
	stems	storage roots	total	stems	storage roots	total	
MCol 1684	7.5	14.4	27.4	3.8	18.2	27.4	26%
MVen 77	11.1	10.4	26.4	5.6	16.0	26.4	54%
MPtr 26	7.8	13.5	26.1	3.9	17.4	26.1	29%
MCol 22	8.4	12.9	27.4	4.2	17.1	27.4	33%
Mean							36%

In the present study, AISS values varied from 1.0-3.6 $t.ha^{-1}$ (Tables 15, 16 and 18). This also resulted in a large variation in the amount of nutrients absorbed by the crop at the start of the storage root filling period (Veltkamp, unpublished results). An efficient nutrient use is of the utmost importance for cassava, because in practice cassava is not usually cultivated on fertile soils (Cock, 1979; Hahn et al., 1979). Therefore, high AISS values can be considered as a waste and are thus not desired. The AISS value is greatly influenced by the characteristics of the leaf canopy. When used as scion in graft combinations, clones with abundant leaf growth, such as MCol 638 and MMex 59 (Fig. 14) showed higher AISS values than MCol 1684, which has a more moderate leaf area development; but there was no linear relationship between LAI and AISS values (Veltkamp, 1985) and therefore LAI is not a good indicator of AISS value.

It can be concluded that high ESRP values and low AISS values are desirable characteristics for cassava clones, but not beyond the point where this is achieved at the expense of light interception by the leaf canopy or the lodging resistance of the crop.

LAI, leaf canopy characteristics and light interception by the canopy

A linear relationship was found between total dry matter production and intercepted photosynthetically active radiation (PAR) (Fig. 12). Translated to LAI values this means that an LAI of about 4 (> 95% light interception) is useful for a high total dry matter production. However, Cock et al. (1979) suggested an optimal

LAI of 3 to 3.5 for storage root filling, which means a light interception of circa 90% (depending on the angle of leaf elevation). For selection of promising cultivars of cassava (i.e. those with high total dry matter yield) light measurements above and beneath the canopy for calculation of the intercepted radiation are very useful and easy to take. The measurements must be taken in the middle of the plots and each plot must be surrounded by at least one border row.

In the clones studied at the practised plant density the period from planting until 50% light interception - a measure of growth vigour in the first part of the growth period - varied from 60 to 90 days (Fig. 10), showing that genetic selection for this aspect is possible. High growth vigour in the early part of the growth period is a desirable characteristic from the viewpoint of weed prevention and erosion control.

For each of the leaf canopy characteristics distinguished (leaf formation rate, leaf life, leaf size, branching pattern) genetic variation is available (Figs. 15, 16, 18 and 19). Daylength and temperature also influence these chracteristics. Interactions were also found between genotype and climate conditions (Chapter 8)(see also Irikura et al., 1979). Before more detailed, sound advice on the desirable characteristics of the leaf canopy components can be given, leaf area development must be modelled and thoroughly tested.

From a study with reciprocal graft combinations it appeared that stock properties also influence the total dry matter production (Veltkamp, 1985), thus further complicating statements concerning the desirable leaf canopy characteristics.

Leaf photosynthetic rate

Genetic differences were found in leaf fotosynthetic rate (Chapter 4) (Mahon et al., 1977b; Palta, 1982; CIAT, 1978). In several crops, such differences have been used as a selection criterion. Unfortunately, the relationship between leaf photosynthetic rate and production is tenuous (Gifford and Evans, 1978). Therefore, at the moment it does not seem to be useful to introduce the leaf photosynthetic rate as a selection criterion in a cassava breeding programme.

Sink potential

Clonal differences in sink capacity were shown to exist in a study (not reported in this thesis) on the reciprocal grafts of three clones. Of the three clones studied (MCol 1684, MCol 638 and MMex 59) MCol 1684 had the greatest sink potential. MCol 1684 as stock produced a 74% higher yield of dry storage roots at 303 days after planting than the average of the two remaining clones (Veltkamp, 1985). Thus, screening for a large sink potential can be useful, but making grafts is laborious.

Knowledge of good growth conditions for cassava

In a separate study (Veltkamp et al., 1985) the growth of cassava plants in the four field experiments described in this study was simulated with a growth model that had been adapted from a summary model, SUCROS, which, in turn, had been derived from extensive growth models (Penning de Vries and Van Laar, 1982). Generally, the results of the simulation agreed well with the field data. It can be concluded that present knowledge of cultivation techniques enables good cassava yields to be obtained.

Potential yield of storage roots per year

With the help of the experimental results presented in the previous chapters, potential yield of storage roots per year can be calculated for the climatic conditions in the experimental area near Cali, Colombia (see Chapter 3) as follows:

$$F * R = I \qquad (1)$$

where:

F = fraction of incoming light intercepted by the leaf canopy

R = amount of incoming PAR ($\mathrm{MJ.ha^{-1}.year^{-1}}$)

I = intercepted PAR ($\mathrm{MJ.ha^{-1}.year^{-1}}$)

Only a fraction of the intercepted PAR is converted to dry matter:

$$I * E = P \qquad (2)$$

E = photosynthetic efficiency (%, divided by 100)
P = energy content of total dry matter produced ($MJha^{-1}.year^{-1}$)

The energy content of the produced dry matter is converted to the weight of the produced dry matter as follows:

$$\frac{P}{C} = D \qquad (3)$$

C = energy content ($MJ.t^{-1}$ dry matter)
D = total dry matter yield ($t.ha^{-1}$)

The potential dry weight of storage roots can be calculated with the help of the formula:

$$(D - A) * S = Y \qquad (4)$$

where:
A = apparent initial start of starch accumulation (AISS) ($t.ha^{-1}$)
S = efficiency of storage root production (ESRP)
Y = potential yield of dry storage roots ($t.ha^{-1}$)

Summarizing formulas (1) to (4) results in the following overall formula:

$$\left(\frac{F * R * E}{C} - A \right) * S = Y \qquad (5)$$

Assuming:
- a light interception by the leaf canopy of 90% (F)
- a yearly incoming PAR of $3450 * 10^4$ $MJ.ha^{-1}$ (or nearly 1900 $J.cm^{-2}.day^{-1}$ global radiation), as was recorded at the experimental site during the period that experiment 1 of this study was conducted (R)
- a photosynthetic efficiency of 2.5% for the whole growth period (E)
- an energy content of dry matter of $16.7 * 10^3$ MJ per ton (Table 7) (C)

- an AISS of 1.5 t.ha^{-1} (A) (Chapter 7)
- an ESRP of 0.66 (Chapter 7) (S),

then the potential yield of dry storage roots is about 30[1] t.ha^{-1}.year^{-1} and the potential total dry matter yield about 46 t.ha^{-1}.year^{-1}. This potential yield of dry storage roots is of the same order as reported by Boerboom (1978b) and by Cock et al. (1979). Assuming a storage root dry matter content of 33%, the potential yield of fresh storage roots will be about 90 t.ha^{-1}.year^{-1}. Such a yield has already been reported by several authors. At the experimental farm of CIAT near Cali, Colombia, the highest recorded yield, namely 82 t.ha^{-1} of fresh storage roots, is of that order and was attained after a growth period of one year (CIAT, 1980).

Cassava growing at higher latitudes

This study has shown (Chapter 8) that one of the clones tested (MCol 22) is suited for growing at daylengths occurring at higher latitudes. This is the first report of a cassava clone whose production of storage roots is nearly day-neutral. Further testing is recommended e.g. at the daylength installation at CIAT (*Fig.* 25) and at higher latitudes. At higher latitudes the length of the growing season must be shortened, because temperatures are lower for part of the year.

[1] $\left(\frac{3450 * 10^4 * 0.9 * 0.025}{16.7 * 10^3} - 1.5 \right) * 0.66 = 30$

SUMMARY

Cassava (*Manihot esculenta* Crantz) is an important crop in many parts of the tropics, being mainly cultivated for its storage roots. Farmers' yields are low and one of the constraints to higher yields is the lack of adequate clones. At the beginning of the 1970s an extensive cassava research programme was started at CIAT (Colombia). One of its aims was to develop high-yielding clones by genetic modification of the plant habitus.

This thesis begins with a literature review in which the available information on the physiological determinants of the yield of cassava storage roots is described.

Next, a series of experiments carried out to deepen and to broaden this knowledge on physiological causes of yield variation in cassava is described. MCol 1684 (the best cultivar of the CIAT cassava germ plasm bank) and MPtr 26 were used as the reference cultivars in the experiments, both in the field and in the greenhouse.

Rate of leaf photosynthesis was measured by infrared gas analysis. Measurements of the photosynthetic rate were carried out using the youngest fully expanded leaf from plants growing outdoors that were 35 - 45 days old. Maximum photosynthetic rates varied from 0.74 x 10^{-6} to 0.81 x 10^{-6} kg $CO_2.m^{-2}$ leaf.s^{-1}. MCol 22 had the highest leaf photosynthetic rate. A relatively low photonflux density level was required for light saturation of the photosynthetic rate. This is characteristic for a plant species with a C_3 cycle. Photosynthesis increased only slightly from 1000 to 1500 $\mu E.m^{-2}.s^{-1}$ PAR (photosynthetically active radiation). Light efficiency at low light intensities (α) varied from 9.0 x 10^{-9} to 12.4 x 10^{-9} kg $CO_2.J^{-1}$. The CO_2 concentration remained at an approximately constant level in the intercellular spaces, independent of the light level, being 212 vppm (0.387 x 10^{-3} $kg.m^{-2}$). At a photonflux density of 1500 $\mu E.m^{-2}.s^{-1}$ mesophyl resistance was higher than leaf resistance to CO_2 (335 $s.m^{-1}$ compared with 185 $s.m^{-1}$). Transpiration rates did not differ between clones, but increased with light intensity. Water use efficiency (WUE) varied from 15.1 to 17.1 mg CO_2 uptake per g H_2O, and was most efficient for MCol 22.

Linear relationships were found between total dry matter yield and the amount of intercepted PAR. Photosynthetic efficiency varied from 1.9% to 2.5%, based on PAR during the first six months of the growth period, and decreased markedly in older plants. The fraction of incoming intercepted PAR varied from 43% to 69% during the first six months. Cultivars had an extinction coefficient (K) of 0.72 to 0.88 and their leaves were dominantly planophile.

A leaf area index (LAI) of 1.0 (about 50% light interception) was attained at 60 to 90 days from planting. An LAI = 3, which coincides with a light interception by the leaf canopy of approximately 90% was reached 120 to 150 days after planting, so about 40% of a growth period of one year had elapsed before complete ground cover was achieved. Genotypes with very different canopy characteristics reached an LAI of 3 in approximately the same time.

Cassava has an indeterminate habit with sympodial branching. The length of the period until first branching depended on genotype and planting date. Large genetic differences were found in leaf life, leaf size, plant age at which maximum leaf size was reached and leaf formation rate per apex. Small variations in environmental conditions caused significant differences in canopy characteristics.

During the growth period of cassava two periods with constant dry matter partitioning could be distinguished, with the apparent initiation of the filling of storage roots (AISS) being the crucial point. A constant proportion of the dry matter formed is distributed to the storage roots: this is the efficiency of storage root production (ESRP). Genetic differences were found for ESRP and AISS.

The influence of daylength on growth and yield was studied. Daylength was increased by light bulbs, while the other growth conditions remained similar. Daylength had only a very slight influence on AISS value. ESRP was negatively influenced by long days. Differences in ESRP were the main cause of differences in yield of storage roots for plants grown at different daylengths. For MCol 22, the ESRP value was also considerably lower under long-day conditions, but the yield of storage roots was nevertheless only slightly reduced, because of the higher total dry matter yield. MCol 22 is the first detected cassava clone whose yield of storage roots is nearly day-neutral and thus it is suitable for cultivation at higher latitudes. Long-day conditions caused a large increase in LAI. The higher LAI values were caused by a higher leaf formation rate per apex and a larger number of apices per m^2. Photosynthetic efficiency was not influenced by daylength.

The implications of the findings are discussed. Plant properties that could be useful for improving storage root yield are: a high ESRP value, a low AISS value, a high growth vigour (short period until 50% light interception), a light interception of about 90% as long as possible, and a good sink potential.

Present knowledge of cassava cultivation techniques is such that high yields are possible. Potential yield of storage roots is about 30 $t.ha^{-1}.year^{-1}$ on dry weight basis and about 90 $t.ha^{-1}.year^{-1}$ on fresh weight basis. The highest recorded yield of fresh storage roots at the CIAT experimental farm is of that order (namely 82 $t.ha^{-1}$), and was achieved after a growth period of one year.

SAMENVATTING

Cassave (*Manihot esculenta* Crantz) is een belangrijk gewas in grote delen van de tropen. Het wordt hoofdzakelijk geteeld voor de verdikte wortels. De gemiddelde opbrengst in de praktijk op de boerenbedrijven is laag (circa 9 ton verse, verdikte wortels per hectare). Eén van de oorzaken van deze lage opbrengst is het onvoldoende beschikbaar zijn van goed producerende klonen. In het begin van de zeventiger jaren werd op het CIAT, het Centro Internacional de Agricultura Tropical, in Colombia een omvangrijk onderzoeksprogramma met cassave gestart. Eén van de doeleinden was het ontwikkelen van zeer produktieve klonen door genetische verandering van de morfologie van de plant.

Dit proefschrift vangt aan met een overzicht van de literatuur, waarin de beschikbare informatie over de fysiologische factoren, die de opbrengst aan verdikte wortels van cassave bepalen, wordt beschreven.

Daarna worden een aantal proeven beschreven en besproken die werden uitgevoerd om de kennis van de fysiologische oorzaken van verschillen in opbrengst aan verdikte wortels van cassave te verdiepen en te verbreden. MCol 1684, de beste cultivar van de op het CIAT aanwezige genenbank van cassave, en MPtr 26 werden in alle proeven gebruikt, dus zowel in het veld als in de kas. In totaal werden er acht klonen gebruikt. De veldproeven werden alle uitgevoerd in de CIAT proeftuin bij Cali in Colombia, terwijl er twee proeven plaatsvonden in één van de kassen van het kassencomplex van de vakgroep Tropische plantenteelt van de Landbouwhogeschool in Wageningen.

De fotosynthesesnelheid van bladeren werd bepaald met behulp van de infrarood-absorptie methodiek. Voor de bepaling van de fotosynthesesnelheid werd het jongste volledig ontvouwde blad gebruikt van 35-45 dagen oude planten die buiten werden opgekweekt. De maximale fotosynthesesnelheid varieerde tussen de onderzochte klonen van $0,74 \times 10^{-6}$ tot $0,81 \times 10^{-6}$ kg CO_2 per m^2 blad per seconde, waarbij de hoogste waarde werd verkregen met MCol 22. Reeds bij een relatief lage lichtintensiteit was er sprake van lichtverzadiging. De fotosynthesesnelheid nam nog slechts in geringe mate toe bij een stijging van de lichtintensiteit van 1000 tot 1500 $\mu Em^{-2}.s^{-1}$ (fotosynthetisch actief licht). Dat is kenmerkend voor een plantesoort met een C_3-cyclus. De fotochemische efficiëntie bij lage lichtintensiteiten varieerde van $9,0 \times 10^{-9}$ tot $12,4 \times 10^{-9}$ kg $CO_2.J^{-1}$. De CO_2-concentratie bleef, onafhankelijk van de lichtintensiteit, ongeveer constant in de intercellulaire holten in de bladeren, namelijk $0,387 \times 10^{-3}$ $kg.m^{-2}$ (212 vdpm). Bij een lichtintensiteit van 1500 $\mu E.m^{-2}.sec^{-1}$ was de restweerstand (mesofyl weerstand)(r_m) groter dan de huidmondjesweerstand voor CO_2 (r_s'), namelijk respectievelijk 345 $s.m^{-1}$ tegen 185 $s.m^{-1}$.

De transpiratiesnelheid verschilde niet tussen de onderzochte klonen, maar nam wel toe met de lichtintensiteit. De efficiëntie van het watergebruik (WUE) varieerde van 15,1 tot 17,1 mg CO_2 per g H_2O, waarbij MCol 22 de meest efficiënte kloon was.

Er werd een rechtlijnig verband gevonden tussen de totale droge stof produktie en de onderschepte fotosynthetisch actieve straling. De fotosynthetische efficiency varieerde van 1,9 tot 2,5% gedurende de eerste zes maanden van de groeiperiode, en nam daarna af. Gedurende de eerste zes maanden van de groeiperiode werd 43 tot 69% van de inkomende straling door het gewas onderschept. De onderzochte cultivars hadden een uitdovingscoëfficiënt (K) van 0,72 tot 0,88. De bladeren waren overwegend horizontaal geplaatst.

Een bebladeringsindex (BI, in het Engels LAI) van 1,0 (ongeveer 50% onderschepping) werd bereikt op 60 tot 80 dagen na het planten van de stekken. Een BI van 3, wat overeenkomt met een lichtonderschepping van circa 90% werd op 120 tot 150 dagen na het planten van de stekken bereikt, zodat pas nadat zo'n 40% van de veel voorkomende groeiperiode van 1 jaar voorbij was het gewas de bodem volledig bedekte. Klonen met een zeer verschillende plantarchitectuur bereikten een BI van 3 in ongeveer dezelfde tijd.

De cassave plant kent geen eindgroei en heeft een sympodiaal vertakkingspatroon. De lengte van de periode vanaf het planten van een stek tot de eerste vertakking hangt af van de kloon en de planttijd. Er werden grote verschillen tussen de klonen gevonden voor wat betreft de levensduur van de bladeren, de bladgrootte, de leeftijd van de planten waarop de maximale bladgrootte werd bereikt en de bladafsplitsingssnelheid per groeipunt. Kleine verschillen in milieuomstandigheden hadden reeds wezenlijke verschillen in de plantarchitectuur tot gevolg.

Er kunnen tijdens de groeiperiode van cassave twee perioden worden onderscheiden waarin een vaste verdeling van de droge stof produktie over de verschillende delen (bladeren, stengels, (verdikte) wortels) plaatsvindt. Het moment waarop de verdikking van de wortels begint neemt hierbij een centrale plaats in. Het gewicht dat de planten hebben bij de start van de wortelverdikking wordt aangeduid met de term AISS-waarde. Het vaste deel van de geproduceerde droge stof, dat nadien terecht komt in de verdikte wortels, wordt aangeduid als de ESRP-waarde. Er werden wezenlijke verschillen gevonden tussen de onderzochte klonen voor wat betreft de ESRP en de AISS-waarde.

Ook werd de invloed van de daglengte op de groei en de opbrengst van cassave bestudeerd. De dagen werden verlengd met behulp van gloeilampen, terwijl de overige groeiomstandigheden niet veranderden. De daglengte had geen invloed op de AISS-waarde. De ESRP-waarde was in alle gevallen kleiner bij lange dagen (16 u licht). De gevonden verschillen in de ESRP-waarden waren de voornaamste oorzaak van de verschillen in opbrengst aan verdikte wortels voor planten die bij verschillende daglengten groeiden. Ook bij MCol 22 was de ESRP-waarde onder lange dag omstandigheden aanzienlijk lager dan bij de natuurlijke daglengte van omstreeks 12 uur, maar toch verschilden de opbrengsten aan verdikte wortels van planten opgegroeid bij verschillende daglengten maar weinig van elkaar. Dat werd veroorzaakt door de grotere totale droge stof produktie bij lange dag omstandigheden. MCol 22 is de eerste cassavekloon waarvan bekend is dat de opbrengst aan verdikte wortels bijna niet wordt beïnvloed door de daglengte. Met andere woorden: MCol 22 is daglengte-neutraal voor wat betreft de opbrengst aan verdikte wortels en kan daarom voor wat betreft de daglengte zonder opbrengstverlies op hogere breedtegraden worden geteeld. Lange dag omstandigheden veroorzaakten een sterke toename van de BI. Deze hogere BI-waarden werden veroorzaakt door een hogere bladafsplitsingssnelheid per groeipung en een groter aantal groeipunten per oppervlakte-eenheid. De efficiëntie van de fotosynthese werd niet beïnvloed door de daglengte.

De gevolgtrekkingen uit de resultaten van dit onderzoek worden besproken. Planteigenschappen die nuttig kunnen zijn om te komen tot een verhoging van de opbrengst aan verdikte wortels zijn: een hoge ESRP-waarde, een lage AISS-waarde, een sterke groeikracht in de beginperiode van het groeiseizoen (anders gezegd: een korte periode tot 50% van de inkomende straling door het gewas wordt onderschept), een lichtonderschepping van circa 90% gedurende een zo groot mogelijk deel van de totale groeiperiode, en een goed vermogen om de droge stof in de zich verdikkende wortels op te slaan.

De huidige kennis omtrent teelttechnieken voor cassave is zodanig dat goede opbrengsten aan verdikte wortels mogelijk zijn. De potentiële opbrengst aan verdikte wortels bedraagt ongeveer 30 $t.ha^{-1}.jaar^{-1}$ op droog gewicht basis en ongeveer 90 $t.ha^{-1}.jaar^{-1}$ op vers gewicht basis. De hoogste tot nu toe op de CIDT proeftuin bij Cali in Colombia verkregen opbrengst bedroeg na een groeiperiode van één jaar, 82 ton aan verse verdikte wortels per hectare.

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CURRICULUM VITAE

H.J. Veltkamp werd op 16 juli 1948 in Warnsveld geboren. Hij bezocht het Baudartius Lyceum in Zutphen en behaalde het diploma HBS-b in 1966. Hij studeerde van 1966 tot 1972 aan de Landbouwhogeschool. In 1972 studeerde hij met lof af in de studierichting Tropische landbouwplantenteelt met als keuzevakken plantenfysiologie en humane voeding. Van 1972 tot 1978 was hij werkzaam bij het Landbouwproefstation van het ministerie van Landbouw, Veeteelt en Visserij in Paramaribo, Suriname. In de periode 1972 tot 1974 was hij hoofd van de afdeling Granenonderzoek, terwijl hij van 1974 tot 1978 als hoofd van de afdeling Kontakten-met-de Landbouwvoorlichting belast was met de overdracht van onderzoeksresultaten van het Landbouwproefstation naar de Landbouwvoorlichtingsdienst. Van 1978 tot 1981 was hij als promotieassistent verbonden aan de vakgroep Tropische plantenteelt van de Landbouwhogeschool en in dat kader als onderzoeker werkzaam op de afdeling Fysiologie van het Cassave-onderzoeksprogramma van het Centro Internacional de Agricultura Tropical (CIAT) in Palmira, Colombia. Na terugkeer in 1981 was hij gedurende bijna één jaar nog als wetenschappelijk ambtenaar werkzaam bij de vakgroep Tropische plantenteelt. Sedert 1982 is hij als docent tropische plantenteelt verbonden aan de Rijks Hogere Landbouwschool in Deventer.