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Manipulation of tuber-size distribution of a potato crop

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Summary

Tuber-size distribution is regulated by many diverse, interacting mechanisms and is therefore difficult to understand and manipulate. It is determined by plant density, number of stems per plant, number of tubers per stem, and yield. Seed size and plant number per unit area are easy to control, but stem number is affected by less controllable factors. Interactions between stems of different types are important for tuber-size distribution.

The hormonal regulation of stolonization and tuberization is still unknown, but under the conditions of north-west Europe the process of tuber set (which is also poorly understood) makes a greater contribution to the final number of tubers than tuberization. The total yield is also relevant, because it affects both the average tuber size and its variation.

Tubers on the same stem differ in timing, rate and duration of growth. The resulting hierarchy in sink strength is not consistent over time. Several mechanisms are suggested for this hierarchy.

Introduction

Potatoes are grown for different markets, each with its own demands. Two important characteristics are the average tuber size and its variation. Many growth processes in different organs and stages of development of the plant affect the final number and size of tubers. This is illustrated in Table 1, in which the agronomic possibilities for manipulation are indicated. All the processes mentioned in the table are strongly affected by environmental conditions, and each process is regulated by balances of internal plant growth regulators in a way still largely unknown. The processes are listed in chronological order, but this order is only valid for an individual tuber. Many processes can occur concurrently within a single plant (Struik & Van Voorst, 1986; Struik et al., 1988; Vreugdenhil & Struik, 1989). This is a complicating factor, but it also provides possibilities for manipulation. The processes listed in Table 1 are not independent and some of them are reversible.

Tuber formation and tuber growth are unique processes in the physiology of the

Table 1. Possibilities for agronomic manipulation of plant processes involved in the determination of tuber-size distribution.

Plant part	Process	Possibility of manipulation *
Seed tuber	Breaking of dormancy	+
	Germination	+
Stem	Emergence	(+)
	Growth	+
	Branching	(+)
	Retardation of growth	(+)
Stolon	Induction	–
	Initiation	–
	Growth	(+)
	Branching	(+)
	Inhibition of elongation	(+)
Tuber	Induction	(+)
	Initiation	(+)
	Set	–
	Growth	+
	Dormancy	(+)

* –, (+), + = no, small and large possibility of manipulation, respectively.

plant and their regulation is not identical with, for example, flower formation, seed set and fruit growth. Tuberization involves the development and growth of a stolon, the inhibition of the elongation of the stolon and the swelling of its tip. Moreover, tuberization is reversible. It may also occur continuously after a certain period of induction. Competition between tubers on one stem should not be compared with the relations between fruits on one plant or from one inflorescence (such as with potato berries, tomato fruits or caryopses on one wheat ear). The potato plant and the individual tuber are very plastic, allowing changes in growth patterns.

This paper analyses the various processes which determine tuber growth and the number of tubers per unit area, and identifies problems which have to be solved to enable tuber-size distribution to be manipulated.

Factors affecting tuber-size distribution

Tuber-size distribution is determined by the following characteristics (Fig. 1).

1. The number of plants per unit area as influenced by the number of seed tubers planted and the percentage emergence.
2. The number of stems per plant, their subsequent development and the inter-stem competition.
3. The number of tubers per stem; this is determined early in the growing season, when stolon formation, tuberization and tuber set have resulted in a final number of tubers that are sufficiently competitive to grow to commercial size. Later in the

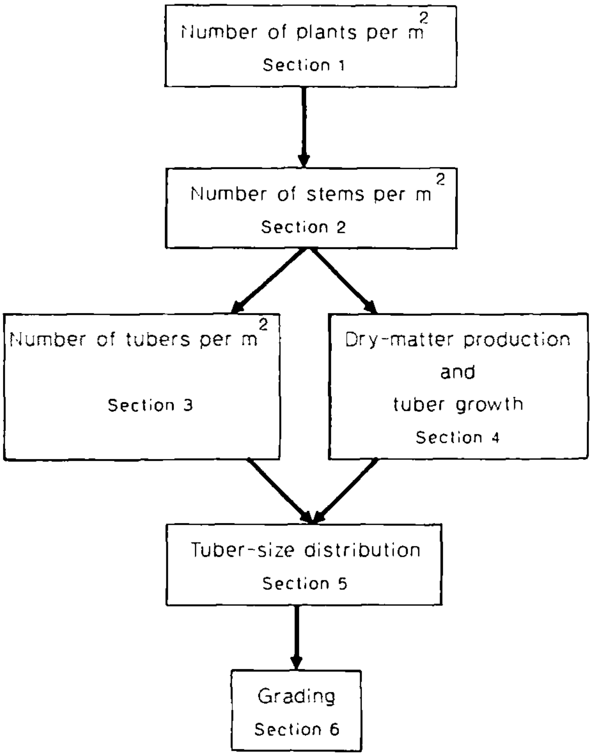

Fig. 1. Relationship between the main characteristics influencing tuber-size distribution.

growing season, the number of tubers may increase due to second growth, or decline due to resorption.

4. The rate and duration of crop growth, which influence both the average size of the tubers and its variation.
5. The size of each individual tuber, which is influenced by its time of initiation and the rate and duration of growth. Tubers from the same plant (or even from the same stem) differ in these three characteristics. There seems to be a hierarchy of tubers on the same stem according to their sink strength. This hierarchy is governed by internal factors, but is also affected by the history of the crop and the environmental conditions during its different stages of growth. Sink-strength hierarchy is not constant during the plant's development (Schnieders et al., 1988; Płodowska et al., 1989), so the differences between tubers in their rates of growth are not constant. Although the size distribution shows a general pattern, which can be determined on the basis of the average tuber size and the spread of yield across size grades (cf. Sands & Regel, 1983; Travis, 1987; MacKerron et al., 1988), deviations from this pattern are possible.
6. The size distribution of the marketable yield differs from the harvestable yield. This difference is influenced by the proportion of tubers showing physiological disorders (second growth, growth cracks, etc.), damage, greening, diseases, etc., or which are

too small and are removed from the lot. Since in most countries grading is not based on weight, tuber shape is also an important factor.

1. Number of plants per m^2. The number of plants per m^2 can be described as:

$$\rho_p = \rho_s \cdot e \qquad \text{Eqn 1}$$

in which ρ_p is the plant density (plants per m^2), ρ_s is the seed-tuber density (seed tubers per m^2) and e is the proportion of emergence (plants per seed).

When seed tubers of good quality and of the proper physiological age are used, the percentage of emergence will be close to 100 %. Thus the number of plants mainly depends on the number of tubers planted. This number can be determined by:

$$\rho_s = w_p / \bar{w}_s \qquad \text{Eqn 2}$$

in which w_p is the planted seed weight (g per m^2) and $\bar{w}_s$ is the average seed size (g per seed).

Plant density can also be derived from:

$$\rho_p = \rho_r \cdot d_p \qquad \text{Eqn 3}$$

in which ρ_r is the row density (rows per m) and d_p is the plant distance within the row (plants per m per row).

ρ_r and d_p define the spatial arrangement of the plants. The potato's large capacity to fill extra space by enhanced stem formation and branching, and by increasing the size of individual stems, means that plant arrangement does not have a large effect, unless the crop is harvested at an early stage (Schepers, 1975a, b). This topic is further discussed in the next section.

2. Number of stems per m^2. Even when there is complete control of pests and diseases, the number of stems per unit area is affected by many factors: the number of plants per unit area, the number of eyes per seed tuber which produced a plant, the number of sprouts per eye, and the proportion of sprouts that will produce an emerging stem.

The number of eyes per seed tuber which produced a plant is influenced by the genotype, shape and size of the mother tuber. The number of sprouts per eye and the proportion of sprouts that will produce an emerging stem are also influenced by genotype and size of the tuber, but also by the physiological status of the mother tuber (and so by conditions during the production and storage of the seed); they can also be manipulated by applications of growth regulators during storage or just prior to planting.

Moreover, the number of sprouts is also affected by the conditions during presprouting and the damage to sprouts during planting. The proportion of sprouts that will produce an emerging stem is also influenced by the conditions after planting (moisture, temperature and structure of the soil), and the size and development of the sprouts at planting, which can be manipulated easily (cf. Schepers & Hoogland, 1968).

Seed size affects the growth vigour of the young potato plant and is the factor most likely to influence the stem and tuber number per plant. Even when the number of stems is not affected by seed size, the yield and tuber-size distribution are influenced: a yield increase, especially of the large tubers, is often observed when large seed is used (cf. Scholte, 1975). When seed tubers with only one sprout are planted, large seed will produce more below-ground branching than small seed (C.B. Bus, unpublished).

The potential to influence the tuber-size distribution by manipulating the physiological status of the mother tuber needs to be studied further. The effects of physiological age of the mother tuber are not limited to the period of sprouting and sprout emergence, but also influence the canopy development as well as tuberization and tuber growth. Methods to analyse physiological age on a routine basis are required. Uncontrollable factors, however, are the growing conditions during the production of the seed tubers and the environmental conditions after planting (cf. Bodlaender & Marinus, 1969; Haverkort et al., 1990a). Growing conditions during the season in which the seed tubers are produced affect the duration of dormancy and the rate of physiological ageing (Wurr, 1978). The mechanisms of this influence are only partly understood.

Not every sprout has the same origin or similar competitive strength, and stems originating from the same seed tuber compete strongly for carbohydrate reserves, water and minerals during sprouting and pre-emergence growth (Morris, 1967; Moorby, 1967; Allen, 1978). During and after emergence, neighbouring plants compete for water, minerals and light (Svensson, 1962; Moorby, 1967; Allen, 1978; Allen & Scott, 1980). It is important to distinguish at least the following types of stems:

- main stems, i.e. stems originating directly from the mother tuber. There can be more than one per eye.
- stems originating as branches of the lower below-ground section of a main stem.
- a branch arising from the subsurface section of a main stem.
- a branch arising in the lower above-ground section of one of the other stem types.

Only the first two stem types usually have the potential to develop tubers, but this potential is not always 100 %, as will be discussed.

Branching of any type is affected by the physiological status of the mother tuber in interaction with its genotype and the environmental conditions (mainly light and temperature). Branching of the last two types above can be influenced by crop management (mainly nitrogen supply and stem density), but its role in determining the tuber number and total yield is poorly understood.

Each type of stem mentioned above can form second-level branches as soon as the main axis has initiated an inflorescence, thereby increasing the leaf area, the leaf-area duration and the duration of tuber growth.

In summary, for good control of the number of stems per unit area, one must control the number of sprouts planted per unit area. The means to do this include the choice of cultivar, the size of seed selected, the shape and physiological age of the mother tuber, pre-treatment of the seed, and the planting technique adopted. Control of the final number of stems and the number of branches is more difficult. The main problems to be solved for an effective manipulation of stem number are the control of the number of main stems per planted sprout, and of the branching of sprouts below or just above the soil level.

Not every emerged stem will produce tubers. Both main stems and below-ground branches may fail to develop tubers, because of early senescence of the stem (cf. tiller death in cereals and grasses; Moorby, 1967; Allen, 1978), incomplete tuber induction (e.g. because of heat; Ewing, 1981) or because of a lack of tuber sites (e.g. because the stem originates just below the surface; cf. Allen & Wurr, 1973). Under inductive conditions, a surviving main stem will usually produce tubers (cf. Allen & Wurr, 1973), whereas the other stem types may not. It is important to know more about the development of the different stem types, and also what consequences the proportion of the different stem types will have, not only for the competition between stems and tubers, but also for the total tuber number, the tuber yield and the tuber-size distribution (cf. Allen, 1978; Christ & Caesar, 1989).

There are at least three further control mechanisms involved in competition between tubers: control of the number of tuber-bearing stems; control of the competition between tuber-bearing main stems for water, light, minerals, nitrogenous compounds and hormones; and control of the competition between tuber-bearing main stems and tuber-bearing branches.

Oparka & Davies (1985) showed that some time after emergence each tuber-bearing main stem functions as an independent unit, with little or no carbon exchange between stems. Competition between tubers should therefore be considered for each individual stem. The tuber number and yield per stem, and tuber sink-strength hierarchy, however, are greatly affected by the above-mentioned competitive relationships between stems.

3. Number of tubers per m^2. Before a stem produces tubers it usually forms stolons. The number of stolons per stem depends on three factors:

- the number of below-ground nodes, which varies with cultivar and environmental conditions (Taylor, 1953) and also depends on cultural practices such as planting depth, hilling and earthing up;
- the proportion of *stolon-bearing* nodes, which is affected by the size of the mother tuber, the number of sprouts per mother tuber (Morris, 1966), the nitrogen supply (Lovell & Booth, 1969) and probably also the environmental factors;
- the number of stolons per stolon-bearing node, which is affected by many intrinsic and environmental factors.

The final number of stolons per unit area is reported to be affected by genotype, seed size and number of stems (Svensson, 1962) and is sensitive to temperature (Borah & Milthorpe, 1962; Morris, 1967; Struik et al., 1989a), and drought (Struik & Van Voorst, 1986; Haverkort et al., 1990b), but not to photoperiod (Struik et al., 1988) or light intensity (Sale, 1973; P. C. Struik, unpublished data). It is not always clear whether these effects are caused by changes in the number of below-ground nodes, the number of stolon-bearing nodes, the number of stolons per node, or by a combination of these factors.

Stolon formation normally follows a pattern along the stem and over time. On plants grown from seed tubers, stolon formation starts at the nodes closest to the mother tuber and progresses acropetally (Plaisted, 1957; Cutter, 1978). The first-formed stolons reach a greater length and are more likely to branch than those initiated later (Lovell & Booth, 1969; Struik & Van Voorst, 1986). Stolon branching is also enhanced by high temperature (Struik et al., 1989a), long photoperiods (Struik et al., 1988), low stem density (Svensson, 1962) and a dry soil in the stolon environment (Struik & Van Voorst, 1986). When a stolon is initiated later, the time between stolon initiation and tuber initiation is shorter (Vreugdenhil & Struik, 1989).

In addition to the pattern of stolon formation there also seems to be a pattern of *time of tuber formation* along the stem and the stolons (Vreugdenhil & Struik, 1989). Tuberization *frequency* also depends on the node of the stem (Wurr, 1977; Cother & Cullis, 1985). The *pattern of tuberization frequency* over the different stem nodes is affected by genotype, environment and number of stolons (Moorby, 1967; Wurr, 1977; Cother & Cullis, 1985). The total proportion of stolons producing tubers also depends on the cultivar (Svensson, 1962; Wurr, 1977), the growing conditions (Haverkort et al., 1990b), cultivation technique (e.g. seed size, planting distance and depth, earthing up, fertilization; Svensson, 1962), but is not reduced by inter-stem competition (Svensson, 1962).

Oparka (1987) showed that excising the apices of primary stolons does not affect the number of tubers or tuber yield, but complete removal of primary stolons greatly reduces the final yield and tuber number. Removal of tuber initials, however, significantly reduces tuber yield, without affecting tuber number. These results clearly illustrate the plasticity of tuber formation.

Haverkort et al. (1990b, c) showed that there is a close relationship between the number of stolons and the number of tubers, whereas the number of stolons is apparently affected by many uncertain factors such as the amount of rainfall early in the growing season and the presence of stolon pruning diseases such as *Rhizoctonia solani* (Cother & Cullis, 1985). Fig. 2 shows an example of the interrelationships between the number of sprouts per tuber, the number of stems per plant, the number of stolons per plant and the number of tubers per plant. This example applies at only one plant density. The coefficient of determination for the relation between the number of tubers per plant and the number of sprouts per seed tuber in this particular example is as high as the coefficients of determination for the intermediate relations. In other examples this relationship is less apparent.

Stolons produce tubers only when conditions for tuberization are favourable. The processes of tuber induction and tuber initiation are poorly understood (Vreugdenhil & Struik, 1989). Recently, two promising new developments have been reported: firstly, Struik et al. (1987) found that extracellular extracts from potato leaves had a stimulatory effect on tuber formation on one-leaf cuttings which were not fully induced to tuberize. This effect was especially marked when extract was used from plants that had not experienced any inductive photoperiod cycles. These results have been confirmed in later experiments with *Solanum demissum*, which has an absolute requirement for a period of short days for tuberization (Helder et al., 1989). Secondly, Koda and coworkers (Koda & Okazawa, 1988; Koda et al., 1988; Y. Koda, personal communication) extracted a compound from leaf tissue that strongly stimulated tuberization *in vitro*. The compound has recently been identified as resembling jasmonic acid (Yoshihara et al., 1988).

In cultivars with a long period of tuber initiation (such as Bintje) it is important to realize that the different stages of tuber development as described by Vreugdenhil & Struik (1989) occur concurrently. That means that the physiological status of stolon tips differs and depends on their location, on the initiation date of the stolon on which the tip is located, and on many other imperfectly understood factors (Struik & Van Voorst, 1986; Struik et al., 1988; Vreugdenhil & Struik, 1989). Since tuberization is regulated separately for each individual stolon tip, examining the tuberization process *per se* does not contribute much to our understanding of the hierarchy within a stem. Moreover, a considerable number of swollen stolon tips may fail to form tubers. Many tuber initials remain very small or are resorbed after a while, causing the total number of tubers present to decline (e.g. Pätzold & Stricker, 1964; Cho & Iritani, 1983). The 'regulation' of the number of tuber sets which will finally produce a marketable tuber usually takes place rapidly, although new tubers can continuously be formed and

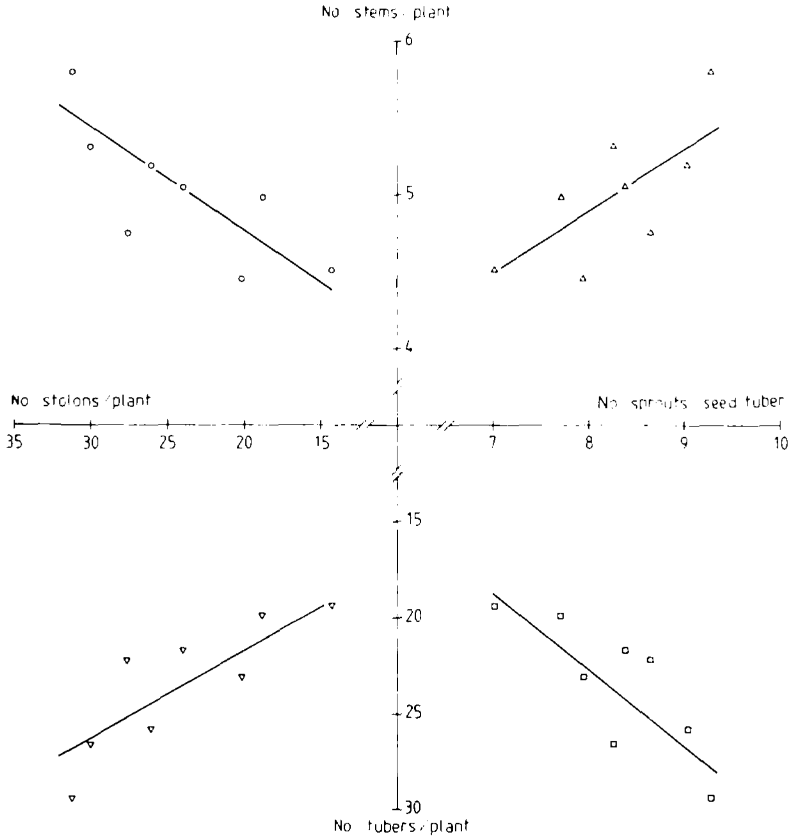

Fig. 2. Interrelationships of numbers of initial sprouts, stems, stolons and tubers per plant of cv. Bintje, grown on a clay soil near Wageningen (the Netherlands) in 1986. From Haverkort et al. (1990c). For the statistical analysis see original publication.

resorbed (Moorby & Milthorpe, 1975). The mechanisms involved in this regulation are still unknown, but are probably as important for the final tuber-size distribution as the process of tuberization itself.

4. Dry-matter production and tuber growth. Various researchers have described the growth of the potato crop (e.g. Allen & Scott, 1980; Spitters, 1990), hence a brief description will suffice here. The rate of crop production is more or less proportional to the rate of photosynthesis, which depends in the first instance on the amount of radiant energy intercepted (Gosse et al., 1986). According to Spitters (1990), the rate of crop growth can be described by:

$$\Delta W_t = f_t \cdot PAR_t \cdot \epsilon \qquad \text{Eqn 4}$$

in which ΔW_t is the rate of growth on day t (g dry matter per m^2 per day), f_t is the fraction of the total photosynthetically active radiation intercepted by the crop (MJ per MJ), PAR_t is the incoming radiation that is photosynthetically active (MJ per m^2 per day), and ϵ is the average light-conversion efficiency (g dry matter per MJ PAR).

From Eqn 4 it can be derived that the amount of dry matter at a certain time can be calculated as:

$$W_t = \Sigma(PAR_t \cdot f_t) \cdot \epsilon \qquad \text{Eqn 5}$$

in which W_t is the dry-matter yield (g dry matter per m^2).

The f_t is not constant during the growing period; it approximately represents the degree of ground cover, which changes in time and is determined by the number of stems and branches, the leaf area per stem or branch, and other factors such as lodging, distribution of leaves and the leaf-angle distribution. The leaf area per stem depends on cultivar, the seed size, the physiological age of the mother tuber, environmental conditions and cultural practices (e.g. Bodlaender & Reestman, 1968; Allen & Scott, 1980; Fahem & Haverkort, 1988; Haverkort et al., 1990a). The leaf-angle distribution may depend on genotype, the time of the day, and the stage of the crop.

The relation between the leaf area per unit area of land and the light interception by a potato crop has been assessed by many authors (e.g. Allen & Scott, 1980; Khurana & McLaren, 1982; Burstall & Harris, 1983). Some authors use the global radiation instead of PAR; global radiation, however, has a lower extinction coefficient and a lower light-conversion efficiency (cf. Spitters, 1987). Light interception can also be estimated by the proportion of the ground which is covered by the green canopy, since a relationship between ground cover and light interception has also been established (e.g. Burstall & Harris, 1983), although it depends on cultivar and planting pattern. Ground cover is easy to estimate non-destructively and precisely by means of a grid (Khurana & McLaren, 1982). Part of the total amount of photosynthetically active radiation is intercepted by the leaves (fraction determined by the leaf-area index), thus enabling the total amount of intercepted radiation to be determined. By applying Eqn 5, the total amount of dry matter produced can be calculated.

Part of the dry matter produced is contained in tuber dry matter and part in the production of other parts. The fractions are determined by external and internal factors and are not constant during the growing season (cf. Van Heemst, 1986).

Tuber yield can be calculated as:

$$W_{\text{tuber, dry}} = W_t \cdot h \qquad \text{Eqn 6}$$

in which $W_{\text{tuber, dry}}$ is the tuber dry-matter yield (g dry matter per m^2) and h is the fraction of dry matter partitioned to the tubers (g per g).

h at time t can be calculated as follows (Spitters, 1987):

$$h_t = h_{\max} \{1 - \exp[-s(t-i)/h_{\max}]\} \qquad \text{Eqn 7}$$

in which $t-i$ is the temperature sum after the beginning of the tuber bulking and s is a function of the maturity class of the cultivar.

The net increase in dry matter which is not contained in tuber dry matter may be used to produce new leaf area, e.g., on second-level branches, and thus contribute to

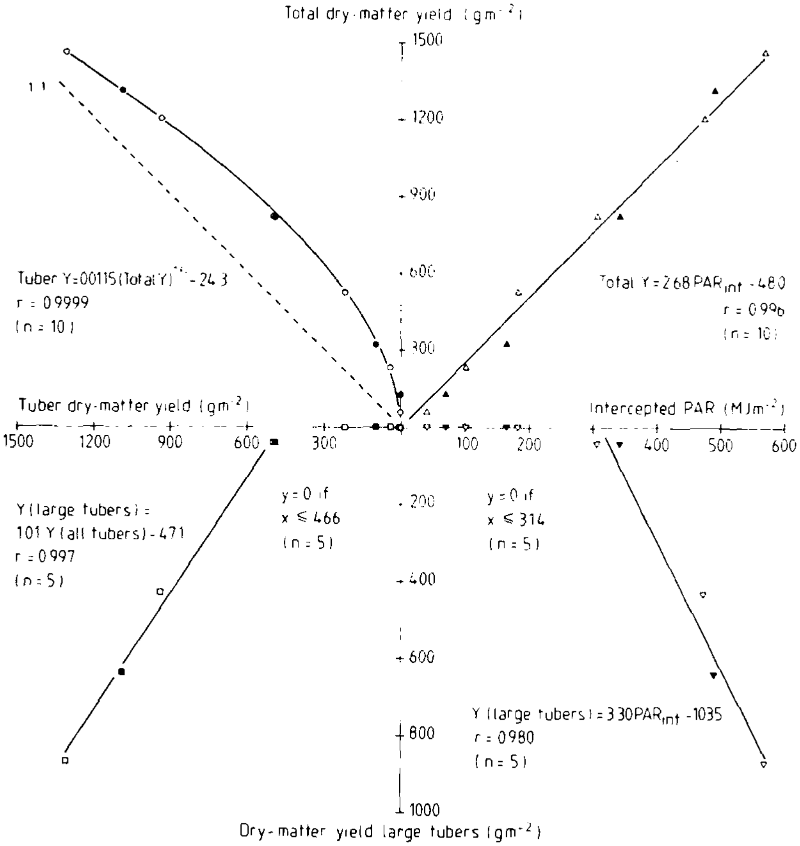

Fig. 3. Interrelationships between the amount of photosynthetically active intercepted radiation (PAR), total dry-matter yield, tuber dry-matter yield and the dry-matter yield of large tubers (>120 g fresh weight). Data from a shading experiment in 1985 with cultivar Bintje (P. C. Struik, unpublished). Open symbols: control; closed symbols; shaded.

the interception of extra light, especially during the later stages of plant growth.

Tuber fresh yield can be calculated as follows:

$$W_{\text{tuber, fresh}} = W_{\text{tuber, dry}}/c_{\text{dm}} \qquad \text{Eqn 8}$$

in which $W_{\text{tuber, fresh}}$ is the tuber fresh-matter yield (g per m^2) and c_{dm} is the tuber dry-matter content (g per g).

Fig. 3 shows an example of a growth analysis in the form of a four-quadrant figure, based on a shading experiment with frequent intermediate harvests (P. C. Struik, unpublished). The total yield is closely related ($r = 0.996$) to the amount of intercepted light. This close relation is partly caused by the fact that two cumulative variables are regressed against each other. The nature of the slope, however, is of great interest; it is constant during the entire growing season. Its value is 2.68 g dry matter per MJ intercepted photosynthetically active radiation. This is a normal value for the light-conversion efficiency (cf. Allen & Scott, 1980; Khurana & McLaren, 1982; MacKerron & Waister, 1985; Haverkort & Harris, 1987; Fahem & Haverkort, 1988; Spitters et al., 1989). The relation between the total yield and the tuber yield is not linear. The yield of tubers larger than 120 g fresh weight shows a close, linear relationship with the total tuber yield (cf. Burstall et al., 1987). Because the harvest index was almost constant for the range above the yield attained when cumulative light interception was more than 300 MJ per m^2, the relation between cumulative intercepted radiation and the yield of large tubers was also linear. The relationships in the lower part of Fig. 3 are strongly influenced by the specific conditions of this experiment and should not be considered to be of general value.

5. *Tuber-size distribution.* Once a certain number of tubers have set, the final tuber-size distribution depends on the growth of the individual tubers and on the competitive relationships between them. Within a cultivar, the average tuber weight and number of tubers define a unique tuber-size distribution (Sands & Regel, 1983; Travis, 1987; MacKerron et al., 1988). The relative variability in tuber size, defined as the standard deviation of the tuber size divided by the average tuber size, is approximately constant for a given cultivar. The changes in and the effects of treatments on the spread of tuber size usually parallel those on the average size (Travis, 1987). However, the link is not a rigid one (Travis, 1987). Therefore, it is possible to manipulate the size distribution at a given yield potential and for a fixed number of tubers by influencing the competition between tubers.

Fig. 4 illustrates the tuber-size distribution on different harvest dates, and shows a shift in the average tuber size to the larger grades and an increase in the variation in size.

Not all tubers on the same plant or stem start their bulking at the same time. This difference is caused by many factors, including the timing of tuber set and the position on the plant. Clark (1921) and Ahmed & Sagar (1981) stated that the duration of the main period of growth and the growth rates vary independently, both influencing the final size of each tuber and thus tuber-size distribution.

Moorby (1967) suggested that only some of the tubers grow rapidly at any one time. When certain tubers approach their final weights, their rate of growth is reduced and other tubers start to grow. Meredith (1988a, b) introduced the concept of twinning, stating that potato plants have a tendency to produce tubers of equal size ('twinning'). In his view twinned tubers are a consequence of discrete episodes of tuber initiation, followed by growth of tubers in cohorts. This theory has been questioned recently by B. Marshall, H. T. Holwerda & P. C. Struik (personal communication).

There are many intrinsic, physiological reasons why it may be necessary for a plant to adjust the rates of growth of the individual tubers to each other. If a hierarchy exists, it is crucial for the final tuber-size distribution. It may act in two different ways: it may determine which tuber sets reach harvestable size and may also affect the rate and duration of tuber growth, thus determining in which size grade a tuber will fall.

Different characteristics have been observed or suggested to be associated with a high rate of individual tuber growth or with a large ability to compete (i.e. with a high ranking in the hierarchy). A precise hierarchy of sink strength among the tubers on one stem is difficult to determine, especially since it may change with time. Moreover, only a few tubers are formed on each stem. The size distribution may therefore deviate

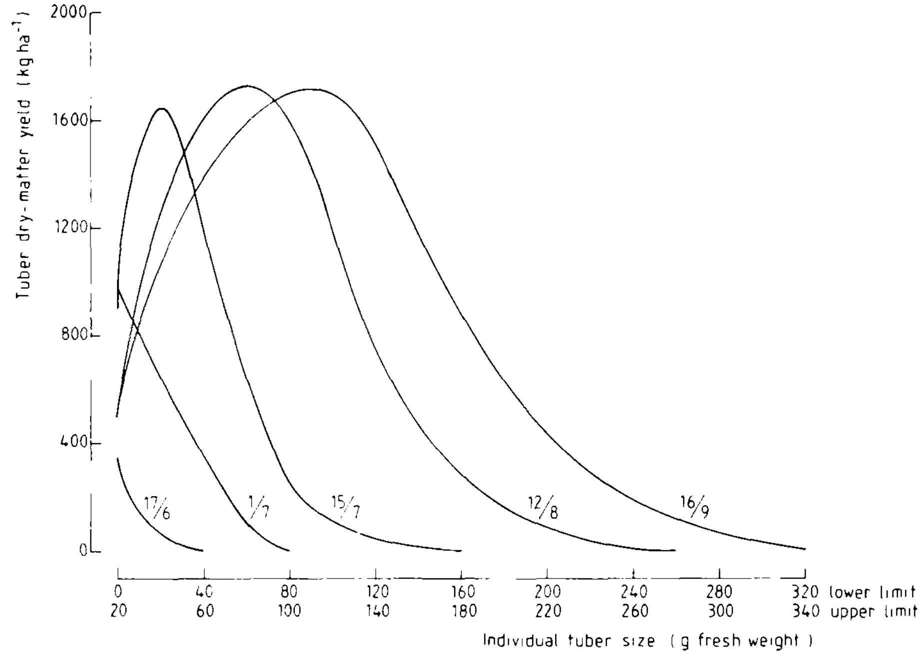

Fig. 4. Accumulation of the dry-matter yields of different tuber-size classes. Data from five harvest dates (P. C. Struik, unpublished).

considerably from the average, without being significantly different from the overall distribution. Thus it is difficult to discriminate between stochastic and physiological differences. The true interactions between tubers occur at the stem level, whereas the size distribution at the crop level is determined by the relative frequencies of the different stem types, their characteristic tuber-size distributions (or relative variability of tuber size) and naturally occurring variation. In order to manipulate tuber-size distribution it is necessary to learn more about the mechanisms which regulate hierarchy, as well as their relative importance.

6. Grading. During grading, the diseased tubers and those showing size and shape defects are removed. The remaining tubers are all marketable, but still need to be graded. Since in most countries grading is done using square meshes, the relation between fresh weight and volume or dimensions is very important. Therefore a tuber-shape factor is relevant for the tuber-size grades.

Tuber shape depends not only on the cultivar and on the physiological age of the mother tuber (Reust & Münster, 1978), but also on the conditions during growth, such as soil type (Reust & Münster, 1978), drought (Reust & Münster, 1978; Van Loon, 1981), and temperature (Epstein, 1966; Struik et al., 1989b; Vreugdenhil & Struik, 1989). The relationships between size grades and the dimensions of the tubers have been assessed in many reports (e.g. McRae et al., 1986; Pitts & Hyde, 1987; Pitts et al., 1987).

Conclusion

Tuber-size distribution can be influenced to some extent by influencing the total tuber yield, the number and size of seed tubers planted, and the number of stems per plant, as well as by manipulating the ratios of the different stem types. When yield must be maximized, the farmer can influence size distribution mainly by the quality of the seed tubers, and by their size and planting density. Under field conditions, however, the stem number and frequency of stem types are hard to control. More research is needed to enable better control of the density of sprouts, the proportion of sprouts that produce an emerging stem, and the degree of branching.

The mechanisms which regulate the distribution of tuber sizes within one single stem are too multifarious and complex to be understood at present, let alone to be used in agricultural practice. Extensive research is required at many levels (the cell, the organ (stolon tip), the stem, the plant and the crop) in order to elucidate the regulation of tuber-size distribution. This research should focus on the tuber-forming potential of stems and branches, the proportion of tuber initials that produce a marketable tuber, and the competition between tubers.

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