2.2 Crop phenology and dry matter distribution

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2.2.1 Introduction

Figure 4 shows the time course of above ground dry matter accumulation of a summer wheat crop during its growth cycle. With respect to the growth rate, three growth stages can be distinguished (Section 2.1). However, a crop not only accumulates weight, it also passes through successive phenological development stages: after sowing or planting, a cereal crop first forms roots, leaves and stems during the pre–anthesis phase, subsequently it flowers, and the seeds set and fill and the crop matures in the post–anthesis phase. These phenological stages are schematically illustrated for a rice crop in Figure 10.

Recognizing the distinction between growth and development, growth is defined as the increase in weight or volume of the total plant or the various plant organs, and development is defined as the passing through consecutive phenological phases; it is characterized by the order and rate of appearance of vegetative and reproductive plant organs. The two processes, growth and development, are often strongly interrelated, which is probably the reason why the term development is used often when growth is meant.

Pre-emergence Seedling Yellows	Tillering Head Development	Heading	Grain Filling + Ripening	
Establishment (0)	Vegetative (1)	Flowering (2)	Yield Formation (3)	Ripening (4)
Nursery Transplanting Field				
25- 35 days ¦ 10 days	40 – 60* days	10 – 15 days	25–35 days	10–20 days

Figure 10. Developmental phases of rice. (Source: Doorenbos & Kassam, 1979)

The order of appearance of the various organs is a species characteristic, it may vary among species and is almost independent of the circumstances. The timing and rate of organ appearance, however, is dependent on environmental conditions and is, consequently, highly variable. Important events in the development of cereals are for instance, emergence, floral initiation, terminal spikelet formation, the moment of flowering (anthesis) and the beginning and end of grain filling. For tuber crops, the onset of tuber bulking is also such an event.

The major environmental conditions influencing phenological development are temperature and day length. Many plant species or cultivars need a period of low temperature to induce flowering, for example winter wheat, winter rye and sugar – beet. The process taking place during this period is called vernalization or jarowization. Summer crops in temperate climates and tropical crops do not need a period of low temperature to induce flowering. For winter crops the low temperature requirements first must be satisfied. For all crops, higher temperatures generally shorten the length of a given phenological phase. Van Dobben (1979) collected data on the length of the period from emergence to anthesis for a number of crop species, grown at various constant temperatures (Figure 11). The shape of the curves relating the number of days to anthesis to temperature suggests a constant product of days and temperature. This product is the temperature sum or the so called Thermal Unit (TU, expressed in units of day degrees). The most common method of obtaining TU values for the duration of a phenological phase is to add average daily temperatures above a threshold value . The range of threshold temperatures

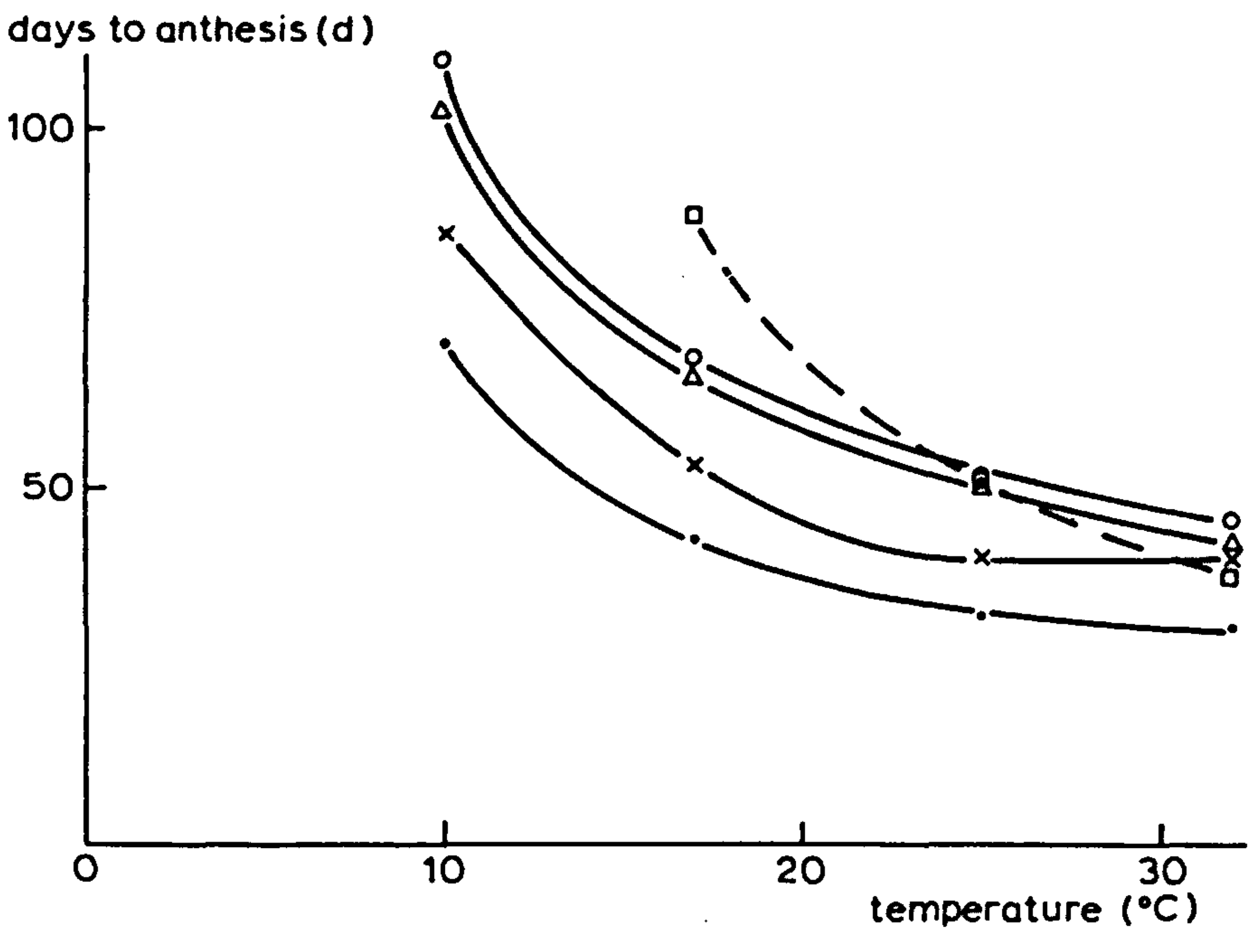

Figure 11. The influence of temperature on the length of the pre-anthesis phase for various field crops. (●) rye; (o) wheat; (Δ) flax; (□) maize; (x) peas. (Source: van Dobben, 1979)

varies between 0 and 10 °C for different species or varieties (Table 7). Sometimes an optimum temperature exists. In that case, temperatures exceeding the optimum, are replaced in the calculation by the optimum temperature itself.

Therefore the higher the temperature, the shorter the length of the total growing period of a crop or, in other words, the higher its rate of development. If development is expressed on a numerical scale, that ranges from 0 to 2, with 0 being emergence, 1 anthesis and 2 maturity, then the development rate is defined as that part of the scale that is accumulated per unit time. Generally a grain crop does not flower in the middle of its growing period. Consequently, the development rate during the pre–anthesis phase differs from the development rate during the post–anthesis phase at the same temperature. If, for example, the time lapse between emergence and anthesis for a certain crop variety in a specific environment is 50 days and between anthesis and maturity 25 days, then the average development rate during the pre–anthesis phase is 1/50 or 0.02 d^{-1}, and during the post–anthesis phase it is 1/25 or 0.04 d^{-1}. The numerical values between 0 and 2, obtained by adding the daily development rates are defined as the development stage.

Exercise 4

Transform the graphs for wheat and maize in Figure 11 into curves of development rate versus temperature. What do you notice about the curves?

For some species or cultivars the effect of temperature on development rate is modified by the influence of the length of the day, or. in fact, the length of the dark period. This effect is called photoperiodism. With regard to this mechanism, plants may be classified into three groups: (i) day–neutral plants, for which development rate is insensitive to day length; (ii) long–day

Table 7. Indicative threshold values, T_o (°C) used for the calculation of TU values for different species.

Crop	T_o
Maize	10
Soybean	10
Sorghum	7-10
Pea	4
Chickpea	4
Wheat	0-5
Rice	0-10

plants, for which anthesis is induced by the occurrence of long days (and therefore short nights); (iii) short – day plants, for which anthesis is induced by the occurrence of short days (and therefore long nights). The reaction to day length may be an important characteristic when a new species or cultivar is introduced in a region, even when it originates from a region at about the same latitude and – consequently – the same photoperiod. The reason is that the growing seasons at the two locations may not coincide due to differences in rainfall pattern. The effects of day length are not treated quantitatively here, because we assume that in each region species with the proper day – length reaction are cultivated.

Although the basic processes governing phenological development and biomass production act independently, both phenomena are strongly interrelated. If the rate of development is high, total biomass production will be low, because the period of linear growth will be short (Section 2.1). Moreover, crops are generally not grown for total biomass, but for their storage organs, such as tubers, grains or pods. These storage organs grow only during the latter part of the growth cycle, after roots, leaves and stems have been produced. A short growing period, resulting in a low vegetative biomass, especially of leaves responsible for light interception, leads inevitably to a poor crop. On the other hand, too much biomass invested in vegetative organs may lead to a relatively low production of storage organs, because in that case the maintenance requirements are high. Therefore, not only total biomass production is of interest, but also its distribution over the various plant parts. The actual proportion of leaves, stems, roots and storage organs in the total biomass at a certain moment depends on the preceding growth rates, which are governed by the weather and the leaf area index in the past, and the partitioning of that dry matter increase over the various plant parts. A fixed distribution pattern, for instance partitioning factors defined as a function of development stage, does not necessarily lead to a constant ratio of various organs. A simple example will illustrate this.

Suppose there is at a certain moment a crop in the field, that comprises 1000 kg ha^{-1} leaves and 400 kg ha^{-1} stems. During the following 10 days, the average growth rate is 200 kg ha^{-1} d^{-1}; the partitioning factors for leaf and stem being 0.6 and 0.4, respectively. In the subsequent 10 day period, the growth rate is only 100 kg ha^{-1} d^{-1} because of a much lower energy availability, and the partitioning factors have changed to 0.3 and 0.7 for leaf and stem, respectively. At the end of the second period the weight of leaves is $1000 + 0.6 \times 200 \times 10 + 0.3 \times 100 \times 10 = 2500$ kg ha^{-1} and the weight of stems is $400 + 0.4 \times 200 \times 10 + 0.7 \times 100 \times 10 = 1900$ kg ha^{-1}. This results in a leaf – stem ratio of 1.32. Now suppose the growth rate in the first period to be 100 kg ha^{-1} d^{-1} and in the second period 200 kg ha^{-1} d^{-1}. Assume too, an identical distribution pattern. Then the weight of leaves at the end of the second period is $1000 + 0.6 \times 100 \times 10 + 0.3 \times 200 \times 10 = 2200$ kg ha^{-1} and the weight of stems $400 + 0.4 \times 100 \times 10 + 0.7 \times 200 \times 10 = 2200$ kg ha^{-1}.

Then the leaf – stem ratio is 1.00.

In this example the development pattern and the time course of partitioning factors were assumed to be identical. However, development is not identical each year, as it responds to differences in environmental conditions. It is therefore not possible to relate the distribution pattern to crop age. Usually the partitioning of the current assimilate supply over the various plant parts is expressed in a distribution pattern in dependence of the development stage of the crop. Such configurations are characteristic for each crop. The effects of environmental conditions other than temperature on the distribution pattern are often very small, especially in the potential production situation; they are therefore not taken into consideration here.

In the next part of this section the partitioning of newly formed dry matter over the various plant organs is treated in relation to the development stage of the crop. Examples will be given for the crops rice, maize and cassava.

2.2.2 *Development and dry matter distribution in rice*

The total growing period of rice from transplanting to maturity generally varies from 90 to 150 days, depending on the variety, temperature and sensitivity to day length (Figure 10). Short duration varieties are in general day-neutral, long duration varieties are short – day plants.

Rice is a species with a terminal inflorescence, and such determinate species show a fixed development pattern: after anthesis leaf, stem and root formation stops and the only organ increasing in weight is the ear. The relation between development rate and temperature is a variety – specific characteristic, which needs to be established experimentally (Section 5.4). As an example, the TU values for two cultivars, the medium – duration breeding line B9C/Md/3/3 and the short duration cultivar IR5, for the pre – anthesis period from transplanting till anthesis are 2700 and 2150 d °C. respectively, taking into account a threshold temperature of 0 °C (van Keulen, 1976). The duration of those periods at 20 °C can be calculated as 2700/20, or 135 days, and 2150/20 or 108 days, respectively. The associated development rates (the inverse of the duration in days) at this temperature are 1/135, or 0.0074 and 1/108, or 0.0093 d^{-1}, respectively. The TU value for the post – anthesis period appeared to be equal for both cultivars, 650 d °C.

Exercise 5

Calculate the duration of the post – anthesis period and the development rate for both cultivars at 20 and 25 °C, respectively.

The similarity of the TU values for the post – anthesis phase for both cultivars is not a coincidence. In wheat too, differences in growth duration between cultivars grown under identical environmental conditions are mainly due to differences in the length of the period from emergence to anthesis (Nuttonson, 1955, 1953).

For actual field situations, the development rate may be deduced from the dates of emergence, anthesis and maturity, and air temperature data from the nearest meteorological station, which should not be too different from the experimental site.

Exercise 6

In Chiang Mai, a province in Northern Thailand, the upland rice breeding line Khichang x RDI was planted at two locations: Phabujom (800 m altitude, average maximum temperature 27 °C, average minimum temperature 20 °C); and at Chang Khian, (altitude 1200 m, average maximum temperature 24 °C, average minimum temperature 17 °C).

Emergence at Phabujom and Chang Khian occurred on 8 June and 5 June, anthesis on 16 September and 1 October, and maturity on 13 October and 2 November, respectively.

Calculate the average development rates for the pre – and post – anthesis phases at both locations, and the TU values for the two phases. A threshold temperature of 0 °C may be assumed.

Construct the relation between average temperature and development rate for this cultivar.

The fraction of the total dry matter increase apportioned to root and shoot, respectively, as a function of the development stage of a rice crop for the period between transplanting (development stage 0) and anthesis (development stage 1) is given in Figure 12a. The partitioning of shoot dry matter increase between leaf blades and 'stems', as a function of the development stage of a rice crop for the period between transplanting and anthesis is given in Figure 12b. It is assumed that after anthesis all dry matter increase benefits the reproductive organs.

Thus, if the growth rate is 200 kg ha^{-1} d^{-1} at development stage 0.5, a fraction of 0.92 of the total dry matter increase, or 184 kg ha^{-1} d^{-1} is apportioned to the shoots. Of that portion, a fraction of 0.50, or 92 kg ha^{-1} d^{-1} is apportioned to the leaf blades and 92 kg ha^{-1} d^{-1} to the 'stems'.

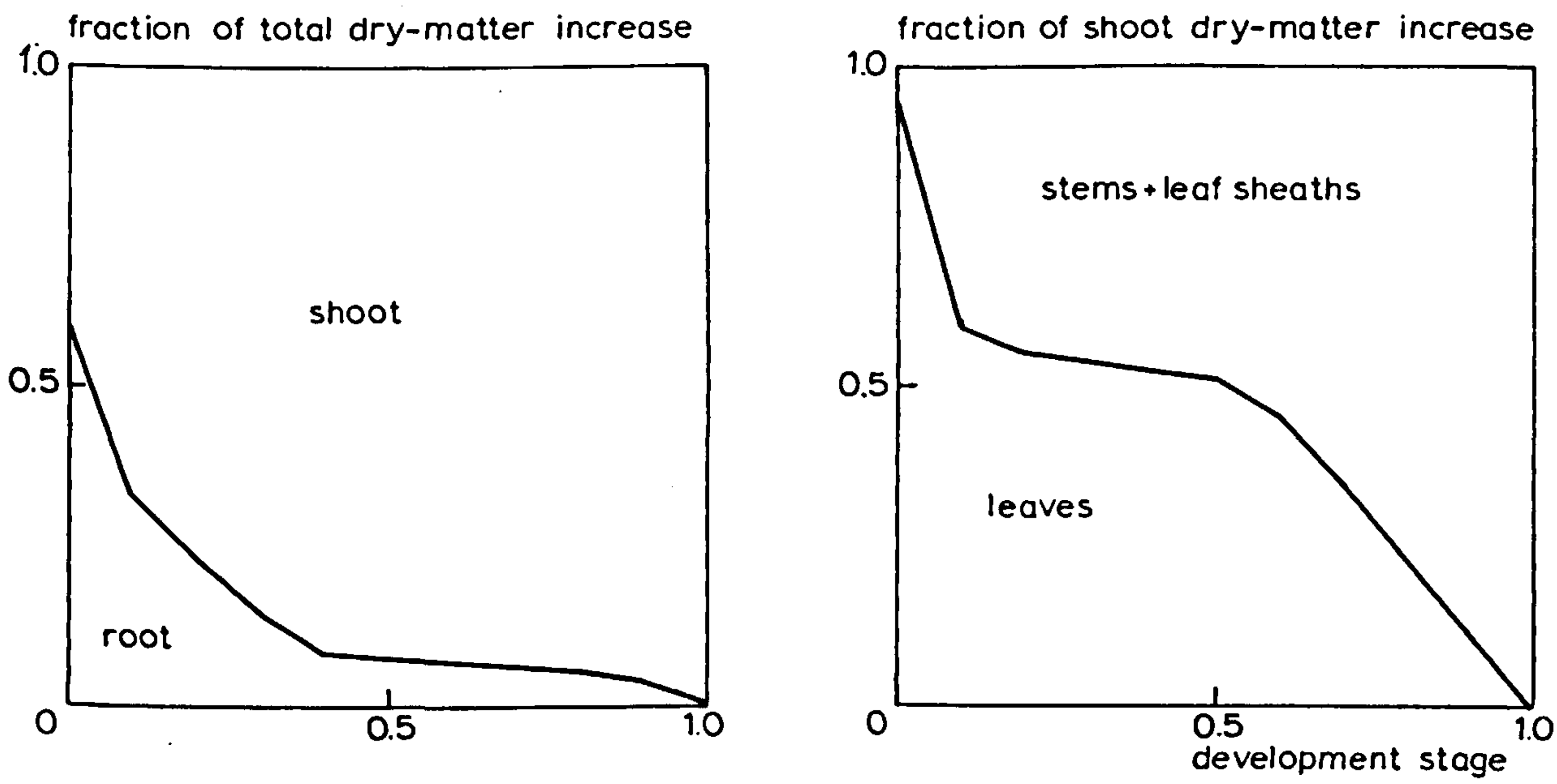

Figure 12. Partitioning factors for plant parts of rice in the course of development.

Exercise 7

Two upland rice varieties are grown at the same location. They are harvested periodically at ten – day intervals. The dry weight of the above ground biomass is given below for the two varieties A and B.

Variety A		Variety B	
harvest day	biomass, kg ha^{-1}	harvest day	biomass, kg ha^{-1}
0	50	0	50
10	100	10	100
20	200	20	200
30	400	30	400
40	800	40	800
50	1400	50	1400
60	2200	60	2200
70	3300	70	3300
80	4600	80	4600
90	6300	90	6300
100	8400	100	8100
110	10500	110	9500
120	11900		
125	12500		

Day 0 is emergence; anthesis for variety A is on day 95 and for variety B on day 80 after emergence.
Calculate for both varieties the dry weight of leaves, stems and grains at the various harvest times. Use for the calculation the partitioning factors given in Figure 12. Assume a constant temperature regime.
(Note: The partitioning factors in Figure 12 are functions of development stage, not age)

2.2.3 Development and dry matter distribution in maize

For maize, the total growing period from emergence to maturity varies from 80 to 110 days for short duration varieties, and from 110 to 140 days for medium duration varieties, when average daily temperatures are above 20 °C. Under cooler conditions, maize is mostly grown as a forage crop because the associated extended length of the growing period does not permit timely maturation, due to the low temperatures, especially towards the end of the growing season.

Maize is considered to be either day – neutral or a short – day plant. The flower has separate male and female parts. The male flowers are in the tassel at the top of the plant; the female flowers are in cobs at nodes along the middle of the stem (Figure 13). The pre – anthesis period ends at silking. The

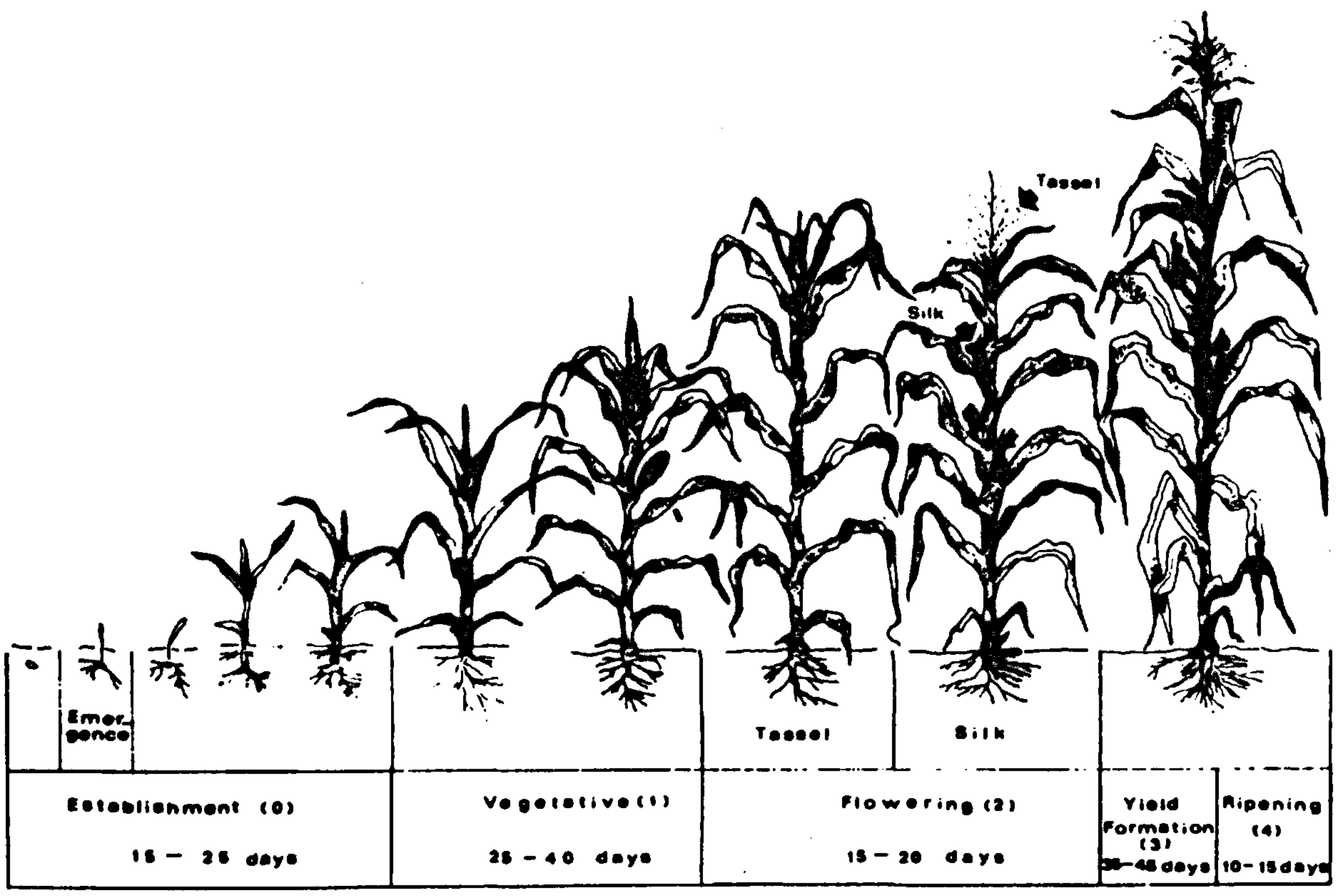

Figure 13. Developmental phases for maize. (Source: Doorenbos & Kassam, 1979)

duration of the interval between emergence and silking is affected by both genetic factors and environmental conditions. For most common cultivars, the time from silking to maturity under normal environmental conditions is identical, an average 50 – 55 days.

The most frequently used method for determining the temperature requirement from emergence to silking is a direct summation of average daily temperatures, taking into account a base temperature of 10 °C. Mederski et al. (1973) established TU values of 625, 640, and 755 d °C for the period between emergence and silking, and 650, 655, and 635 d °C for the post – silking period for the varieties Ohio 401, DeKalb XL45 and Pioneer 3306, respectively. The latter values may vary with the definition of maturity. In this case, it is defined as the moment that a black layer develops at the base of the kernel, which marks the end of the period of effective grain filling. Similar to rice, the TU value for the post – silking period is almost identical for the three varieties at 650 d °C. The average duration of that period at 20 °C is 650/(20 – 10) = 65 days; at 25 °C it becomes 650/(25 – 10) = 43 days (the base temperature is 10 °C!). The corresponding development rates are 1/65, or 0.0154 d^{-1}, and 1/43, or 0.0233 d^{-1}, respectively.

Exercise 8

A maize variety is grown at a location (air temperature given in Table 8), for which a TU value of 760 d °C has been established for the period between emergence and silking, and one of 660 d °C between silking and maturity. For both periods a threshold value of 10 °C may be taken into account. The crop emerged 1 June.

Calculate the dates on which development stages 0.2, 0.4, 0.6, 0.8, 1.0, 1.5, and 2.0 are reached.

What are these dates if emergence takes place on 15 June.

Calculate the average development rates for the pre – silking and post – silking periods for both emergence dates.

Exercise 9

A maize crop is harvested periodically at ten – day intervals. The harvested plants are separated into leaves and stems. The dry weights of the plant parts are given below:

Date	leaf weight ($kg\ ha^{-1}$)	stem weight ($kg\ ha^{-1}$)
10 June	200	0
20 June	1400	300

30 June	2800	800
10 July	4500	2000
20 July	5700	3800

Emergence date is 1 June; silking date is 5 August.
Draw a graph of the fraction of the weight increment allocated to the leaves as a function of the development stage of the crop. Assume a constant temperature regime.

Table 8. Average air temperatures (°C) to be used in Exercise 8.

	Month			
Date	June	July	August	September
1	16	20	24	33
2	15	22	26	30
3	14	21	25	30
4	16	19	26	29
5	18	18	27	28
6	17	18	24	30
7	16	20	25	29
8	13	19	24	28
9	10	21	26	29
10	9	21	27	28
11	12	22	28	27
12	16	23	30	30
13	20	30	31	26
14	23	20	28	25
15	22	24	31	26
16	19	24	30	25
17	18	23	29	24
18	18	22	28	27
19	16	23	31	24
20	20	20	32	25
21	22	22	31	24
22	21	23	30	22
23	24	24	29	23
24	21	23	29	22
25	20	24	30	23
26	19	26	26	22
27	20	25	33	24
28	19	26	28	25
29	23	25	29	24
30	18	24	26	23
31		25	33	

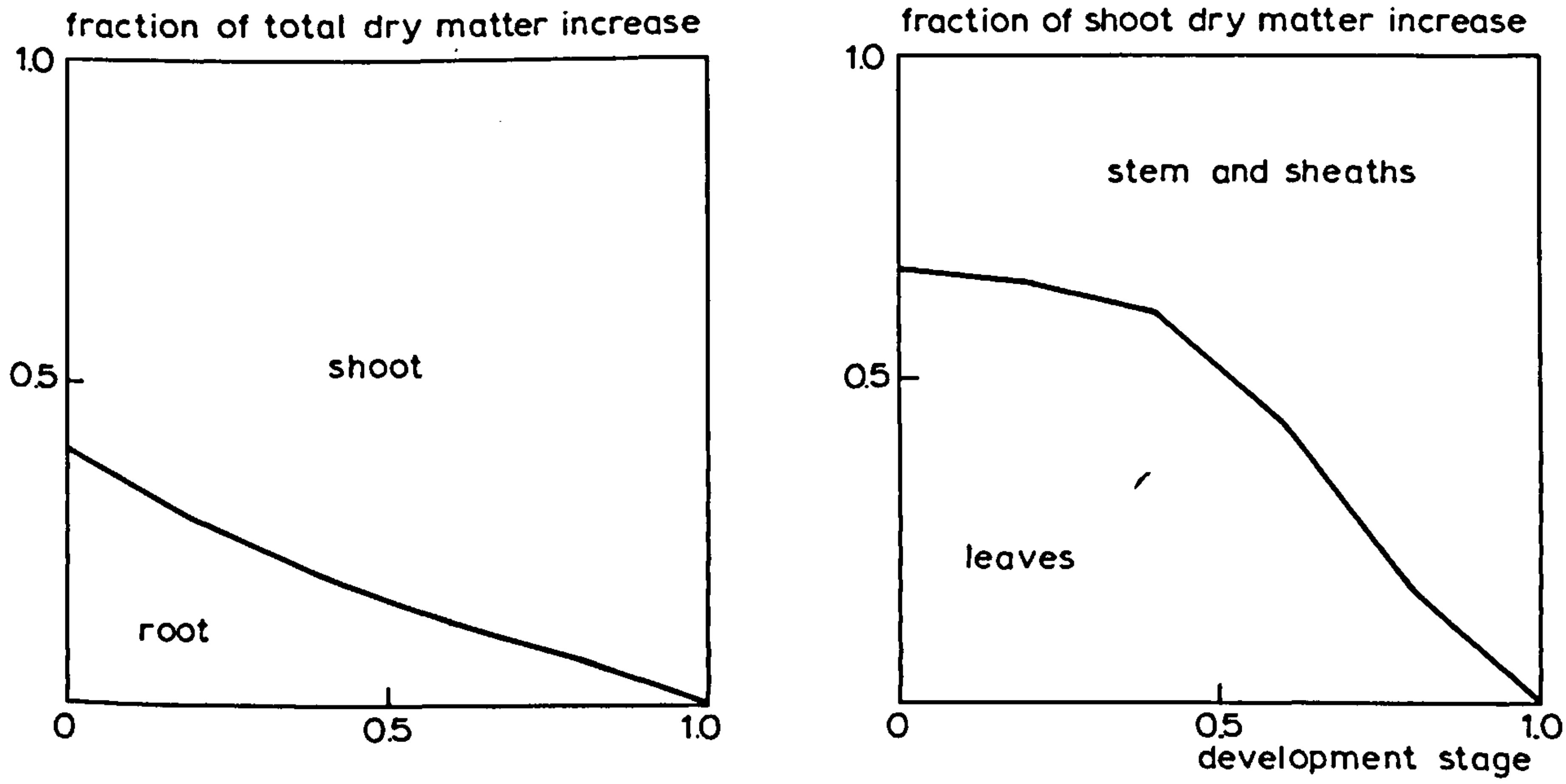

Figure 14. Partitioning factors for plant parts of maize in the course of development.

The distribution pattern for maize (Figure 14) is constructed from experimental data in the same way as is done for a part of the pre–silking period in Exercise 9.

2.2.4 *Development and dry matter distribution in cassava*

Cassava is a perennial plant that, for agricultural production, is propagated almost exclusively through stem cuttings. Many cultivars exist, their development pattern varying according to ambient climatic conditions. Short–duration cultivars are harvested 6–12 months after planting; long duration cultivars are often left in the field for periods of two years or more. Unlike rice and maize, the economic product is not the grain, but the storage root, which consists predominantly of starch. If environmental conditions are conducive for initiation storage roots are initiated about eight weeks after planting, which is mainly under photoperiodic control. Under short–day conditions, storage root initiation occurs readily, but it is delayed when day length exceeds 10–12 h, and consequently yields are lower. For this reason, cassava is most productive between 15° N and 15° S latitudes.

In the development of cassava, three phases may be distinguished:
– establishment,
– early growth and foliage formation,
– simultaneous formation of foliage and starch accumulation in the storage roots. The last phase may continue for more than a year. In Figure 15, dry–matter accumulation for various plant parts of cassava is shown for a period of two years. The graph shows that starch accumulation in the roots starts some four months after planting, that leaf weight shows a seasonal

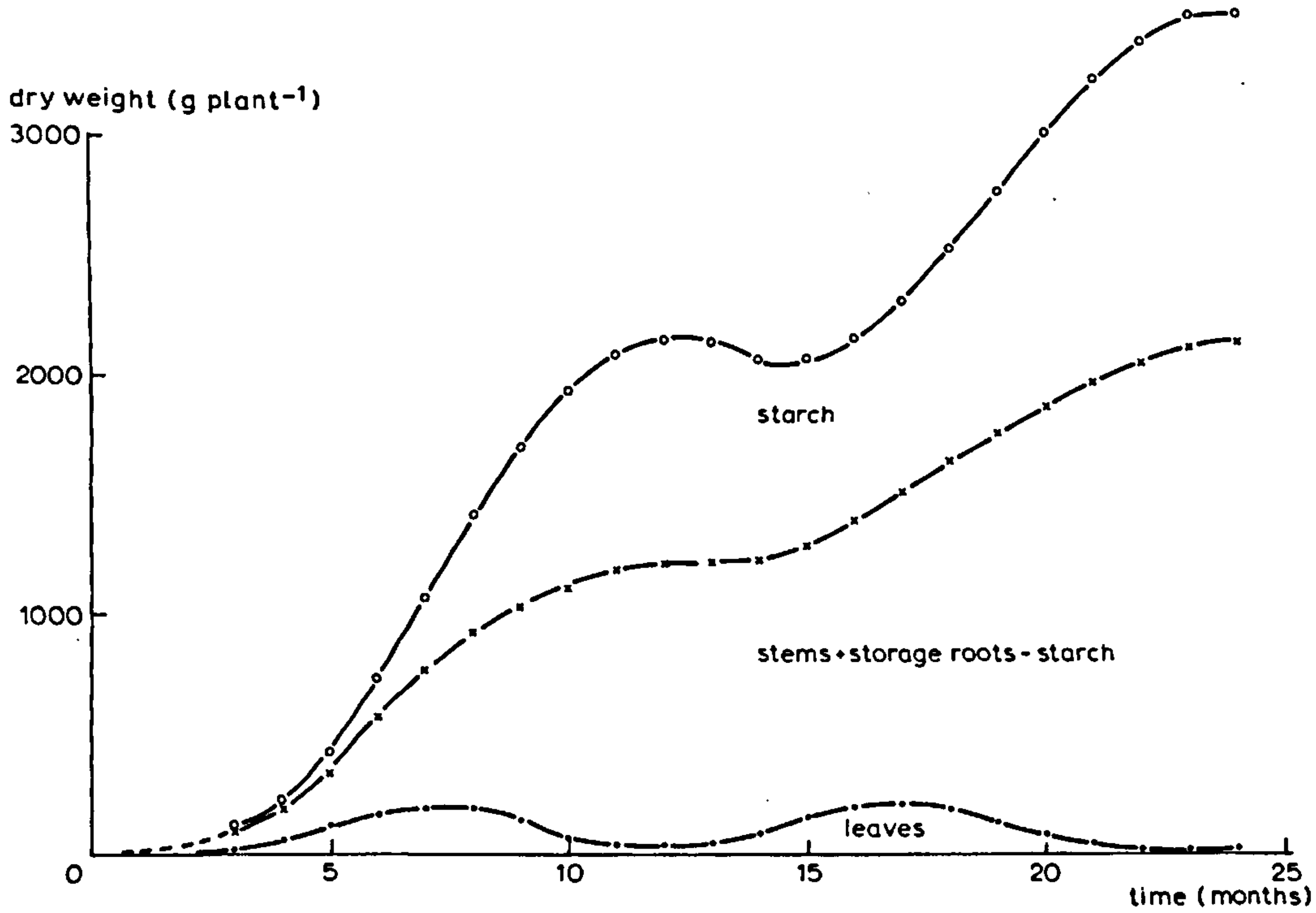

Figure 15. Dry weight of various plant parts of cassava in the course of time. (Source: Cours, 1948)

pattern of increase and decrease, and that this pattern is reflected in the dry matter accumulation in the other plant parts.

Boerboom's (1978) analysis of cassava production shows that the distribution of dry matter over the storage roots and stem or shoot is invariable with

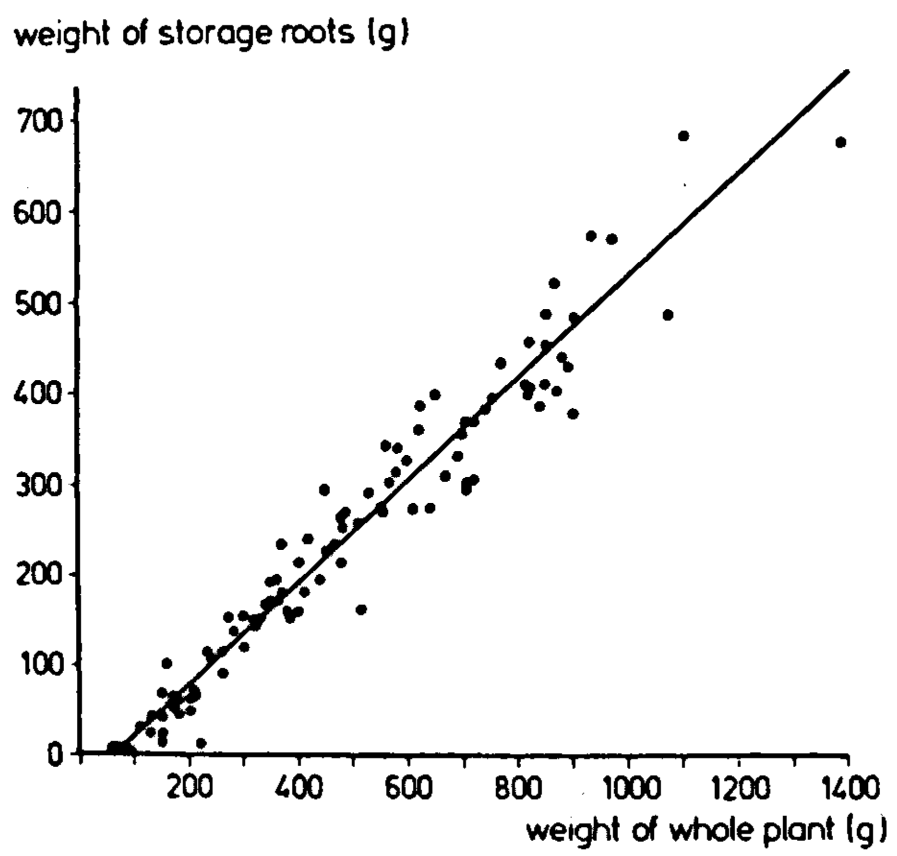

Figure 16. Relationship between dry weight of whole plant and dry weight of storage roots for cassava plants. (Source: Boerboom, 1978)

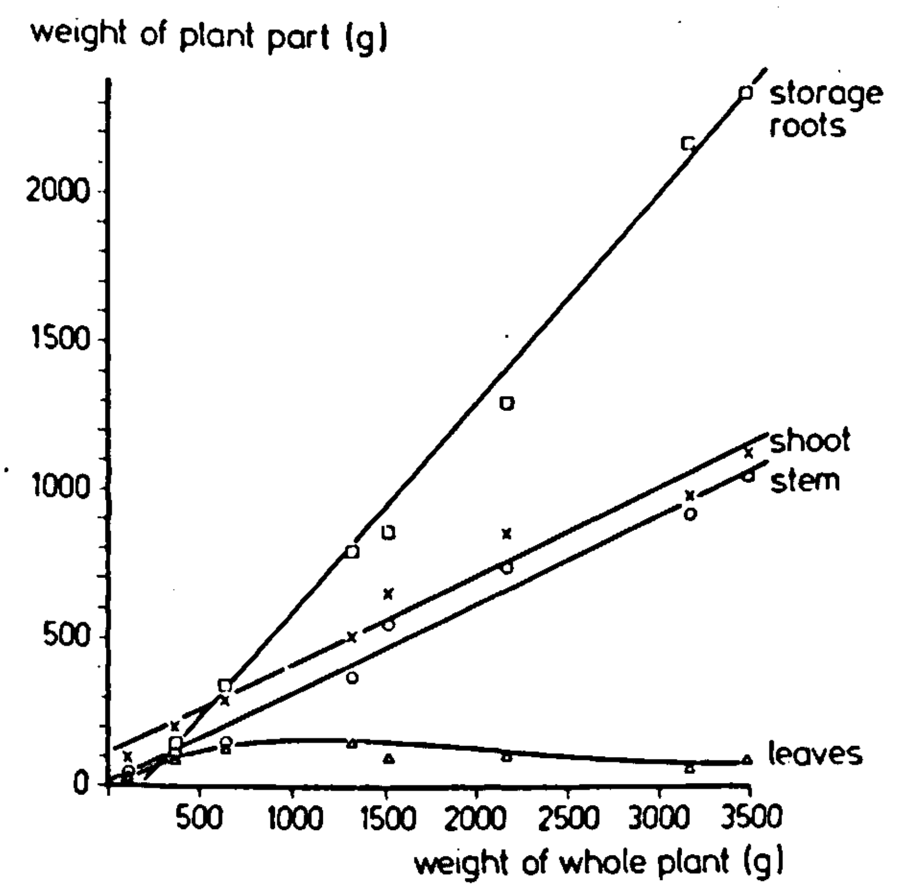

Figure 17. Relationships between dry weight of whole plant and dry weight of plant parts for cassava cv. SPP. (Source: Boerboom, 1978)

time for an extended period (Figures 16 and 17). The main parameters describing the distribution pattern over the different plant parts are: the total plant weight at which storage root production starts, represented by the intercept with the x axis and the efficiency of storage – root production, represented by the slope of the regression lines in Figures 16 and 17.

Experimental data were used to determine the partitioning factors in the same way as for rice (Figure 18). For the present procedure, the growth period

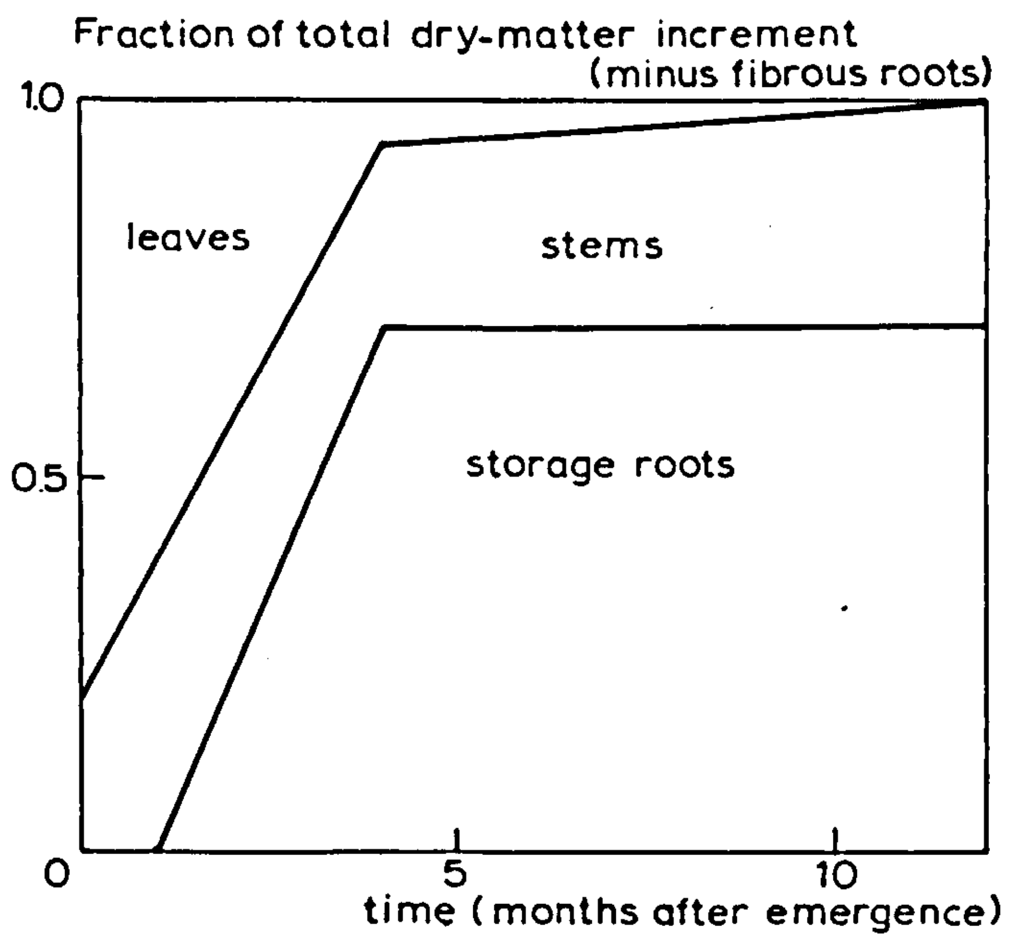

Figure 18. Partitioning factors for plant parts of cassava in the course of time.

is restricted to one year, because it is impossible to determine the partitioning factors for longer growth periods, as foliage formation in the second year mainly occurs at the expense of existing reserves and not from current dry matter production (Figure 15).

The independent variable in Figure 18 is not the development stage, as for rice and maize, but time after emergence. The experiments to which this graph refers were carried out at Buitenzorg, (Java, Indonesia) having a photoperiod of about 12 hours, i.e. under optimum conditions of day length. This description was adopted because it appeared impossible to determine temperature requirements for reaching the various development stages, or to establish development rates from existing experimental data. To achieve consistency in data handling, a constant development rate over the year could be assumed, giving an x axis with a scale from 0 to 1, i.e. adopting a development rate of 1/365, or 0.00274 d^{-1}.