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Possible mechanisms of size hierarchy among tubers on one stem of a potato (*Solanum tuberosum* L.) plant

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Summary

The tubers on one potato stem vary greatly in size and their size distribution may be described by their number and their average size and its variation. These components are mutually and closely related.

The variation is partly caused by stolon characteristics, including their date of initiation, position and size. Tuber size is therefore partly determined before tuberization. Tuber-specific factors, such as the position and activity of the tuber initial also play a role, but the date of initiation of an individual tuber is not crucial. Later on, during tuber bulking, the activity of enzymes involved in starch metabolism, the levels of hormones, the mineral composition and the turgor potential are associated with the tuber growth rate.

The growth characteristics of individual tubers may also vary since they are exposed to different conditions because of differences in position or growing period.

Introduction

Potato (*Solanum tuberosum* L.) plants form tubers on stolons, if conditions are favourable. There can be numerous sites of tuber formation on a single potato stem. Tuber formation consists of many different steps, such as stolon formation and growth, inhibition of stolon growth, and tuber induction, initiation, set and growth (Struik et al., 1988a; Vreugdenhil & Struik, 1989; see also these papers for definitions); each step is regulated by balances of internal plant growth regulators in a way still largely unknown. Because several of these steps can occur concurrently on one stem (Struik & Van Voorst, 1986; Struik et al., 1988a; Vreugdenhil & Struik, 1989), the tubers of a single stem depend on the characteristics of the stolon to which they are attached, such as the position of that stolon on the stem, and the date of initiation of the stolon, etc. Due to these differences and other (partly unknown) specific influences associated with the position of the stolon tip, there are differences in the date of initiation and

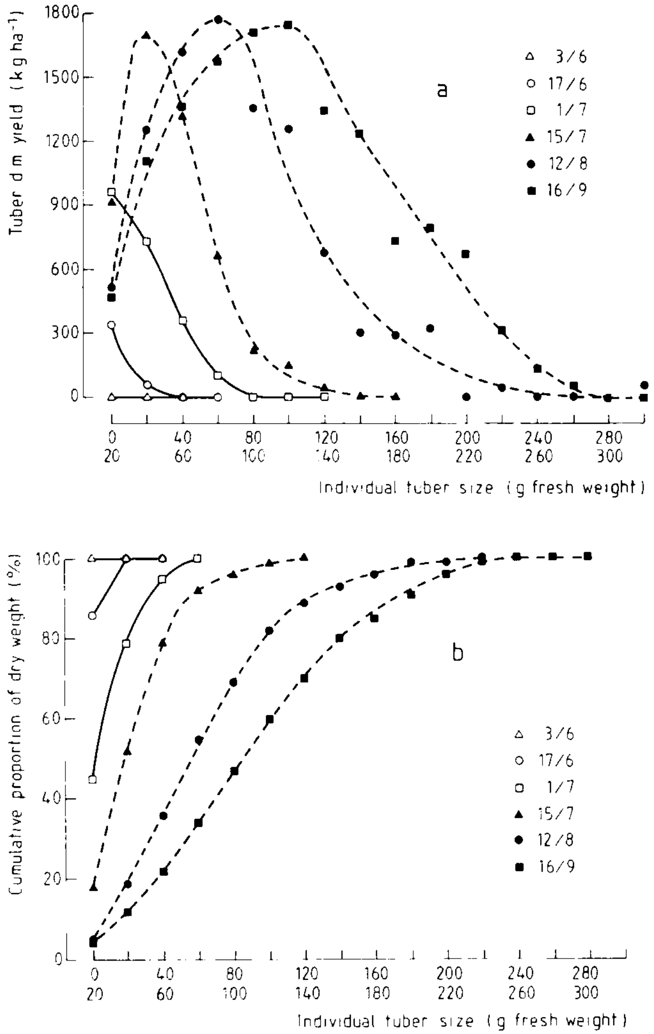

Fig. 1. Development over time of the tuber-size distribution of a potato crop in the Netherlands.
1a. Tuber-size distributions at different dates of lifting, plotted as dry-matter yields of a given grade against individual tuber fresh weight.
1b. Tuber-size distributions at different dates of lifting, plotted as cumulative proportions of the dry weight of a given grade against the individual tuber fresh weight.

set of the tubers, and also in their chances to grow.

At any given time, the tubers on one stem vary in size for reasons that are poorly understood. The differences in size are partly related to differences in the date of tuber set and in the rate of growth. However, it is commonly believed that the rate of growth of each individual tuber fluctuates (Moorby, 1967, 1968; Gray, 1973; Wurr, 1977;

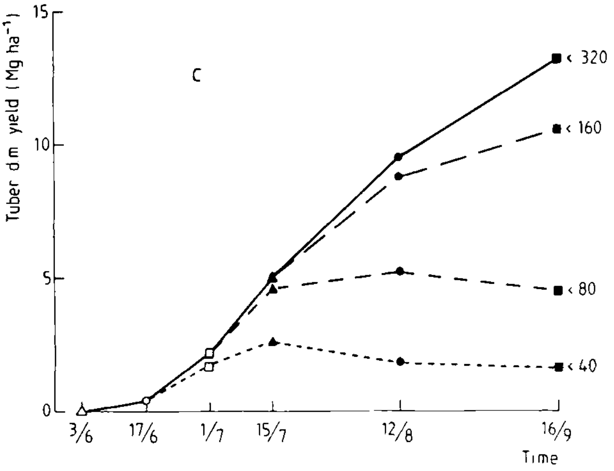

Fig. 1c. Development over time of the dry-matter yield of tubers smaller than a given size.

Ahmed & Sagar, 1981; Engels & Marschner, 1986a, b, c; Schnieders et al., 1988; Struik et al., 1988b) and that the duration of the main period of growth and the rate of growth vary independently between tubers (Clark, 1921; Ahmed & Sagar, 1981).

Shortly after tuber set, there seems to be some relationship between the 'sink strength' of a tuber and its size as is shown, for example, between the size of the tuber or its growth rate and its content of labelled carbon when $^{14}CO_2$ is provided to the plant (Oparka, 1985; Engels & Marschner, 1986c). These initial differences in the rate of tuber growth may be important for the final size distribution. However, the relationship weakens during later stages of growth (Moorby, 1970; Oparka, 1985): the sink strength of a tuber no longer depends on its size alone, but also on other characteristics such as the activity of certain enzymes in the tubers, the tuber position, etc. (cf. Engels & Marschner, 1986a, b, c).

The tuber-size distribution of a potato crop is affected by many factors (Struik et al., 1990). The size distribution of one plant depends on the 'sink strength' of its individual tubers, which is affected by various characteristics whose relative importance changes with time. In this paper we discuss the factors which have been suggested to be associated with the rate of growth of tubers or with their ability to compete. The factors can be divided into four groups, depending on their relationship to: 1) the position, date of initiation and size of the stolon to which the tuber is attached; 2) the date of initiation of the tuber and its initial activity; 3) internal tuber characteristics, such as turgor potential, hormone concentrations and enzyme activities; 4) variation in external conditions over time or within the plant.

We first describe the normal tuber-size distribution of a potato plant.

Normal tuber-size distribution

Within a cultivar, the average tuber size (μ), the variability of tuber size (σ) and the number of tubers define a unique tuber-size distribution (Sands & Regel, 1983; Marshall & Thompson, 1986; Travis, 1987; MacKerron et al., 1988; Fig. 1). The average size increases during the growing season (Fig. 1a), whereas the number of tubers that will reach marketable size is usually fixed at some given time after tuber set. Concomitantly, the range of the sizes increases. There is a close link between the increase in average size and in spread. The increase in spread is illustrated by Fig. 1b which shows that the later the crop is harvested the larger the range of sizes. Fig. 1c illustrates that the yield of the large sizes increases at the expense of the smaller sizes: the lower the upper limit of the individual tuber size, the earlier the maximum yield of this grade is obtained. This means that after a certain stage of growth, a tuber outgrows, say, size grade 80–160 g and then falls into the next grade, 160–320 g, but it is not at once replaced by a tuber in the smaller size grade 40–80 g growing into the next grade, 80–160 g.

There is a negative correlation between the relative variability of tuber size (σ/μ, i.e. the coefficient of variation) and the number of tubers per unit area (Fig. 2). The characteristic spread is often small when tuber density is high. Such an effect means that when competition becomes strong many tubers suffer, whereas when it is weak only a few are able to exploit this situation (MacKerron et al., 1988). However, Fig. 3 shows that the relationship shown in Fig. 2 is not always true when data from individual plants of one crop are pooled according to the number of their tubers. Over a wide range of tuber numbers the relative variability of tuber size slightly increases with an increase in the number of tubers per plant.

At the crop level the following statements are probably true:

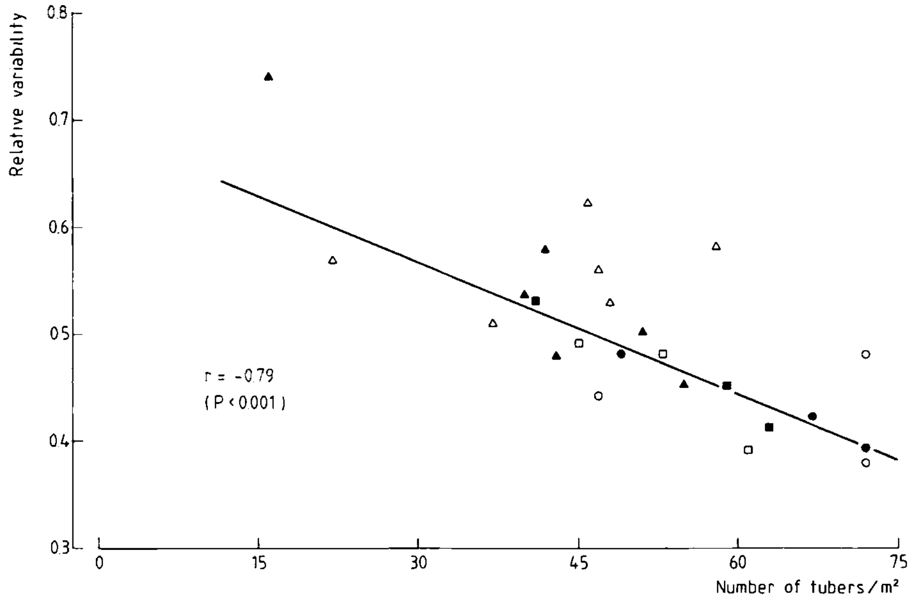

Fig. 2. Relationship between the relative variability of tuber weight distributions and the number of tubers per unit area. ○ = 1983; △ = 1984 harvest 1; □ = 1984 harvest 2. Open symbols unirrigated; closed symbols irrigated. Redrawn from MacKerron et al., 1988.

- the largest tuber at one time is also the largest one at later stages of growth (cf. Krijthe, 1955);
- the largest tuber at one time also has the largest rate of growth, thereby causing the tuber sizes to diverge (cf. Krijthe, 1955; MacKerron et al., 1988) or the spread of sizes to increase proportionally with an increase of the average tuber size;
- there is a continuous and gradual shift from one size class to the larger ones;
- the differences between tubers in chances to grow to large sizes depend on the number of tubers.

At the individual plant level, however, the following may be observed:

- at any one time only a few tubers grow rapidly. When certain tubers approach their final weights, their rate of growth is reduced and other tubers start to grow more quickly (Moorby, 1967, 1968);
- all tubers have similar chances to grow at a certain rate; some tubers continue to grow for a longer period, thus reaching a larger final size (Moorby, 1970; Cother & Cullis, 1985);
- tubers show fluctuating rates of growth so that a large tuber at one time may not be the largest one at a later stage of the plant's development (Moorby, 1967; Gray, 1973; Wurr, 1977; Ahmed & Sagar, 1981; Engels et al., 1986a, b, c; Schnieders et al., 1988; Struik et al., 1988b; Płodowska et al., 1989a). Measuring the growth rates of individual tubers can be done only by frequently disturbing their growth medium or by letting them grow under unnatural conditions. Although this may affect some tubers more than others, it is likely that the observations reported by these authors reflect what happens in undisturbed soil in the field. Initial differences in size caused by differential timing of onset of rapid growth, may be followed by differences in rate of growth such that the ranking order of tubers from the same plant

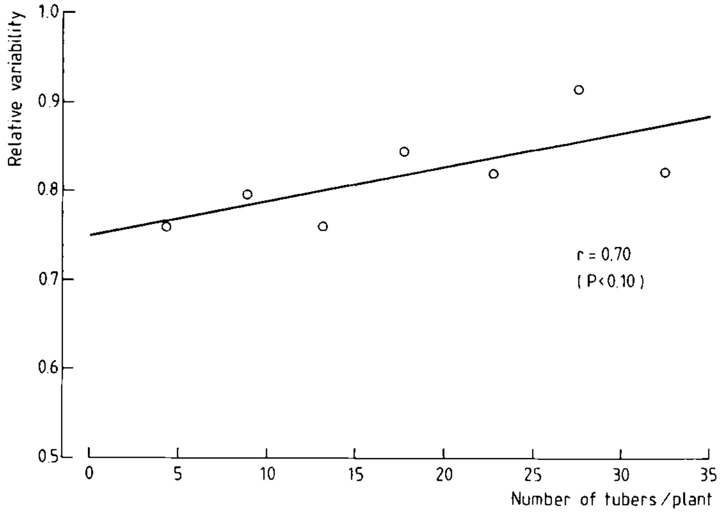

Fig. 3. Tuber-size distribution of plants from one crop showing different numbers of tubers per plant. μ and σ are obtained without truncation of the Gaussian distribution, using also the very small tubers.

or stem changes with time (Schnieders et al., 1988; Struik et al., 1988b; Płodowska et al., 1989a).

The level of integration, which may vary from one stem via a plant to the whole crop, is relevant to any discussion on mechanisms involved in the regulation of tuber size or tuber-size distribution. Struik et al. (1990) described the mechanisms at crop level; in this paper we will discuss those factors that act at the level of the individual stem.

Factors related to the position, date of initiation and size of the stolon to which the tuber is attached

Different patterns within a stem that are relevant to tuber-size distribution (Struik et al., 1990) are:

1) stolon formation along the stem and over time; although there is an influence of cultivar and propagule, stolon formation usually starts at the nodes closest to the mother tuber and progresses acropetally (Plaisted, 1957; Cutter, 1978). Stolons that are first formed reach a greater length and are more likely to form branches than those initiated later on (Lovell & Booth, 1969; Struik & Van Voorst, 1986), and thus have higher numbers of potential tuber sites. The distribution of marketable tubers over the stem also depends on the number of stolons formed; for example, when many stolons were present the probability of marketable tubers at the lower positions declined (Cother & Cullis, 1985);

2) time of tuberization; the stolons initiated early on take longer to tuberize than ones formed later (Vreugdenhil & Struik, 1989);

3) the proportion of stolons producing a tuber (named 'tuberization frequency' after Svensson, 1962); there is usually a pattern of tuberization frequency along the stem (Moorby, 1967; Wurr, 1977; Cother & Cullis, 1985) which depends on cultivar and environment but it is difficult to generalise about this;

4) the frequency of large tubers; not all the tubers that are initiated have similar chances to grow out. There is a tendency for tubers on the upper stolons to be smaller than those on stolons lower down but this effect is not clear (Clark, 1921). Tubers on the lower stem nodes probably form first and show a faster relative growth rate than those formed further from the stem base and the length of the tuber-bearing stolons declines the further they are from the stem base (Gray, 1973). Plaisted (1957) and Cother & Cullis (1985) observed that marketable tubers are more likely to be formed on basal (old) stolons than on top stolons although the probability of marketable tubers may be largest in the middle of the below-ground stem part, a pattern probably affected by the number of stolons initiated (Cother & Cullis, 1985). Krijthe (1955) observed that the largest tubers were formed on stolons positioned on the nodes 3, 4 and 5 from the base of the stem.

These patterns may be affected by the distance of the stolon from the mother tuber, the stem apex and other above-ground plant parts, gravity controlled transport of growth regulators, the site specific mechanical resistance of the soil, the range of nodes over which tubers are formed, and the competition for photosynthates within a node (Cother & Cullis, 1985). Water supply shortly after emergence also affects the number of stolons formed (MacKerron & Jefferies, 1986; Haverkort et al., 1990).

The time of initiation of a stolon may influence the final tuber-size distribution (Struik & Van Voorst, 1986; Struik et al., 1988a) and is more important than the time

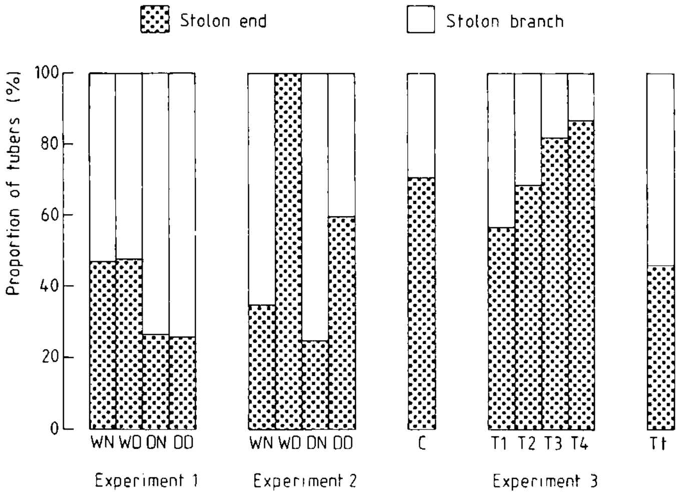

Fig. 4. Effect of environmental conditions on the position of tubers with a dry weight >8.0 g, in different experiments. In Experiments 1 and 2 the effects of drought in the stolon or root environment during the tuberization period were investigated (after Struik & Van Voorst, 1986); treatment codes Experiments 1 and 2: WN is control; WD is drought in root medium; DN is drought in stolon medium; DD is drought in both root and stolon media. In Experiment 3, the effects of short periods of long photoperiods during different stages of development were investigated (after Struik et al., 1988a); treatment codes Experiment 3: C is control; T1 is long-day treatment from 14–30 days after planting (DAP); T2 is long day from 22–38 DAP; T3 is long day from 30–46 DAP; T4 is long day from 38–54 DAP; Tt is long day from 22–62 DAP.

of initiation of the individual tubers. Struik & Van Voorst (1986) and Struik et al. (1988a) proved that the position of large tubers could be affected by environmental factors and Fig. 4 shows that large tubers may be more frequent on stolon ends.

The effect of position of the stolon on tuber size might also be due to the vascular associations between leaves and other organs. In crops other than potato, such associations were demonstrated by Wardlaw (1964). Gray & Smith (1973) suggested that for potato too, there is a high degree of vascular continuity between tubers and the supplying leaves. However, vascular bundles from one leaf are not necessarily restricted to only one side of the stem (Artschwager, 1918) and the observed anastomosis of bundles at nodes may enable redistribution of assimilates (cf. Oparka, 1985). Nevertheless, Moorby (1968) suggested that in the potato plant certain leaves or groups of leaves are responsible for certain tubers; thus rapidly growing tubers would be those with a direct vascular connection with a photosynthetically active leaf. Once this leaf becomes senescent, ‘its’ tuber may end its phase of rapid growth.

Schnieders et al. (1988) suggested that the hypothesis of Moorby (1968) might also imply that the diurnal fluctuation in tuber volume caused by the water movement out of and into the tuber could be variable and dependent on the transpiration of certain leaves or groups of leaves. Indeed, Płodowska et al. (1989b) showed that there are large differences in diurnal fluctuation in the volumes of individual tubers on one stem of a plant that is water-stressed and that there are strong similarities between the reaction of the leaf thickness and of tuber volume to the stress. However, there were not enough data to establish a relationship between individual tubers and specific leaves. Moorby's hypothesis and Schnieders' suggestions are still no more than suppositions that need to be investigated. However, since anastomoses occur this hypothesis can be valid only if there is proved to be a resistance to compensatory cross-over.

Experiments with labelled carbon showed, indeed, that sometimes most of the labelled carbon is recovered at a particular side of the stem (Gray & Smith, 1973; Oparka & Davies, 1985). However, there is not always a proven correlation between tuber size and the amount of photosynthates transported to them during a given period (Moorby, 1968; Gray & Smith, 1973). Oparka & Davies (1985) showed that some time after emergence, each tuber-bearing stem functions as an independent unit with little or no carbon exchange between stems. Later on, import of photosynthate into stolon tips prior to the onset of tuberization can vary greatly. They also found some relationship between certain groups of leaves and certain tubers, but the distribution patterns were not rigid.

There may be other differences between tubers associated with the efficiency of their transport systems: these may differ,

- because of differences in the ability to accept and process assimilates (Milthorpe & Moorby, 1969). This topic will be discussed below and is mainly relevant for later stages of tuber development;
- because of varying diameter of the vascular bundles within stolons or of the volume of the stolon to which the tuber is attached, or because of other stolon characteristics; the effects of the stolon characteristics are discussed below in more detail.

The diameter of the stolon end does not appear to change after tuber initiation (unpublished data of B. O. M. Dirks & P. C. Struik). Engels & Marschner (1986c) observed a logarithmic relation between tuber volume and stolon diameter or stolon volume suggesting that the tuber size may depend on the growth characteristics of the stolon before tuberization takes place, mainly because this growth affects the import of materials necessary for tuber growth. However, the correlation coefficients were low; moreover, the same authors (1987) showed that the transport capacity of stolons was not limiting the yield of the tubers attached to them.

Clark (1921) did not find an effect of stolon length on tuber size, but Engels & Marschner (1986c), using the data of Crafts (1933), found strong correlations between tuber size and cross-sectional area.

Another characteristic which may enhance the growth of tubers attached to a given stolon is the presence of stolon roots which affect the uptake of water and nutrients by the stolon (see, e.g., Kratzke & Palta, 1985, 1986). Water uptake affects the diurnal fluctuation in tuber growth (Schnieders et al., 1988; Płodowska et al., 1989b) and nutrient uptake essential for tuber initiation and tuber growth, especially that of Ca which is transported only with difficulty to the stolon tips or tubers if taken up by stem roots (Krauss & Marschner, 1974; Kratzke & Palta, 1986). These aspects of mineral nutrition are discussed in detail in another section of this paper.

There are several reports describing the effects of stolon tip removal by artificial methods (e.g. Oparka, 1987) or by fungal infection (e.g. Cother & Cullis, 1985). Oparka (1987) showed that excising the apices of primary stolons did not affect the number of tubers or tuber yield, but that complete removal of primary stolons greatly reduced the final yield and number of tubers. Removal of tuber initials, however, significantly reduced yield without affecting number. Cother & Cullis (1985) found a stolon pruning threshold of 18 % below which yield was not reduced and that for every 20 % increase in pruning above this threshold yield was reduced by only 6 %. These results illustrate the plasticity of tuber formation and growth of the potato plant.

Other fungal diseases that plug the transport system (such as infection by *Verticillium* spp.) may also have a specific but minor effect on tuber-size distribution.

Factors related to the date of initiation of the tuber and its initial activity

Because tubers that are able to grow into marketable sizes are usually initiated during a short period of time (Krijthe, 1955; Struik et al., 1988a), there is usually little evidence of a close correlation between the date of initiation and final size. Wurr (1977), Struik & Van Voorst (1986), Struik et al. (1988a) and Vreugdenhil & Struik (1989) all have questioned whether there is any strong relationship between the date of initiation of a tuber and its chances of growing. The hypothesis that the largest tuber at one time remains so from the moment of its formation until maturity (Krijthe, 1955; Gray, 1973; MacKerron et al., 1988), does not require that such a relationship exists, because tuber formation may be defined in such a way that a tuber has already passed the stage of tuber 'set' before it is counted as a tuber. However, Oparka & Davies (1985) observed large differences in the rate of photosynthate import between stolon tips, suggesting that there are already significant differences in sink strength before tuberization takes place.

However, Struik et al. (1990) concluded that the process of tuber 'set' (being the final phase of the early tuber development after which the small tuber definitely has the ability to produce a marketable tuber) is at least as relevant for final tuber-size distribution as is the process of tuberization, although tuber 'set' is still both poorly defined and poorly understood. Under conditions or with cultivars where the variation in date of initiation and set of harvestable tubers is much larger, there may be a certain correlation between date of tuber initiation or set and final size. For example, Meredith (1988a, b) stated that potato plants have the tendency to produce tubers of equal size ('twinning') as a consequence of discrete episodes of tuber initiation, followed by growth of tubers in cohorts. The analysis by Meredith was questioned by Marshall et al. (1991).

It is thus clear that the rate of initial growth rather than the timing of first swelling may be important. Plaisted (1957) showed that many processes take place during the formation of the tuber incipient; cell division, cell enlargement and starch and protein synthesis must take place at the same time. Reeve et al. (1973) found that the slow-growing tubers at later stages of development are those in which the mitotic processes are restricted in early phases of growth. There are also differences in the activities of enzymes involved in starch synthesis: in the early stages of tuber growth, the activity of starch phosphorylase is high, whereas later that of ADP-glucose pyrophosphorylase increases (Mingo-Castel et al., 1976; Hawker et al., 1979; Obata-Sasamoto & Suzuki, 1979). Moreover, whereas the formation of adequate phloem tissue may be important for the likelihood of growth of an initial into a tuber, Engels & Marschner (1987) found that the transport system probably does not limit the potential for further growth during the later stages of development.

Many factors that determine the initial activity of a tuber also remain important for its later growth rate although their relative importance may change.

Factors related to internal tuber characteristics, such as enzyme activities, hormone concentrations and turgor potential

Tubers on one stem compete for assimilates, nitrogenous compounds, nutrients, hormones and, probably, even for the water that is necessary for their cell enlargement and the transport of nutrients and other substances.

After the initial phase, during which growth of an individual tuber is mainly determined by cell divisions (Plaisted, 1957; Reeve et al., 1973; Schnieders et al., 1988), other factors determine differences in the growth rate of individual tubers. During the early phases of growth there is often a significant relationship between labelled carbon and tuber size (Gray & Smith, 1973; Oparka, 1985; Engels & Marschner, 1986b) but later on this relationship weakens. The differences between tubers in competitive strength may be related to differences in their ability to convert photosynthates into starch (Lovell & Booth, 1967; Moorby, 1968; Mares & Marschner, 1980). Synthesis and degradation of enzymes may exert overall control over starch synthesis (Sowokinos, 1976; Hawker et al., 1979; Mares & Marschner, 1980) within which there may be lesser but important effects resulting from the regulation of the activity of one or more enzymes, for example ADP-glucose pyrophosphorylase (Preiss, 1982; Sowokinos & Preiss, 1982). Obata-Sasamoto & Suzuki (1979) indicated that the activities of phosphorylase and granule-bound starch synthase increased rapidly during swelling of the stolon tip and remained constant afterwards, whereas the activities of soluble starch synthase and ADP-glucose pyrophosphorylase increased only in the later stages of growth.

Moorby (1968) suggested that in slow-growing tubers the enzymes necessary for the synthesis of starch have a low activity. Subsequently there have been many reports claiming significant correlations between the growth rate of individual tubers and their ADP-glucose pyrophosphorylase, starch synthase or starch phosphorylase activity, in particular claiming a low activity of ADP-glucose pyrophosphorylase in small tubers but a much higher activity in large tubers (e.g. Hawker et al., 1979; Krauss & Marschner, 1984; Marschner et al., 1984a; Engels & Marschner, 1986a, b). The best relationship was usually found when growth rate was related to the ratio ADP-glucose pyrophosphorylase/starch phosphorylase; the activity ratio ADP-glucose pyrophosphorylase/phosphorylase was low in slow growers and high in fast growers (Hawker et al., 1979; Krauss & Marschner, 1984; Marschner et al., 1984a; Engels & Marschner, 1986a).

Engels & Marschner (1986a) reported linear relationships between ^{14}C import and the starch synthase activity or the starch phosphorylase activity, whereas they observed exponential relations between ^{14}C import and the ADP-glucose pyrophosphorylase activity or the activity ratio ADP-glucose pyrophosphorylase/starch phosphorylase.

Photosynthate supply and the activities of starch synthesizing enzymes are influenced by the mineral nutrition of the plants. When potassium supply is insufficient, less assimilates are translocated to the tubers than when its supply is adequate (Haeder et al., 1973), an adequate supply increasing the yield of large tubers and decreasing that of small tubers (Beringer et al., 1983). The activities of starch synthase and ADP-glucose pyrophosphorylase in vitro were more than doubled in the presence of 100 mM K^+ as compared with the activities in the absence of K^+ (Hawker et al., 1979).

Starch synthesis is also controlled by the level of inorganic phosphate, high levels being inhibitory (Mohabir & John, 1988; Anderson et al., 1989).

Photosynthate partitioning and activities of starch synthesizing enzymes might also be under hormonal control. Marschner et al. (1984a, b) reported that there was a statistically highly significant, negative correlation between growth rate and the content of abscisic acid (ABA) of the tuber, a significant, positive correlation between growth rate and the content of gibberellic acid (GA) and a highly significant, positive correlation between growth rate and the content of indol acetic acid (IAA). The correlation was also high when the ratio ABA : IAA was used rather than their individual levels; rapidly growing tubers had a low ABA content, a high IAA content, a high GA content, or a low ABA : IAA ratio. These results partly differ from those of Krauss (1981), who found no or only weak correlations, but agree with those of Bialek & Bielinska-Czarnecka (1975), who also observed high GA-activity during rapid tuber growth. However, the results were dependent on the time at which the samples were taken and, moreover, the hormone concentrations (especially ABA; Krauss, 1981) vary greatly within one tuber.

Application of GA3 to the surface of stolons of growing tubers markedly affects enzyme activity even before the application influences the rate of tuber growth itself (Mares et al., 1981). There was a reduction in both the activity of ADP-glucose pyrophosphorylase and of the ratio ADP-glucose pyrophosphorylase/starch phosphorylase and an increase in the activity of UDP-glucose pyrophosphorylase. The activity of starch phosphorylase initially increased slightly but then fell, whereas no changes were detected in the activity of starch synthase.

Mingo-Castel et al. (1976) reported that, in vitro, kinetin-induced tuberization stimulated the activity of phosphorylase in the early stages and of ADP-glucose pyrophosphorylase in the later stages of tuberization; starch synthase activity was not affected.

It is not yet possible to conclude which of the factors noted above (enzyme activities, minerals, hormones) is the primary regulator in the control of photosynthate partitioning and carbohydrate storage. Engels & Marschner (1986a) doubted whether the relationships between enzyme activities and tuber growth rates reflect the true regulatory mechanisms in vivo.

Oparka & Wright (1988), among others, suggested that both a temporary (diurnal fluctuation in tuber volume) and a long-term (drought) decline in turgor potential of a tuber influenced the partitioning of sucrose into starch with an optimum, thus affecting tuber growth as well; such declines in turgor potential are likely to differ among tubers of one stem (cf. Płodowska et al., 1989b).

Factors related to variation in external conditions over time and within the plant after tuber initiation

Tubers on the same stem may also vary in rate and duration of growth because the mechanisms discussed above are affected differentially when the tubers are exposed to different conditions. Soil environmental factors (e.g. temperature, moisture content, and mechanical resistance) may vary greatly over a short distance within a ridge. By suitably changing the temperature around one tuber, the rate of its growth can be reduced; the growth of the other tubers then increases (Engels, 1983; Krauss & Marchner, 1984). The reason for this single reduction can be a change in enzyme activity, hormone contents, or both. For cv. Désirée, there is a sharp optimum temperature for starch synthesis of 21.5 °C (Mohabir & John, 1988); if the temperature of a tuber is increased to 30 °C, its growth ceases and the activity of certain enzymes is depressed more than that of others resulting in a reduction of the starch content and an increase of the sucrose content (Krauss & Marschner, 1984). Moreover, since not all tubers grow rapidly at the same time, the conditions to which the entire plant is exposed during the rapid growth of a particular tuber may vary from tuber to tuber. Short periods of long days (Struik et al., 1989a), low light intensity (Struik, 1986; 1987a, b), high temperature (Struik, 1987b, 1989; unpublished data), drought (Struik & Van Voorst, 1986; Płodowska et al., 1988a, b), or increased carbon dioxide concentration in the air (P. C. Struik, unpublished data) all affect the number of tubers and the tuber-size distribution. Shifts to larger or smaller size grades were observed, associated with or without changes in the number of tubers, depending on the timing of the treatment and on the other environmental conditions.

These results are not in agreement with those of other authors. Moorby et al. (1975) stated that probably all tubers were affected in a similar way by drought. MacKerron et al. (1988) observed that the effects of drought on the tuber-size distribution were not atypical: they could be described by the effects on yield and tuber number, but the relative variability remained unaffected. Yet it seems logical to surmise that the large differences between years in the tuber-size distribution of a given cultivar must mainly be attributed to variation in temperature and water supply during certain stages of growth and in the total amount of radiation intercepted (cf. Struik et al., 1990).

The many factors that influence the yield of a single stem, the number of tubers and the characteristic spread of tuber sizes, together with the many factors that influence the hierarchy among tubers and the fact that different processes are affected during different periods of the tuber development, all combine to make it difficult to determine a pattern of hierarchy. A statistical approach as used by Marshall et al. (1991) may be helpful. In this approach the frequency of occurrence of two tubers of similar size ('twinning') on the same plant is simulated using normalized logarithmic curves of the size distribution based on dry weight. Although twinning frequencies of up to 55 % were observed, the simulated and observed frequencies were not significantly different. There seems to be no physiological basis for the occurrence of twinning.

Discussion

The mechanisms of hierarchy are manyfold, complex and also change during the development of the plant. Fig. 5 presents an overview of the most relevant factors involved and their interactions.

We believe that the pattern of stolon formation and development is crucial for the final size distribution of tubers, especially the number of stolons, their position, time of initiation and their growth. Thus the hierarchy of tubers is already partly fixed before tuberization takes place but can be modified by many tuber characteristics after tuber set. The pattern of stolon formation is determined by the presence of the mother tuber and the growing shoot and affected by genotype, environmental conditions and cultural practices. The mechanisms of hierarchy may be different in plants that are produced from other types of propagules, such as true potato seed or microtubers.

The influence of stolon formation on tuber-size distribution is caused by its effect on tuber set, on the possibilities to transport photosynthates, amino acids, hormones and water to the growing tips and by direct and indirect effects on the initial activity of the stolon tip, the tuber initial or the small growing tuber. In this way the stolon system determines to a large extent the number, position and potential size of the

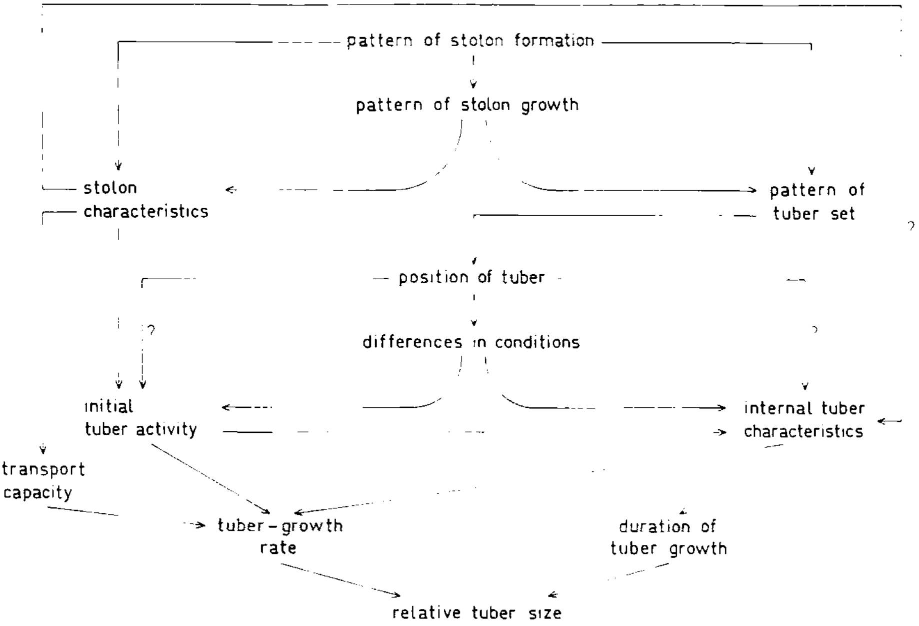

Fig. 5. Scheme of the factors influencing the final tuber-size distribution during the different stages of development.

tubers. In practice, it is possible to influence the number and size of stolons and the structure of the stolon system, for example by plant density, planting depth, build up of the ridges, nitrogen fertilization, irrigation, control of *Rhizoctonia solani*, etc. (see Struik et al., 1990).

When conditions for tuberization are favourable, the number of tuber initials formed is abundant. Tuberization is not an important factor in determining the number of marketable tubers. The process and pattern of tuber set and the initial activities of tubers set have a much larger effect on the number of marketable tubers and the final tuber-size distribution. Although tuber set is known to be strongly affected by genotype, temperature, water supply and productivity of the plant, it is, nevertheless, a process that is poorly understood. The number of tubers that will finally grow out is probably fixed in a short period of time but it is difficult for the grower to know exactly when this short period starts and finishes, so that tuber set is hard to manipulate. Also the effects of environmental factors are so large that the effect of any attempted manipulation of set is often unpredictable.

The final size of a tuber results from duration and rate of its growth, characteristics that are mutually independent. The duration of growth of the individual tuber may be strongly affected by the quality of the transport system because of possible connections with leaves that may remain active until the end of the growing season. It is difficult to influence the rate of tuber growth and, as yet, impossible to control differences in rate of growth between tubers. These differences, however, are very important for the final size distribution, especially if they are consistent for a long time.

The best ways of influencing tuber-size distribution of single plants are to manipulate the productivity of the plant and its number of stolons. Another possible influence may result from manipulation of the water supply during tuber set. Since stolon number, tuber set and the interactions between tubers are hard to control, it is very difficult to manipulate tuber-size distribution in the field. Therefore, more research is required to elucidate the physiological aspects of formation, quality and behaviour of stolons, of tuber set and of interactions between tubers after tuber set to improve the chances of manipulating tuber-size distribution with greater precision.

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