

Plant development in potato

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3

Plant development in potato

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3.1 Introduction

Potato (*Solanum tuberosum* L.) is a perennial herb but used as an annual crop. Traditionally, it is propagated using seed tubers, but the species is very versatile in its methods of multiplication (Struik and Wiersema, 1999). It can be multiplied in vivo by seed tubers, minitubers, true potato seed (TPS), nodal and apical cuttings, sprout cuttings, etc. There are also many in vitro methods of multiplication, including individual cells, meristems, (in vitro) microtubers, in vitro plantlets, etc. In these different methods of multiplication, there is usually a trade-off between level of differentiation and rate of multiplication: the less differentiation, the higher the rate of multiplication. The big exception to this rule is the production of TPS where very high rates of multiplication can be achieved with highly specialized organs (flowers, berries, and true seeds). The best method of multiplication depends on the desired rate of multiplication in combination with the desired, minimum vigor of the propagule and given the cost of production and value of the produce produced from it.

Growing potato crops from open pollinated TPS has been investigated for many decades but never reached a high level of adoption. Since recently, tetraploid cultivars based on TPS are available, whereas also breeding programs have been initiated based on hybrid diploid breeding using TPS as starting material, at least in the very early stages of the seed system. Hybrid TPS breeding has great promise by combining speed breeding with high rates of multiplication (Kacheyo et al., 2022). The biggest advantages of this new technology are through the rapid progress in stacking genes and combining new traits, while multiplying very rapidly through sexual reproduction. In order to have enough vigor, it is possible to create seedling tubers or produce seed tubers after several generations of tuber production. The different options are illustrated in Fig. 3.1. The different basic methods of multiplication make it relevant to compare plant development (both above-ground and below-ground) of plants grown from true seed, seedling tubers and latergeneration seed tubers.

In this chapter, I use the term *seedling tuber* to describe tubers derived directly from TPS. Such seedling tubers can be used as seed tubers or ware potatoes (Struik and Wiersema, 1999; Almekinders et al., 2009; Stockem et al., 2020; Kacheyo et al., 2021). The term *seed tuber*, on the other hand, refers to the end-use of tubers derived from mother plants grown from either seedlings, seedling tubers or any other tuber propagules (Struik and Wiersema, 1999; Almekinders et al., 2009; Stockem et al., 2020; Kacheyo et al., 2021). The term ware potato or ware tuber refers to any commercial end-use of tubers derived from mother plants grown from any possible type of starting material of potato and are fit for processing into all kinds of possible end uses and consumption (Haverkort et al., 2022).

Since expectations are that there will be increasing interest in plants grown from different types of starting materials or propagules, I will compare the plant development from different propagules. The cycles are illustrated in Fig. 3.2. A seedling will also produce tubers to be used as either seed tubers or ware potatoes (Fig. 3.1).

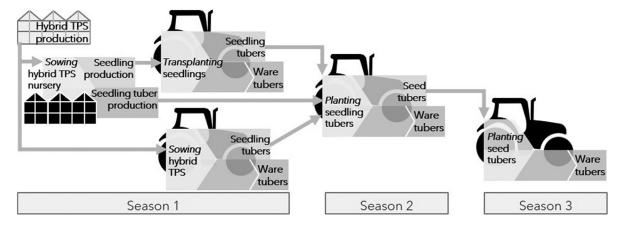


FIGURE 3.1 Different ways of using different types of propagules across different generations (van Dijk et al., 2021). Source: From van Dijk, L., Lommen, W.J.M., de Vries, M.E., Kacheyo, O.C., Struik, P.C., 2021. Hilling of transplanted seedlings from novel hybrid true potato seeds does not enhance tuber yield but can affect tuber size distribution. Potato Res. 64 (3), 353–374. https://doi.org/10.1007/s11540-020-09481-x.

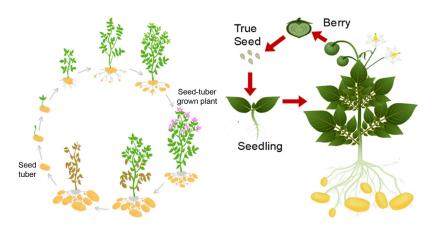


FIGURE 3.2 Two contrasting in vivo ways of multiplying the potato plant, either through seed tubers (left) or through true potato seed (right). Seed tubers can be harvested and stored until they lose dormancy and start to produce sprouts. Before or after sprouting seed tubers can be planted and will then produce news plants that may consist of multiple stems and produce progeny tubers (either for seed or ware). On the other hand, true potato seeds may be harvested from the berries, stored until they lose their natural dormancy and sown at a shallow depth to produce a seedling.

3.2 General morphology

Fig. 3.3 shows the general morphology of the potato (S. tuberosum spp. tuberosum) plant, grown from either a seed tuber or a true seed with all its details. The figure describes (A) the entire plant grown from a seed tuber; (B) the flower; (C) the berries; (D) a seedling; (E) the below-ground plant parts of a seed-tuber grown plant; (F) a tuber; and (G) a sprout on a single tuber. A seed tuber can only produce a new plant after dormancy has been broken. Dormancy of a seed tuber can be defined as the physiological state of the seed tuber during which there is no visible sprout growth, even not when conditions for sprout development and growth are conducive. When grown from a nondormant seed tuber, the morphology of the entire plant strongly depends on the size and the physiological age of the seed tuber. Physiological age is defined as the stage of development of a seed tuber as it progresses through time depending on conditions during growth and storage and as it affects its vigor when planted. The size of the seed tuber determines to some extent the number of eyes present, the proportion of the eyes producing one or more sprouts, and the proportion of the sprouts producing a stem, thus determining the final number of stems developing per seed tuber. The size of a seed tuber has an impact on the development of the physiological age, while the physiological age also has its direct impact on the proportion of eyes producing one or more sprouts and the proportion of sprouts producing a stem, thus also determining (in close interaction with seed tuber size) the number of stems produced by a single seed tuber. For our descriptions, we take a normal-sized seed tuber (about 40−80 g fresh weight stored in darkness at about 4°C for about 8 months) as starting point.

Also, a TPS will only produce a seedling after the dormancy of the true seed (i.e., the incapacity of a viable seed to germinate under favorable conditions) has been broken, either by naturally or by physical or chemical

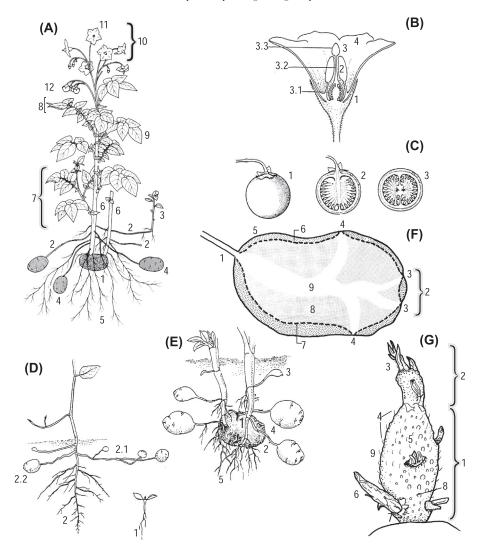


FIGURE 3.3 Morphology of the potato (*S. tuberosum* spp. *tuberosum*) plant. (A) Overview of entire plant grown from a seed tuber: 1. Seed tuber; 2. Stolon; 3. Stolon, turning into a below-ground lateral stem; 4. Progeny tuber; 5. Roots; 6. Main stem; 7. Above-ground lateral stem; 8. Compound leaf; 9. Leaflet; 10. Inflorescence; 11. Flower; 12. Berries. (B) Flower: 1. Calyx; 2. Stamen, consisting of a filament and an anther; 3. Female structure, with 3.1. Ovary; 3.2. Style; 3.3 Stigma; 4. Corolla, consisting of five petals that are often fused. (C) Berries: 1. General appearance; 2. Longitudinal cut showing the position of the true seeds; 3. Transversal cut, showing the position of the true seeds. (D) Seedling: 1. Seedling shortly after emergence; 2. Seedling shortly after tuberization with 2.1. Tuber-bearing stolon; 2.2. Small tuber. (E) Below-ground plant parts of a plant from a seed tuber. 1. Seed tuber; 2. Tuber-bearing stolon; 3. Incipient tuber; 4. Small tuber, with eyes consisting of an eyebrow and buds and with lenticels (not visible) that are important for gas exchange; 5. Roots. (F) Tuber: 1. Basal (heel or stolon) end. 2. Apical (or rose) end; 3. Apical eyes; 4. Lateral eyes; 5. Skin; 6. Cortex; 7. Vascular system; 8. Storage parenchyma; 9. Pith. (G) Single sprout on a seed tuber: 1. Basal part. 2. Tip; 3. Terminal bud; 4. Hair; 5. Undeveloped bud; 6. Developed bud for lateral stem; 7. Root tips; 8. Lenticel; 9. Main sprout developing into main stem. Source: *From Struik, P.C., Wiersema, S.G., 1999. Seed Potato Technology. Wageningen Academic Publishers, Wageningen, the Netherlands.*

means. In this case there will be only one single stem per plant. That single stem might branch profusely, especially at the lower part of the plant.

Despite considerable differences in physiological and morphological characteristics, plants grown from TPS and from seed tubers are relatively similar (see Figs. 3.4 and 3.5).

3.3 Descriptions of phenological stages of potato

Descriptions of phenological stages have been developed for many crops. They are relevant as such descriptions, often in the form of a digital scale, allow to systematically compare plant growth and development and can

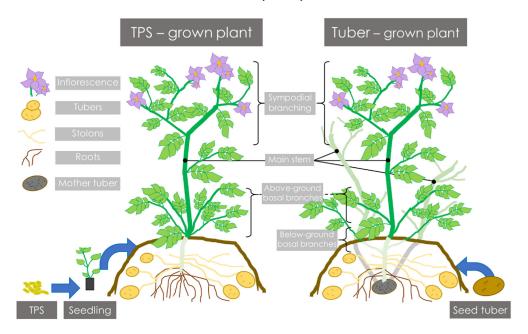


FIGURE 3.4 A single-stemmed potato plant grown from true potato seed (left) and a multistemmed potato plant grown from a seed tuber (right) stressing the similarity of the two plant types. Source: From Kacheyo, O.C., van Dijk, L.C.M., de Vries, M.E., Struik, P.C., 2021. Augmented descriptions of growth and development stages of potato (Solanum tuberosum L.) grown from different types of planting material. Ann. Appl. Biol. 178 (3), 549–566. https://doi.org/10.1111/aab.12661.

Potato canopy structures

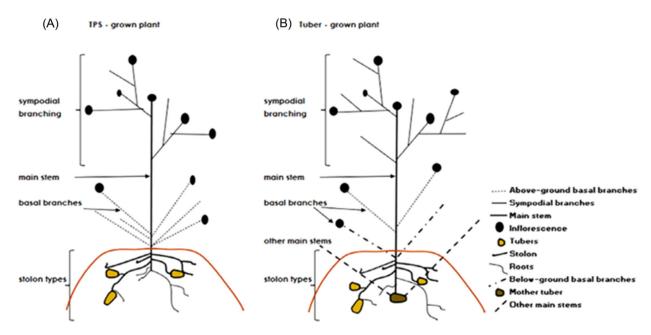


FIGURE 3.5 Different types of branches on a true-potato-seed grown plant (single stemmed; A) and a seed-tuber grown plant (multiple stemmed; B). Note that part of the differences in morphology is due to the shallower planting of the true potato seed (although earthing up is the standard practice after emergence) in comparison to the seed tuber, resulting in more diverse types of branches below- and above ground. Source: From Kacheyo, O.C., van Dijk, L.C.M., de Vries, M.E., Struik, P.C., 2021. Augmented descriptions of growth and development stages of potato (Solanum tuberosum L.) grown from different types of planting material. Ann. Appl. Biol. 178 (3), 549–566. https://doi.org/10.1111/aab.12661.

3.6 The leaves 61

standardize methodologies and their descriptions in agronomic research. Also for potato (S. tuberosum L.), phenological scales of plants derived from seed tubers have been developed. Examples are the scales of Anonymous (1987) and Griess (1987, 1989). Jefferies and Lawson (1991) also developed a scale and also indicated that most developed potato scales were not representative of all the stages of plant development of the potato plant. Some scales fail to detail important stages such as the preemergence phase, stolon formation, sympodial branching from the axils of the upper leaves as well as branch growth and development at lower parts of the plant. Furthermore, there might be significant differences in growth and development stages of plants grown from different types of starting material, for example, differences among plants grown from seed tubers, TPS, or in vitro plantlets. Such significant differences have often not been stipulated in most of the existing scales, although Hack et al. (1993) published a scale based on both seed-tuber grown plants and true-potato-seed grown plants. Kacheyo et al. (2021), therefore, designed an augmented and very detailed development scale based on the Biologische Bundesanstalt, Bundessortenamt and CHemical Industry (BBCH Scale) (Meier et al., 2009). Fig. 3.5 describes the most important differences in phenological development between plants grown from a seed tuber and those grown from TPS. Most significant differences can be found in the root systems, the appearance of the plant at emergence, the leaf development, and the development of the different types of shoots, stolons, and branches. For a full description of the augmented scale which still complies to the basic principles of the BBCH Scale I refer to the original publication by Kacheyo et al. (2021) in the journal Annals of Applied Biology.

3.4 Sprout development

When the plant is grown from a seed tuber, the development of the sprouts on such a seed tuber is crucial for the appearance and structure of the plant. Fig. 3.3 already showed sprout development in some detail. Fig. 3.6 shows the development of the sprouts on a seed tuber with increasing physiological age. In the same figure, the resulting above- and below-ground structures are pictured and further explained in its caption. This impact of the seed tuber on sprout development and subsequent crop development is unique for seed-tuber grown crops. It provides opportunities to adjust physiological age and subsequent crop management to specific outlets. It is also important for regions with more than one growing season per calendar year. The influence of the true seed on the physiology of the germinating seedling is much smaller, but seedlings often become bushier than seed-tuber grown plants demonstrating strong branching at the base of the plant.

3.5 The shoot system

The potato plant has a complex structure (Kacheyo et al., 2021), both when grown from true seed and when grown from seed tubers. When grown from true seed, there will be strong branching at the bottom of the plant, with often less profusive sympodial branching. When grown from a seed tuber, there can be multiple stems (either originating from the same eye or from different eyes), which demonstrate sympodial branching. Sympodial branching may be intense, especially when nutrient supply is abundant and for indeterminate types. In such a case, the canopy may consist of a constellation of stems, each comprising many different types of stems and stem parts, lower and apical branches, etc. During the first part of the growing season, these stems share the resources from the same mother tuber, but gradually they become independent units with their own resource capture, albeit in competition with each other for light, water, and nutrients. A complex single stem is actually a stem system, consisting of a primary stem segment, which ends in a terminal inflorescence (first level main stem). Such a stem may have basal lateral stems, either originating below ground or above ground. Once a primary stem has produced an inflorescence, it can produce higher-order stem segments through sympodial branching. Under optimal conditions sympodial branching may include several layers of second level secondary stem segment, several layers of tertiary stem segments, followed by quaternary levels, etc. For further details, see Almekinders and Struik (1996) and Struik (2007).

3.6 The leaves

The potato plant grown from a seed tuber has one major leaf per node and demonstrates a spiral phyllotaxis. The early leaves are small but later foliage leaves are compound leaves which can reach substantial sizes. Such

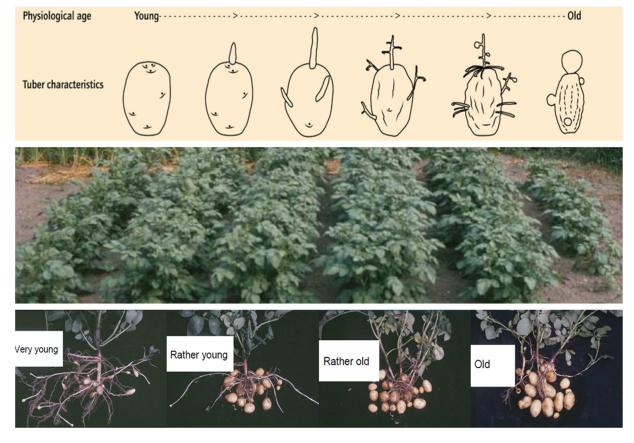


FIGURE 3.6 Physiological age of the seed tuber determines sprouting behavior, above- and below-ground developments. Seed tuber drawings show various stages of physiological ageing: dormancy, apical dominance, multiple sprouting, multiple sprouting and branching of sprouts, senility of sprouts, and little tuber formation. When planted at the same time in separate rows such seed tubers will provide different canopies (canopy picture in the middle), ranging from no emergence because of dormancy (extreme left), via single-stemmed plants to multiple-stemmed plants with maximum vigor (central row) to multiple-stemmed plants (central row) with decreasing vigor to no plants because of little tuber formation (extreme right). For below ground, only the contrast between very young, rather young, rather old, and very old is pictured, without the extremes from the upper and central part of the figure. Note the differences in number and length of stolons and in number and size uniformity of tubers in the pictures of the below-ground structures. Because of the impact of physiological age on the crop cycle length, the seed tubers that are rather young or rather old will give the highest yield (depending on the duration of the growing season), whereas the size distribution of the crop from rather old seed tubers will be shifted to smaller sizes compared with the crop from the rather young seed tubers. Based on Struik and Wiersema (1999).

leaves are imparipinnate, with small additional leaflets (also called folioles) intervening between the larger pinnae. Usually, these compound leaves have three or four pairs of large leaflets with the small folioles in between. The large leaflets are ovate to ovate-elliptical. The small leaflets are subsessile and ovate to suborbicular. The rachis of the compound leaf ends in a single top leaf which is sometimes different in shape compared with the large leaflets and often is the largest one. In plants grown from TPS, the first leaves are cotyledon leaves and are followed by the first true leaves. In TPS-grown plants, only later foliage leaves will show the typical compound leaf structure.

The number of leaves of the primary stem segment of a seed-tuber grown plant is usually rather constant, certainly when the seed tubers are properly presprouted. However, the number of leaves on the basal lateral branches varies depending on the environmental conditions (such as temperature and photoperiod), and also strongly depends on the position along the primary main stem segment: the lower the position of the basal branch is the higher the number of leaves that will be produced before a basal branch starts to produce a terminal inflorescence. The lowest basal branch may even have more leaves than its main stem. Also, the number of leaves per apical sympodial branch changes: the number of leaves per stem segment declines with an increase in level because the meristem switches to reproductive development increasingly rapidly. Fig. 3.7 illustrates the number of leaves per stem segment over time. A typical leaf appearance rate is 0.53 leaves per day or one leaf per 28°C · day calculated on the basis of a base temperature of 0°C (Vos and Biemond, 1992). Vos (1995) showed data from different cultivars and different average temperature and came to a range of leaf appearance rates of

3.6 The leaves 63

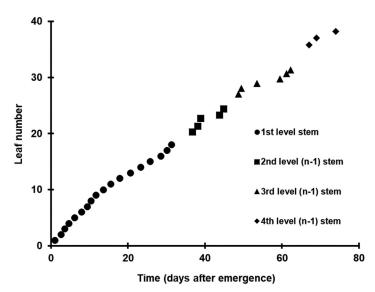
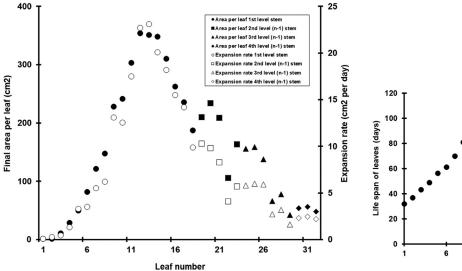


FIGURE 3.7 The number of leaves on a single main stem as a function of time for cv. Bintje, grown from a seed tuber in a cooled greenhouse, under abundant nutrient supply and abundant light. Source: From Struik, P.C., 2007. Above-ground and below-ground plant development. In: Vreugdenhil et al. (Eds.), Potato Biology and Biotechnology. Elsevier Science BV, pp. 219—236 based on data from Vos, J., Biemond, H., 1992. Effects of nitrogen on the development and growth of the potato plant. 1. Leaf appearance, expansion growth, life span of leaves and stem branching. Ann. Bot. 70, 27—35.



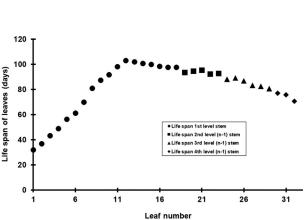


FIGURE 3.8 Relationship between leaf position (*x*-axis, leaf 1 being the first leaf to appear) and final area per leaf (in cm²), expansion rate (in cm² per day), and life span (in days) of a potato main stem grown from a seed tuber. This main stem of cv. Bintje produced several sympodial branches (up to the fourth level). Source: *From Struik*, *P.C.*, 2007. Above-ground and below-ground plant development. In: Vreugdenhil et al. (Eds.), Potato Biology and Biotechnology. Elsevier Science BV, pp. 219–236 and based on a plant with abundant nutrient supply and abundant light and grown in a cooled greenhouse. Data taken from Vos, J., Biemond, H., 1992. Effects of nitrogen on the development and growth of the potato plant. 1. Leaf appearance, expansion growth, life span of leaves and stem branching. Ann. Bot. 70, 27–35.

0.33-0.53 leaves per day or 0.0242-0.0317 leaves per $^{\circ}\text{C} \cdot \text{day}$ which results in one leaf per $32-41^{\circ}\text{C} \cdot \text{day}$. Fleisher et al. (2006) derived a phyllochron of $24.3-28.2^{\circ}\text{C} \cdot \text{day}$ per leaf with a base temperature of 4°C .

Data on leaf appearance rate of TPS-grown plants are scarce. It is our experience that leaf appearance rates are lower for TPS-grown plants than for seed-tuber grown plants due to the lower early vigor. However, this effect is partly compensated by the smaller size of individual leaves during early stages of growth.

Fig. 3.8 demonstrates the growth characteristics of the different leaf ranks (or leaf numbers, counted from below) by presenting the expansion rate, the final (maximum) individual leaf area, and the life span of individual leaves of a plant grown from a seed tuber. The rate of increase in leaf area (the expansion rate) strongly depends on leaf rank and increases with an increase in leaf rank (or leaf number or leaf insertion number) until about leaf number 13 (depending on cultivar and pretreatment). The final leaf area follows the curve of the expansion rate rather closely suggesting that the expansion duration is not very different for the different leaf ranks, at least not

for the first level stem segment. The maximum expansion rate is reached before second and third level leaves appear. Higher level leaves have lower rates of expansion and a lower final area per leaf than the leaves of the first level. Leaves with a low leaf rank have a shorter life span than leaves of a higher rank, until about leaf number 13. Beyond that leaf number a slow decrease of the life span occurs. Similar detailed information on leaf appearance rate, final leaf area and life span for TPS-grown plants are currently produced but are not available for publication yet.

3.7 Canopy development

The crop canopy cover at each time point during the growing season is the resultant of the rate and duration of canopy growth and the rate of canopy senescence (or the timing of the haulm killing) (Khan et al., 2019). Under optimal conditions and with long growing seasons, the early establishment of full canopy cover and its maintenance over a long period lead to a high biomass because of abundant interception of incoming radiation. However, the biomass needs to be partitioned to tubers in the right fractions in order to obtain economic yield. Therefore, canopy cover and tuber yield are closely related, but in a different way for early and late maturity cultivar types. The proper quantification of canopy dynamics and dry matter partitioning is essential for accurate modeling of potato production (Khan et al., 2019; Ospina Nieto et al., 2021). The canopy structure strongly depends on propagule type, seed quality, seed physiological age, and crop management. Genotypic variation in potato canopy dynamics is huge, governed by many interacting genes each with only a small effect and showing a strong genotype-by-environment ($G \times E$) interaction (Ospina Nieto et al., 2021). For a stable crop growth of both early and late maturing cultivars, the dry matter partitioning during the growing season should be stable, predictable, and properly managed if disturbed by stresses, such as water limitation or temporary heat. Moreover, it is essential to obtain more knowledge about the senescence phase as this phase is very important for the timely maturation and quality of the tubers (including duration of dormancy). Fig. 3.9 provides some examples of canopy development over thermal time. Note the differences in maximum canopy cover reached and the duration of maximum canopy cover between environments and between cultivars.

Crops grown from TPS have a much slower initial rate of increase of the canopy cover and demonstrate a much bushier appearance. Because of their appearance, such plants can easily lodge with important consequences for canopy structure. Hilling needs to be done carefully and relatively late during crop development.

Table 3.1 presents the proportional distribution of leaf area over the main stem and different types of branches. Not all leaves will contribute to tuber formation in the same manner and therefore this proportional distribution is relevant for canopy development and the interactions between above- and below-ground development. Obviously, the contribution of the apical lateral branches increases over time. The contribution of the basal lateral stems very much depends on the cultivar in this example, and can also become significant during later stages of canopy development.

Similar data are not available for TPS-grown crops but at our laboratory we are currently comparing in great detail leaf area allocation to different branches as well as leaf and whole-plant photosynthesis of the same genotypes grown in greenhouse conditions and in the field from seedling tubers and transplants produced from true seeds.

3.8 The stolon system

Diageotropic (or plagiotropic) shoots arise on below-ground stem parts. These are actually botanically rhizomes but are usually called stolons. Per node several stolons may arise: one main stolon and two axillary ones. Their structure is very similar to shoots, but they have rudimentary leaves and a hooked tip. They can easily branch, thus increasing the number of sites from which tubers may arise. Stolons can also produce roots thereby taking care of the capture of their own nutrient and water resources. When the tip of the stolon becomes above ground, it will demonstrate phototropic growth and develop into a leafy shoot, with its below ground branches then becoming ordinary stolons. In modern cultivars, stolonization does not require (much) induction but the process is very sensitive to moisture conditions, especially during early growth. It is believed that stolonization starts at the nodes of the main stem closest to the seed tuber and subsequently progresses acropetally; however, this pattern is not always very clear cut (Struik, 2007). It is commonly believed, however, that the first stolons on a seed-tuber grown plant grow faster and for a longer period of time than

3.8 The stolon system 65

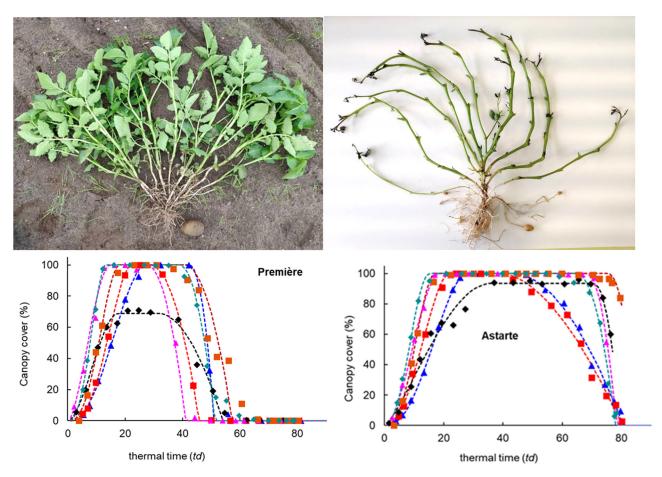


FIGURE 3.9 Single seed-tuber grown plant during early stages of canopy cover (upper left), a true-potato seed plant with leaves removed (upper right), canopy cover development in early cultivar Première under different levels of nitrogen supply (lower left) and canopy cover for late cultivar Astarte under different levels of nitrogen supply (lower right). Canopy cover percentages are plotted against thermal time: one unit is one day under optimal conditions. Source: Jiahui Gu (personal communication) and Sohail Khan (personal communication).

TABLE 3.1 The proportional distribution in percentage of leaf area over main stems (i.e., first-order main stem segment) and apical (sympodial; higher-order stem segments) branches and basal branches at different moments after planting for the cultivars Bintje and Saturna, grown from seed tubers at normal planting densities under Dutch field conditions. The table also contains the total leaf area index (i.e., area leaf per area ground).

Cultivar	Time (days after planting)	Main stem segment First order (%)	Apical lateral stems		Basal lateral stems	Total leaf area
			Second order (%)	Third order (%)	(%)	index (m ² /m ²)
Bintje	50	100	0	0	0	3.8
	83	55	31	4	10	6.3
	131	21	55	21	3	3.1
Saturna	50	82	0	0	18	4.4
	83	35	26	7	32	8.6
	131	6	18	23	53	3.6

Based on Struik, P.C., Wiersema, S.G., 1999. Seed Potato Technology. Wageningen Academic Publishers, Wageningen, the Netherlands.

later-initiated stolons. This means that the oldest stolons are much longer than younger stolons. Moreover, there is a strong tendency among the first stolons of one and the same main stem to have a longer period of time between stolonization and tuberization when the stolons have been initiated earlier. For later stolons, this relationship weakens, especially under variable conditions of water supply and temperature. Other researchers

have found that the first two or three stolons have a lower rate of elongation growth; the following four to eight stolons then demonstrate a very high rate of elongation growth, followed by an increasingly lower rate of elongation growth for subsequent stolon ranks.

However, it is very important to realize that for modern cultivars and for seed-tuber grown crops, there is no clearly separated cascade of events: stolon formation, stolon swelling into tuber incipients, and early tuber growth all happen at the same time on the same stem. In early cultivars, the transition from stolonization to tuber bulking may be more abrupt than for late cultivars. There is also not a strict relation between below-ground developmental processes (such as tuberization) and above-ground developmental processes (such as flowering).

Based on the trends illustrated above, the stolon system of a potato plant/crop is shaped by the differences between stolons in time of initiation, rate of growth, and the time between stolon initiation and tuber initiation on that stolon, all at least partly determined by their position on the stem (Struik, 2007). Potato plants develop different stolon types: tuber-bearing and nontuber-bearing stolons, as well as long and short stolons (Struik, 2007). Long stolons can branch profusely and are often nontuber bearing. Continued growth of long stolons can result in development into an above-ground shoot, similar to a below-ground branch (see also above). If stolons remain too short, there is not enough space for all tubers to grow. Because of all these differences, there is a stolon hierarchy and resulting from that a tuber hierarchy, which can vary during the bulking period, that is strongly determined by the supply of nutrients from below ground and the supply of energy from above ground (Struik et al., 1991).

The stolon system of a TPS-grown plant is different from that of a seed-tuber grown plant. The patterns described above are not applicable as the stolons on a TPS-grown plant are originating very close to each other and often partly at or just above the surface. Earthing up is therefore very important in TPS-grown plants.

3.9 The tubers

Tubers are the swollen parts of the stolons and are globose or ellipsoid in shape. They have a tuber skin (periderm) with lenticels for gas exchange and with scars of scale leaves (eyes) which contain buds that can produce one or more sprouts that can develop into shoots (see Fig. 3.3). They even can have roots. Tubers can also be formed on other parts of the plant than stolons and are then often sessile, for example, in the axils of leaves or even in inflorescences. This can happen under the induction of physiological triggers or because pathogens block the normal downward stream of assimilates. Normal tubers have a structure very similar to a swollen stem with various meristems from which sprouts can emerge after breaking of dormancy and apical dominance. Tubers can very much vary in shape, size, color of the skin, eyes and flesh, skin texture, and deepness of the eyes. They can also vary in chemical composition (dry matter concentration, starch content, protein content and quality, pigments, Vitamin C, antioxidants, etc.). Tuber bulking is a process that is very sensitive to environmental conditions, including temporary stresses such as drought, heat or excess water in the soil. Tubers, therefore, can have a wide diversity of physiological disorders, including knobbiness, growth cracks, secondary growth, heat sprouts, hollow hearts, translucent ends, etc.

An important trigger for tuber formation is the change of the plane of cell division and a strong increase in radial cell expansion. More or less at the same time, there is a strong increase in dry matter concentration because of accumulation of storage carbohydrates (starch), associated with a change in sugar metabolism and storage proteins (patatins).

The tuber system is strongly influenced by the stolon system and therefore differs between plants grown from seed tubers and those from TPS. The tuber system is characterized by tuber initiation, growth and resorption, the number of tubers, tuber bulking, tuber—tuber relationships, tuber shape, tuber disorders, tuber size distribution, and seed behavior (Fig. 3.10; Struik, 2007). Tuber formation in potato consists of a complex and dynamic sequence of several, partly independently regulated, events, including induction, initiation, set, bulking, and maturation. These events require that environment-dependent steps occur in an orchestrated way, regulated by specific genes, including the arrest of stolon growth, initiation of radial growth, and storage of patatins and starch. Tuber bulking is a complex phenomenon and can easily be reversed when environmental conditions suddenly change.

In Fig. 3.10, the dynamics of the number of tuber incipients or tubers per unit area over time and development are described. The figure provides a contrast between two situations that might occur in different years for one and the same cultivar. The figure describes the initiation of tubers, their growth, and possible resorption when conditions are not conducive to let all tuber incipients or small tubers grow out to marketable sizes. This results in two curves for each of the two situations: one curve for the total number of incipients/tubers and one for the number that finally reaches marketable sizes (in this case of seed tubers). In Situation 1, there is a large overkill of tuber initiation, resulting in a small fraction of the tuber incipients that really will grow out and a significant

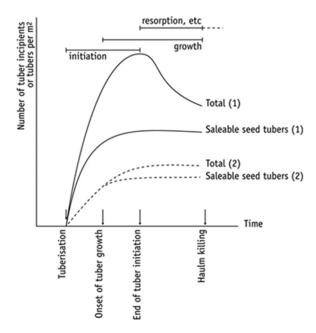


FIGURE 3.10 The tuber system, with a schematic representation of the changes over time of different types of processes and structures. As an example, we have taken saleable seed tubers as the main target, but similar figures would also apply to other types of end products. The figure describes two contrasting situations. See text for further explanation. Source: From Struik, P.C., Wiersema, S.G., 1999. Seed Potato Technology. Wageningen Academic Publishers, Wageningen, the Netherlands.

loss of small tubers that are being resorbed. In the other situation, there is very little tuber initiation and almost all tuber incipients will finally grow out into marketable sizes with very little loss of tuber initials and very little resorption of small tubers. Nevertheless, the final number of saleable seed tubers can still be very much in favor of the first situation.

Initiation, resorption, hierarchy, and fraction of marketable sizes are only partly under the control of the farmers. Proper management of water supply during early stages of growth (during stolonization and tuberization), proper ridge or bed structure, and crop management that aims at maintaining conducive conditions for tuber bulking without temporary disturbances of tuber growth (like those caused by irregular irrigation, short heat waves, drought) are important to steer the right number of tubers per stem. Number of stems per unit area can then be controlled by presprouting, physiological age and size of the seed tubers planted, plant density, and hilling.

The common belief is that the largest tuber at one point in time will also be the largest tuber at the end of the growing season. However, the growth rate of an individual tuber might vary in close interaction with the other tubers on the same stem, Moreover, the duration of growth of individual tubers may vary within one stem as well. It is very difficult to link these tuber growth characteristics to position on the plant or connecting them to certain branches or leaves. This certainly is true for a complex crop where yields of individual plants may vary very much and might vary more because of variation in number of tubers per plant than because of strong variations in size of the tubers. Nevertheless, during a growing season and once the number of tubers is more or less fixed, the relative variability in tuber size or weight (i.e., the coefficient of variation of the tuber size or weight) is relatively constant. That causes a strong correlation between yield and yield of large tubers within a cultivar as long as that cultivar is grown under similar conditions and has the same number of daughter tubers per unit area. That also makes the development over time of the tuber size distribution predictable as long as there are no strong changes in number of tubers per unit area (Situation 2 in Fig. 3.10).

3.10 The organs of sexual reproduction

Almekinders and Struik (1996) described the development of inflorescences on seed-tuber grown plants in great detail. Kacheyo et al. (2021) paid special attention to the reproductive development of the potato plant

(including inflorescences, flowers, berries, and seeds), especially when grown from TPS. We refer to these two papers for details. The text below on the organs of sexual reproduction is partly based on Struik (2007).

The inflorescence of a potato plant is a cymose panicle. Potato inflorescences can be formed at the end of the various types of stem segments described earlier in this chapter. That means that potentially a potato plant can produce a large number of inflorescences over a long period of time, provided these inflorescences can compete with the tubers for resources required for their growth and development. The number of inflorescences, therefore, strongly depends on the growing conditions and on crop management. Important factors influencing the number of inflorescences include: photoperiod, temperature, plant density, stem number per individual plant, physiological age and size of the seed tuber, and nitrogen supply.

Also, the number of flowers per inflorescence can vary considerably. This number of flowers per inflorescence is influenced by the same environmental and management factors as mentioned for the number of inflorescences. It is also important to note that the number of flowers per inflorescence strongly depends on the order of the stem segment, with higher order stem segments having fewer flowers per inflorescence.

An individual flower consists of a greenish campanulate calyx composed of five sepals, and five petals varying in color (possible colors include at least white, yellow, and violet). Each flower has five stamens. The anthers of the stamens are joined laterally, forming a cone-shaped structure, concealing the ovary, but with the (female) stigma protruding from it.

Successful pollination results in the formation of berries, which are globular and contain two carpels and many seeds. Berry size and number of seeds per berry depend on the position of the berry within its inflorescence and the position of that inflorescence within the plant. Berry weight, number of seeds per berry, and 100-seed weight are interrelated.

3.11 The root system

The root systems of a seedling and of a seed-tuber grown plant are very different. In TPS-grown plants, a radicle is formed at germination, which develops into the root system of the seedling. In seed-tuber grown plants, root primordia are formed on sprouts and below-ground stems develop the root system further. The differences between seminal roots of TPS-grown plants and adventitious roots of seed-tuber grown plants are essential in their history, anatomy, and morphology. However, in both cases, the root system is relatively weak, making the crop sensitive to water and nutrient (especially nitrogen and phosphorus) shortages. This is particularly true for early cultivars. It makes the crop less efficient in water use and nutrient use and makes the crop sensitive to poor soil structure and salinity.

In seed-tuber grown crops, root initials can already be present on the sprouts during presprouting (see Fig. 3.3). These can be essential in capturing phosphorus and other nutrients during crop establishment, especially in cold soils shortly after planting in areas with early spring planting of potato. Late cultivars usually have larger root systems than early cultivars, which is relevant as that means that late cultivars suffer later and less from the decline in intensity of root growth after the onset of tuber bulking.

Roots do not only arise on the main stems and the below-ground branches but also arise on stolons and even on tubers. Such roots can support the supply of nutrients to rapidly growing tubers that might be poor sinks for nutrients in comparison to the foliage.

3.12 A few comments on the relations between above-ground and below-ground development

The haulm strongly interacts with the below-ground plant parts. The sink—source and the sink—sink relationships are very complicated in a potato crop, but essential for the proper number of tubers per stem and per plant, marketable tuber yield, and tuber quality (physical and chemical quality, size distribution, duration of dormancy, growth vigor of seed tubers). These relationships are very much influenced by (changes in) environmental factors, such as temperature and photoperiod (Struik, 2007) and crop management, such as nitrogen supply (Ospina Nieto et al., 2021).

It is important to realize that there are many different types of branches on one plant. Given the complexity of the shoot system, the stolon system, and the tuber system, there are different types of interactions between shoots and tubers. Some shoots will mainly contribute to the maintenance of the above-ground machinery, whereas other shoots might focus more on producing assimilates for below-ground plant parts, including the tuber. This

References 69

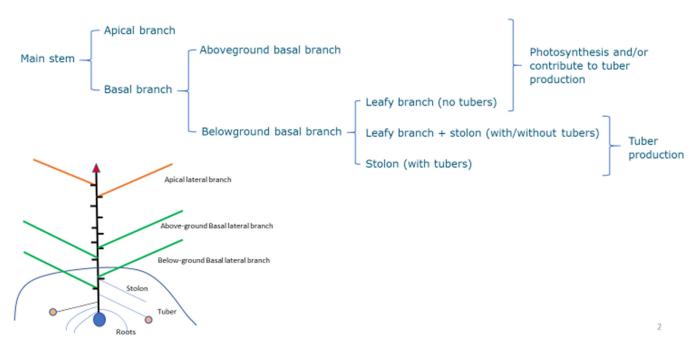


FIGURE 3.11 Different types of branches and stem segments, including stolons and tubers, contributing in different ways to tuber yield. Note that the blue colored propagule could be either a seed(ling) tuber or a true potato seed when there is significant earthing up. Source: *Jiahui Gu (personal communication)*.

is illustrated in Fig. 3.11. The precise quantification of the sink—source relationships will require detailed experimentation based on analysis of plants grown from different types of starting material.

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