Received: 17 March 2020 | Revised: 5 October 2020 | Accepted: 20 October 2020
DOI: 10.1111/aab.12661

PLANT PHENOLOGICAL GROWTH STAGES

Annals of Applied Biology
An international journal of the aab
WILEY

Augmented descriptions of growth and development stages of potato (*Solanum tuberosum* L.) grown from different types of planting material

Olivia Cynthia Kacheyo[1] | **Luuk Christiaan Maria van Dijk**[1,2] | **Michiel Erik de Vries**[1] | **Paul Christiaan Struik**[2]

[1]Solynta, Wageningen, The Netherlands
[2]Centre for Crop Systems Analysis, Wageningen University and Research, Wageningen, The Netherlands

Correspondence
Paul Christiaan Struik, Centre for Crop Systems Analysis, Wageningen University and Research, Bornsesteeg 48, 6708 PE Wageningen, The Netherlands.
Email: paul.struik@wur.nl

Funding information
Nederlandse Organisatie voor Wetenschappelijk Onderzoek, Grant/Award Number: NWO 313-99-301; Solynta

Abstract

The recent invention of hybrid breeding technology for potato has led to an increased interest in hybrid potato R&D. Hybrid true potato seeds (TPS) are used to produce planting materials such as transplants and seedling tubers, but can also be used for direct seeding of seed or ware crops. Transplants and seedling tubers can be used to produce seed tubers or ware tubers. The rise in R&D in hybrid breeding creates the need for phenological scales of growth and development of plants produced by the various planting material types of hybrid-TPS. The BBCH (Biologische Bundesanstalt, Bundessortenamt and CHemical Industry) scale is one of the phenological scales developed for the description of the growth and development stages of plants. In 1993, a BBCH scale with descriptions for potato plants was released. The original BBCH scale gave standardised descriptions for TPS- and tuber-grown plants. Differences in the morphology of plants originating from the different planting materials in terms of types of branches and differences in below-ground growth and development were not included. Moreover, for reproductive growth stages, crucial for hybrid breeding, the original scale is incomplete as it does not carefully take the complex sympodial branching into account. Methods of describing growth of tubers and berries are complex and impossible to use when final tuber mass or berry size is unknown. The current paper augments the original BBCH scale, while retaining its structure and logic. It provides alternative and comprehensive descriptions of growth stages suitable for potato plants grown from different types of planting materials, and for all end uses of these plants. The proposed scale is detailed enough for research and breeding but still general enough for agricultural use.

KEYWORDS

above-ground, BBCH scale, below-ground, plant growth stage scale, planting material types, potato growth and development, stolon, sympodium, TPS-grown plants, tuber-grown plants

1 | INTRODUCTION

Descriptions of phenological stages have been developed in order to systematically compare plant growth and development. For potato (*Solanum tuberosum* L.), various phenological scales of plants derived from seed tubers have been developed (Anon, 1987; Griess, 1987, 1989). Jefferies and Lawson (1991) indicated that most developed potato scales were not representative of all the stages of plant development as some scales fail to detail important stages such as the pre-emergence phase, sympodial branching from the axils of the upper leaves as well as branch growth and development. Furthermore, differences in growth and development stages of individual plants grown from different planting material types have not been stipulated in most scales.

2 | THE BBCH SCALES

The BBCH scale, abbreviation derived from Biologische Bundesanstalt, Bundessortenamt and CHemical Industry (BBCH Scale) (Meier et al., 2009), is one of the phenological scales developed for the description of the phenological growth and development stages for monocotyledonous and dicotyledonous plants. Over the years, the BBCH scale has been further developed and adopted for various crop species, including *Solanum* species such as potato (*S. tuberosum*; Hack et al., 1993), tree tomato (*Solanum betaceum*; Acosta-Quezada et al., 2016), cocona (*Solanum sessiliflorum*;Moreno, Quiñones, & Jiménez, 2016) and eggplant (*Solanum melongena*; Feller et al., 1995a, 1995b), among others.

The scales are organised by 10 distinct growth and development stages in the plant's life cycle. These principal growth and development stages are described using numbers from 0 to 9 with each number distinctively representing a growth and development stage in sequential ascending order of the numbers (Meier et al., 2009). The ascending order of the numbers does not define a strict sequence of the principal stages but because of the very different plant species, shifts in the course of the development or omission of certain stages may occur in some species. Additionally, stages may sometimes occur simultaneously in certain species; therefore, the order of occurrence of the principal stages during growth and development may differ from one species to another (Meier et al., 2009).

The BBCH scales also describe short growth and development steps characteristic of certain plant species, which are termed secondary stages (Meier et al., 2009). These are stages used when steps in plant growth and development must be indicated precisely through further breakdown of principal stages into sub stages. The secondary stages are also coded from 0 to 9 and are passed successively during the respective principal growth and development stages. The combination of the principal stage and the secondary stages gives a two-digit descriptive code, where the first digit is the principal stage and the second digit represents successive stages within the particular principal stage. In other crop species, where further subdivisions of a principal stage are required beyond the secondary stages in the two-digit scale, meso stages coded from 0 to 9 are used between the principal stage and the secondary stage resulting in a three-digit scale (Hack et al., 1992; Meier, 1997; Meier et al., 2009).

2.1 | The original BBCH scale for potato

Hack et al. (1993) describe, in the German language, an extended BBCH scale for potato grown from seed tubers and true potato seeds (TPS). The first publication with English descriptions can be found in the publication Meier (1997). The scale describes the 10 principal stages of plant growth and development as observed from tetraploid seed tubers as well as tetraploid TPS. As tetraploid potato is largely vegetatively propagated by seed tubers, the development of the potato BBCH scale from seed tubers was useful as it addressed the need for a worldwide adopted scale for research, breeding and other disciplines. The scale uses both two- and three-digit descriptions with the meso codes 0 to 9 describing the various levels of sympodial development, that is, 0 defines the primary level of branching and 2 defines the second level, etcetera.

2.2 | Diploid hybrid F1 true potato seeds

The recent invention of an F1 diploid hybrid breeding system for potato, as described by Lindhout et al. (2011), provides us with diploid hybrid F1 TPS. The parents of the cross are required to be high-attribute parental plants and highly homozygous in order to achieve high uniformity in the F1 materials obtained from the cross. The cross results in one plant producing up to thousands of F1 hybrid botanical potato seeds, which are commonly referred to as TPS (Almekinders, 1995; Almekinders, Chujoy, & Thiele, 2009; Jansky et al., 2016; Muthoni, Shimelis, & Melis, 2013; Struik & Wiersema, 1999) and can be used as planting material for producing new potato varieties (Lindhout et al., 2011).

Hybrid TPS are therefore flexible and versatile as they allow for the adoption of three possible systems of potato production: through direct sowing of F1 hybrid seeds, through transplanting seedlings derived from hybrid TPS or through the use of tubers derived from directly sown or transplanted seedlings (Almekinders, Chilver, & Renia, 1996; Almekinders et al., 2009; Almekinders & Struik, 1996; Struik & Wiersema, 1999). In addition to the three systems, the use of various types of seed tubers is still the norm in potato production. Seed tubers are daughter tubers used as planting material, irrespective of their origin (i.e., whether their mother plant is produced from a seed tuber or from true seed). The term seed tuber reflects the use, not the origin of tubers. However, in this paper, the term seed tuber is used to describe tubers derived from mother plants also grown from seed tubers and the term seedling tuber is used to describe tubers derived from TPS (Almekinders et al., 2009; Stockem et al., 2020; Struik & Wiersema, 1999), thus introducing two types of vegetative potato seed: seedling tubers and seed tubers. This is to provide a clear distinction of planting materials and their respective origins.

2.3 | Limitations of the original BBCH scale

The application of the original BBCH scale (Hack et al., 1993) to potato plants grown from different planting materials—directly sown TPS, transplants from TPS, seedling tubers or seed tubers—has proven to be limiting due to the standardised descriptions of the various principal stages in the original scale. Significant differences in the development of leaves and types of leaves in TPS-grown and tuber-grown plants have been observed as early as at emergence (Struik, 2007a). Some of the methods used to describe development stages such as tuber development and berry development require final tuber and berry sizes for stage description which proves difficult especially in the absence of final harvest data (Hack et al., 1993). Additionally, descriptions of various branch types (below-ground basal branches in tuber-grown plants) as well as detailed stages of stolon development were not described in the original scale.

2.4 | Morphology of the potato plant

Observations on TPS-grown and seed tuber-grown plants have shown differences in plant morphology and patterns of growth and development, especially in relation to the development of the root system, the form of the plant shoot at emergence, leaf development, the number of stems and the various types of stems (Figure 1; Wohleb, Knowles, & Pavek, 2014; Struik, 2007a; Struik & Wiersema, 1999).

In TPS-grown plants, at germination, a radicle is formed which develops into the root system of the seedling and elongation of the hypocotyl leads to the development of the main stem of the plant. TPS-grown plants develop a single stem per plant (Struik & Wiersema, 1999; Vos, 1999). In contrast, tuber-grown plants usually produce a collection of main stems developing from one or more axillary buds, commonly known as eyes, on the tubers (Struik & Wiersema, 1999; Vos, 1999).

Potato is known to develop a sympodial shoot, which allows for multiple levels developing after termination of the main stems (or the lower-order levels) into inflorescences (Almekinders, 1995; Struik, 2007a; Vos, 1999). Leaf development is significantly different between the two planting materials, TPS and seed tubers. In TPS-grown plants, after emergence, apical meristem growth results in the development of the first true leaves. For tuber-grown plants, early leaves are visible at sprouting and elongation of the main stem leads to the gradual unfolding of individual leaves on the stem. A fixed number of leaves develop on the stem before its termination into an inflorescence. Sympodial branching starts in the axils of upper leaves of the main stem (Jefferies & Lawson, 1991). A lower number of apical branches are observed in TPS-grown plants than in tuber-grown plants, which have more excessive apical branching, especially when nitrogen supply is abundant.

In addition to the sympodial development of the main stem, potato plants grown from tubers generally develop different types of stems: the main (primary) stem(s), basal branches that develop from above-ground basal nodes (herein referred to as above-ground basal

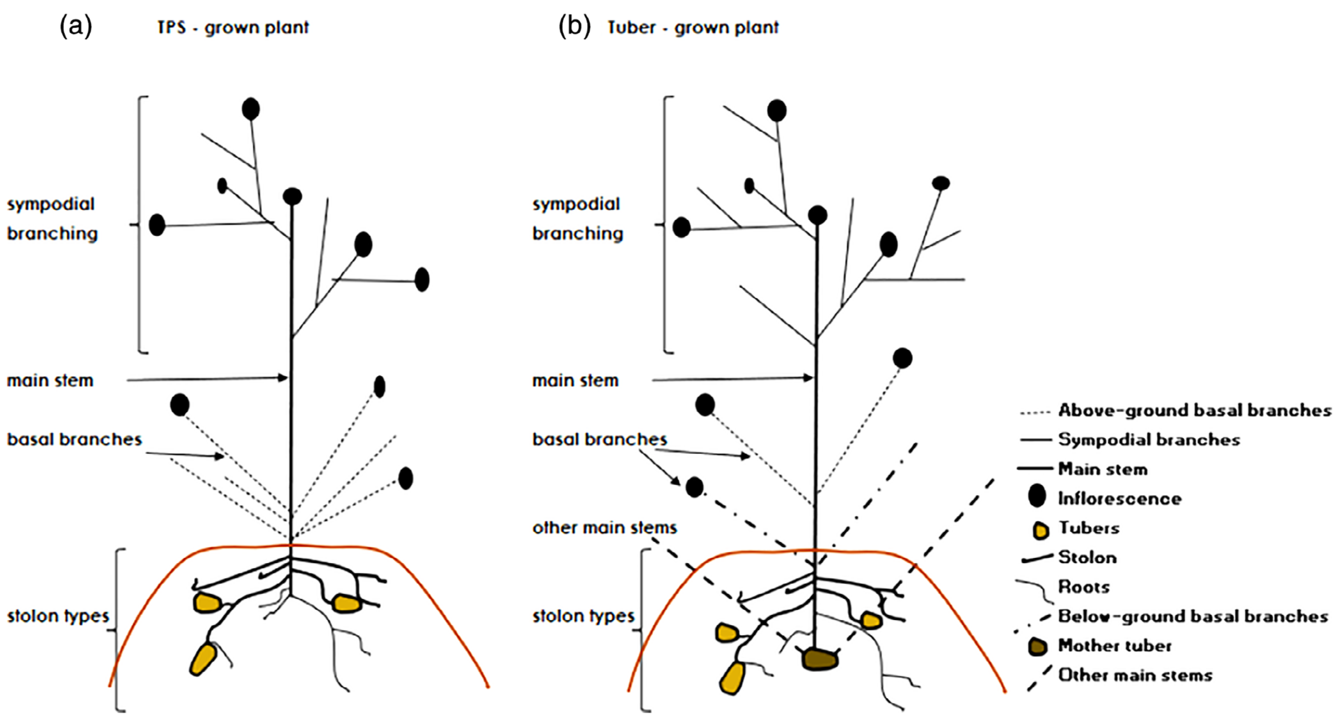


FIGURE 1 Structure of above- and below-ground plant parts of a potato plant for both true seed-grown and tuber-grown plants, adapted from: Struik (2007a), Struik and Wiersema (1999), Almekinders and Struik (1996) and Vos (1995)

branches), basal branches that develop from below-ground nodes but are visible above ground as branches (herein referred to as below-ground basal branches) as well as stolons, which are diageotropic stems (Almekinders & Wiersema, 1991; Struik, 2007a; Struik & Wiersema, 1999; Vos, 1999). The above-ground basal branches are non-tuber bearing, whereas the main stems and below-ground branches can be tuber bearing as they are capable of developing stolons on their below-ground nodes. This can however be affected by different field management operations such as "hilling" or "earthing-up," which involve the covering of the basal part of the stems thus causing formation of stolons on the now below-ground branches. Some shoots that originally behave like stolons (diageotropic growth) may also turn into below-ground branches with their initial stolon branches developing into regular stolons (Struik, 2007a). In TPS-grown plants, the main stem also produces above-ground non-tuber bearing basal branches (Struik, 2007a; Struik & Wiersema, 1999). No below-ground basal branches develop from below-ground nodes in TPS-grown plants, except when they start as stolons. The original BBCH scale for potato uses the term side shoot to define basal branches developing both above and below ground, however for purposes of distinction between TPS-grown and tuber-grown plants as well as mislabelling of other main stems as side shoots in tuber-grown plants, basal branches will henceforth be the term used to describe side shoots (Figure 1).

Potato plants develop different stolon types: tuber-bearing and non-tuber-bearing stolons as well as long and short stolons (Figure 1; Struik, 2007a; Vos, 1999). Long stolons are observed to branch profusely and are often non-tuber bearing. Continued growth of long stolons can result in emergence from the soil surface and subsequent development into an above-ground shoot (as a below-ground branch) (Struik, 2007a). Stolons on TPS-grown plants also develop below ground directly from below-ground nodes. Some stolons on TPS-grown plants may also develop into below-ground basal branches when they grow out of the soil surface as in tuber-grown plants. As stolon development is a precursor of tuber development, tuber development steps are normally described from stolon initiation to tuber maturity (Celis-Gamboa, 2002). From tuber initiation, when the tips of tuber-bearing stolons swell to twice the diameter of the subtending stolon, tuber growth starts and the size of the tubers increases (Celis-Gamboa, 2002).

During the development of reproductive stages, sympodial branching causes a complex branching pattern where several branches develop at the axils of the leaves (Struik, 2007a; Struik & Wiersema, 1999; Vos, 1995). The first inflorescence on the potato develops after termination of leaf appearance and elongation of the main stem. The apical meristem develops an inflorescence which may either abort or fully develop during the course of the growing period (Struik & Wiersema, 1999). The inflorescence contains more than one flower bud and one or more buds may develop and mature at the same time on one inflorescence. Flower development follows full development of flower buds but this may not always be the case as bud and flower abortion may occur leaving the peduncle of the inflorescence still attached to the plant (Almekinders, 1991). Development of the inflorescence on the main stem leads to the beginning of vegetative growth in the axillary buds of one or more leaves below the primary inflorescence on the main stem. This leads to development of an order of branching which also develops leaves and later terminates into an inflorescence on its meristem. Continuous vegetative growth leads to further layering of the branching pattern of a sympodial branch (Struik, 2007a; Struik & Wiersema, 1999). The number of leaves per branch becomes lower with an increase in order but also depends on the position of the branch on the sympodium (Almekinders & Struik, 1996).

2.5 | Complementing the original BBCH scale for potato plants from various planting materials

The use of various other planting materials in addition to regular seed tubers has increased with the introduction of potato hybrid breeding reported by Lindhout et al. (2011). This development makes it topical to create a scale that works for plants from all planting materials. To address the limitations of the original scale, alternative or additional but compatible descriptions of various stages of growth and development are required to complement the original scale as described by Hack et al. (1993). The new alternative or additional descriptions—from now referred to as augmented descriptions—will thereby help in the description and coding of all important stages of growth and development, including the stages that were omitted in the original scale.

Research and development, plant protection, variety release, and commercialisation of diploid hybrid potato calls for detailed descriptions of growth and development stages of plants from the various types of planting material of hybrid potato. This motivates an urgent need for codification of growth and development stages of potato taking into account the various sectors that use the BBCH scales. With an increase in the use of technology as well as software tools in various aspects of plant research, potato crop growth stages and crop management practices can be easily aligned through standardised coding using the original BBCH scale augmented with additional and adapted descriptions.

The new augmented descriptions will provide distinction of principal growth and development stages when critical differences in morphology of the plants or timing of occurrence of development stages are distinct between plants from different planting material types. Addition of further descriptions to the original scale will clearly define the differences in each planting material type and will detail other morphological changes in the plants in parallel to those already discussed in the original scale. This will help address the need for proper phenological descriptions of potato plants worldwide. The new alternative and additional descriptions do not violate the basic rules of the BBCH scales nor are they in conflict with the original BBCH scale for potato. They do provide alternative and additional descriptions of growth and development stages that make the new scale applicable to potato plants grown from different planting materials.

This paper proposes additional or alternative descriptions of selected potato growth and development stages in the original BBCH scale; it also provides new suitable, objective descriptions of other stages detailed by Hack et al. (1993). It also describes a BBCH scale coding for plants originating from diploid hybrid potato planting materials, including TPS and seedling tubers.

3 | MATERIALS AND METHODS

Complete life cycles of the potato plants were observed in two growing seasons in the field and a growing season in a greenhouse. General observations and destructive harvests were used to determine the growth stages of hybrid diploid potato, *S. tuberosum* L. The descriptive stages as detailed here represent growth and development stages of normal growing plants with no observable abnormalities in growth due to either mutations or those caused by abiotic or biotic stresses.

Potato plants grown from F1 diploid hybrid TPS of experimental hybrids were used for observations of growth and development in various experiments during two field seasons. Greenhouse and field trials were conducted for clear observation of the experimental hybrids under both conditions. Experimental hybrids were used to observe growth and development in field experiments through direct sowing as well as transplanting of greenhouse-raised seedlings. The field experiments were conducted during the 2018 and 2019 growing seasons at UNIFARM fields of Wageningen University and Research, located in Bennekom, the Netherlands. Greenhouse experiments and observations were conducted in the Nergena greenhouse of the UNIFARM facilities of Wageningen University and Research. Three planting material types, seedling tubers, transplants as well as directly sown TPS, were used for the observations throughout the experimental period.

Observations of nursery materials were performed on directly sown TPS in seedling nurseries in a greenhouse in 2018. Studies on germination stages were also conducted in aseptic laboratory conditions, where TPS were sown on MS media (Murashige & Skoog, 1962) to further observe germination stages of the hybrid TPS in 2018. Additionally, observations on germination were performed in a laboratory on river and fine sand as well as glass beads. The hybrids used in the experiments originated from the Solynta breeding programme, described in detail by Lindhout et al. (2018). The field performance of this plant material has been analysed in detail by Stockem et al. (2020).

Photographs of different plant growth stages were taken from various plants in the greenhouse, field and laboratory to provide a general outlook of the various plant growth stages. The pictures were therefore taken under a variety of lighting conditions and angles. Therefore, to provide clear and visible depictions of the stages, where necessary, the photographs were subjected to corrections for sharpness, temperature, contrast and brightness using Microsoft Word.

The original BBCH scale for potato described by Hack et al. (1993) is published in the German language, however, for the purposes of this paper, all text of the descriptions of growth and development stages referring to the original BBCH scale will be adapted from the text of the original English BBCH scale found in Meier (1997).

TABLE 1 Original and alternative descriptions of the potato Biologische Bundesanstalt, Bundessortenamt and CHemical Industry (BBCH) scale. Bold text indicates principal stages where augmented descriptions have been added to the original scale as well as alternative descriptions which do not compromise the authenticity of the original scale

Stage	Description for seed-grown plants (directly sown/ transplants)	Description for tuber-grown plants
0	Germination	Sprouting
1	Leaf development	Leaf development
	Stem elongation and development of sympodial stem	**Stem elongation and development of sympodial stem**
2	**Formation of above-ground basal branches**	Formation of above-ground basal branches
		Formation of below-ground basal branches
3	Main stem elongation (crop cover)	Elongation of main stems (crop cover)
4	Tuber formation (% of final tuber mass reached)	Tuber formation (% of final tuber mass reached)
	Tuber bulking (Harvest index)	**Tuber bulking (Harvest index)**
5	Inflorescence emergence	Inflorescence emergence
	Augmented descriptions of inflorescence development (highlighting clear sympodial branching patterns)	**Augmented descriptions of inflorescence development (highlighting clear sympodial branching patterns)**
6	Flowering (% flowers in population)	Flowering (% flowers in population)
	Flower development (morphological development of flowers on plants)	**Flower development (morphological development of flowers on plants)**
7	Development of fruit (% of berries at full size in fructification)	Development of fruit (% of berries at full size in fructification)
8	Ripening or maturity of berries and seeds	Ripening or maturity of berries and seeds
9	Senescence	Senescence

4 | RESULTS

Augmented descriptions of growth and development in potato have been developed to ease application of the scale to various planting materials of Hybrid-TPS as well as to provide alternative and compatible descriptions of the BBCH scale when applicable. The augmented descriptions complement the original scale and describe growth and development stages using mainly the three-digit codes of the BBCH scale. In order to conserve the basic rules of the BBCH scale used in developing the original scale, for potato, Table 1 provides a general overview of the principal stages of the scale and the stages where augmented descriptions have been proposed.

4.1 | Vegetative growth and development

4.1.1 | Principal Growth Stage 0: Germination/sprouting

The first principal stage, Stage 0 of the BBCH scale, details germination or sprouting of TPS- or tuber-grown plants, respectively. TPS- and tuber-grown plants show differences in development in this principal stage of the BBCH scale (Figure 2; Table 2). During the germination process, seeds imbibe water (Stage 001) when exposed to moisture, which triggers the start of the physiological process of germination. The radicle emerges (Stage 005) and develops into a root system. The hypocotyl develops (Stage 007) next and further develops into the stem of the plant after emergence (Stage 009) (Figure 2; Table 2).

Seed tubers and seedling tubers start the first principal stage dormant with no visible sprouts at Stage 00 (000) and sprout

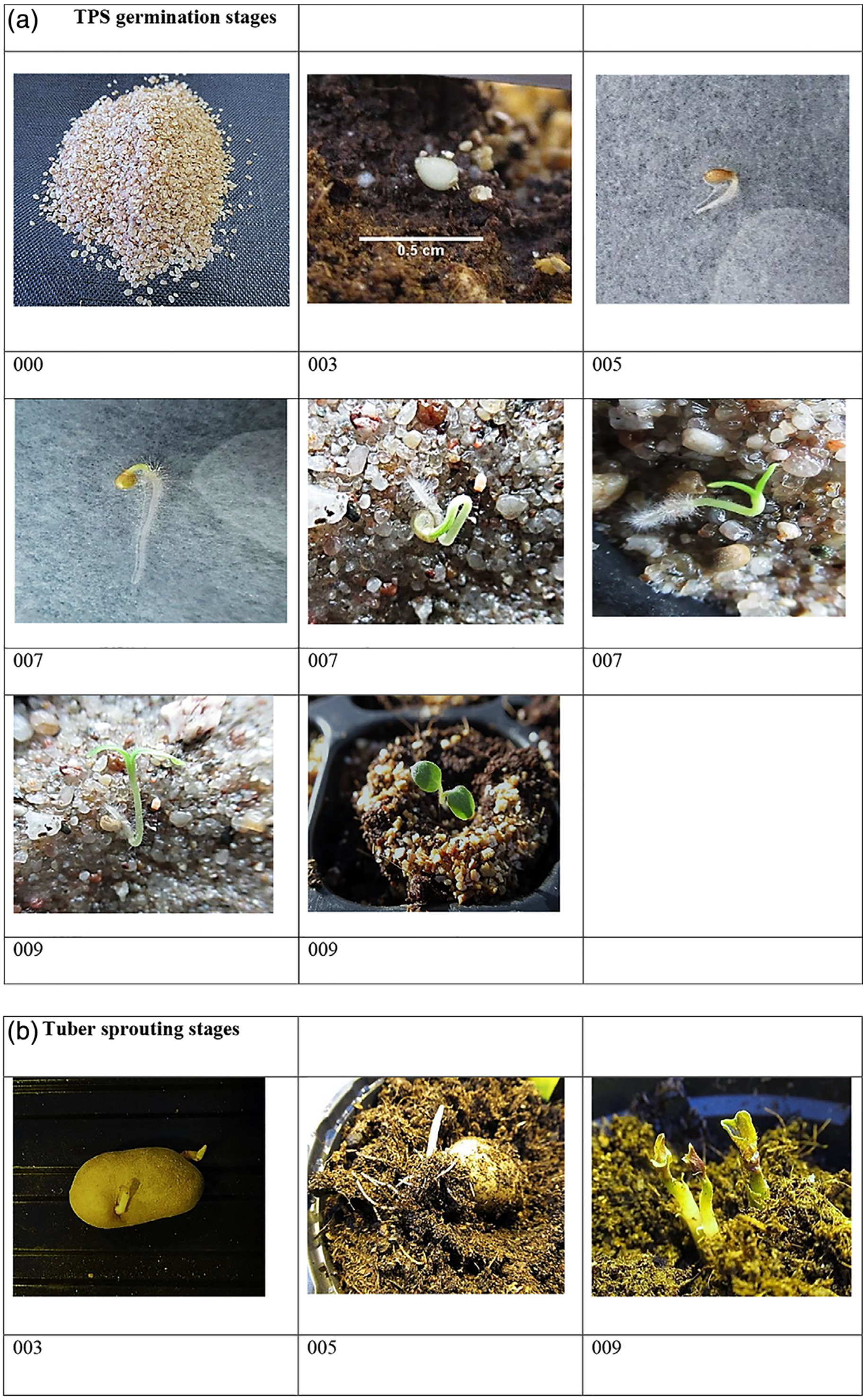


FIGURE 2 Depiction of germination and sprouting stages of Principal Stage 0 on the potato Biologische Bundesanstalt, Bundessortenamt and CHemical Industry (BBCH) scale in true potato seeds (TPS)-grown and tuber-grown plants with corresponding codes for each stage. Pictures belong to different hybrids and were taken at different moments during the course of observation of growth and development stages of diploid hybrid potato. (a) Depicts germination in TPS-grown plants sown on peat moss, river sand and filter papers in Petri dishes in the laboratory and (b) depicts sprouting in tuber-grown plants grown in a greenhouse compartment

TABLE 2 Description of the phenological growth stages of true potato seeds (TPS)-grown and tuber-grown plants of F1 diploid hybrid plants in the Principal Stage 0 according to the basic (two-digit) and extended (three-digit) Biologische Bundesanstalt, Bundessortenamt and CHemical Industry (BBCH) scale (with adaptations from Hack et al., 1993)

Two-digit code	Three-digit code	TPS-grown plant description	Tuber-grown plant description
00	000	Dry seeds	Innate or enforced dormancy: tuber not sprouted
01	001	Beginning of seed imbibition	Beginning of sprouting: sprouts visible (<1 mm)
02	002		Sprouts upright (<2 mm)
03	003	Seed imbibition complete	End of dormancy: sprouts 2–3 mm
			Sprouts upright
05	005	Radicle emerged from seed	Beginning of root formation
07	007	Hypocotyl with cotyledons breaking through seed coat	Beginning of stem formation
08	008	Hypocotyl with cotyledons growing towards soil surface	Stems grow towards soil surface
09	009	Emergence: cotyledons break through soil surface	Emergence: stems break through the soil surface: Formation of scale leaves in the axils of which stolons will develop later
			Sprouting of 1st main stem
	021–029		Sprouting of 2nd main stem in tubers
	0N9		Sprouting N^{th} main stem in tubers

development follows until the sprouts emerge at Stage 09 (009) (Figure 2). As a collection of stems originates from the same seed tuber or seedling tuber, multiple sprouts are observed at emergence Stage 09 (009) unless the tubers were planted when still in the phase of apical dominance (Struik & Wiersema, 1999) leading to the development of a single stem. Description of other sprouts developing from the same mother tuber can be detailed through further descriptions as indicated in Table 2 from Stage 021 for the second sprout to 0N9 for development in the N^{th} sprout. The root system of plants from seed tubers or seedling tubers forms at Stage 05 (005) (Table 2).

4.1.2 | Principal Growth Stage 1: Leaf development

Leaf development is the second principal stage on the BBCH scale, and it depicts the development of full compound leaves on the plant which occurs as the main stem elongates (Table 3). In the original scale, a 4 cm size is used as a basis of determining a developed leaf; however, because compound leaves may also be fully developed at a size below 4 cm, the use of size may limit the application of the scale. A leaf will be determined as developed when it fully unfolds from the main stem and one or more discrete pairs of leaflets are visible (Figure 3). In TPS-grown plants, the first leaves visible at Stage 100 are cotyledon leaves that develop during the Germination Stage 0 (Figure 2). An apical meristem becomes visible and further growth leads to the development of the first true leaves. The stages in leaf development are determined by observing the order of the leaves developing on the main stem from the first leaf to the ninth leaf to explain Stages 101 to 109 on the three-digit BBCH scale. For each level of sympodial branching, a decrease in the number of leaves in reference to the main stem is observed.

4.1.3 | Principal Growth Stage 2: Formation of basal branches

The Principal Growth Stage 2 describes the growth and development of both above- and below-ground basal branches in tuber-grown plants as well as above-ground basal branches in TPS-grown plants (Table 4). The term "basal branches" is used to describe "side shoots," which is the term used in the original BBCH scale for potato, to clearly distinguish the branching patterns of the different planting materials (see morphology of the potato plant, Figure 1). The growth and development of both above-ground and below-ground basal branches are unique to tuber-grown plants and occur *concurrently*, thereby requiring a description of growth stages for both branch types in the Principal Growth Stage 2 in contrast to the original scale (Table 4). Over 5 cm of growth is used to determine a branch to distinguish a branch from stolons which may later turn into basal branches if emerged from the soil (Figure 4; Table 4). As no below-ground basal branches are visible in true seed-grown plants, the Principal Stage is described from 201 to 209 in the three-digit coding system.

4.1.4 | Principal Growth Stage 3: Main stem elongation (canopy cover)

Principal stage 3 describes main stem elongation based on canopy cover (Table 5). Progress in the stages in the original scale is

TABLE 3 Description of the phenological growth stages of true potato seeds (TPS)-grown and tuber-grown F1 diploid hybrid plants derived from directly sown true seeds during Principal Stage 1 according to the basic (two-digit) and extended (three-digit) Biologische Bundesanstalt, Bundessortenamt and CHemical Industry (BBCH) scale

Two-digit code	Three-digit code	Description of leaf and stem development in TPS-grown plant	Description of leaf and stem development in tuber-grown plants
10	100	Onset of leaf development:	Early leaves visible on main stems
		Cotyledons completely unfolded	First leaves begin to extend
		Onset of main (1st level/primary stem) stem elongation	Onset of main (1st level/primary stem) stem elongation
11	101	1st leaf of main stem fully unfolded	1st leaf of main stem fully unfolded
12	102	2nd leaf of main stem fully unfolded	2nd leaf of main stem fully unfolded
13	103	3rd leaf of main stem fully unfolded	3rd leaf of main stem fully unfolded
		Continued elongation of main stem	Continued elongation of main stem
	10n	Stages continue until…	Stages continue until…
19	109	Nine or more leaves of main stem unfolded	Nine or more leaves of main stem unfolded
		Main stem terminates into inflorescence	Main stem terminates into inflorescence
	120	Onset of leaf development (2nd level)	Onset of leaf development (2nd level)
		Onset of formation of one or more sympodial stems (2nd level)	Onset of formation of one or more sympodial stems (2nd level)
	121	1st leaves unfolded (2nd level)	1st leaves unfolded (2nd level)
		Elongation of one or more sympodial stems (2nd level)	Elongation of one or more sympodial stems (2nd level)
	129	Nine or more leaves of one or more sympodial stems unfolded (2nd level)	Nine or more leaves of one or more sympodial stems unfolded (2nd level)
		One or more meristems terminate(s) into inflorescence (2nd level)	One or more meristems terminate(s) into inflorescence (2nd level)
	130	Onset of leaf development (3rd level)	Onset of leaf development (3rd level)
		Onset of formation of one or more sympodial stem(s) (3rd level)	Onset of formation of one or more sympodial stem(s) (3rd level)
	131	1st leaves unfolded (3rd level)	1st leaves unfolded (3rd level)
		Formation of one or more sympodial stem(s) (3rd level)	Formation of one or more sympodial stem(s) (3rd level)
	13n	Stages continue until…	Stages continue until…
	1Nn	n leaves unfolded (N^{th} level)	n leaves unfolded (N^{th} level)
		Formation of one or more sympodial stem(s) (N^{th} level)	Formation of one or more sympodial stems (N^{th} level)

determined using the percentage of plants meeting between the rows (Hack et al., 1993). This, although informative, limits the applicability of the scale when diverse cultivation practices such as potting or field cultivations on mounds or beds are used. The percentage of canopy cover offers a clear description for the principal stage as compared to the use of plants meeting between the rows as described in the original scale (Hack et al., 1993). Haverkort (2018) provides a detailed method for measuring canopy cover in potato cultivated in the field. Description of the principal stage now details the accumulated percentage of crop or canopy cover at the time of observation from stage 300 to 309 describing 10 to about 90% cover.

4.1.5 | Principal Growth Stage 4: Tuber bulking

In addition to the original description of the stage by Hack et al. (1993), alternative stages 410 to 419 have been developed herein to describe the process of tuber bulking by determination of the harvest index (HI) of the plant at each moment of harvest (Table 6). This is proposed to allow for description of the stage in the absence of final tuber mass to determine the stage. The stages 410 to 419 are alternatives describing the principal stage and should therefore not be used in parallel to the original description outlined by Hack et al. (1993). The HI should be calculated as defined in Equation (1).

$$\mathrm{HI} = \frac{\text{Total tuber dry weight (g)}}{\text{(Total above ground dry biomass (g) + total below ground dry biomass (g))}} \quad (1)$$

4.2 | Reproductive growth and development

4.2.1 | Principal Growth Stage 5: Inflorescence emergence

The development of inflorescences on the plant determines the beginning of Principal Stage 500. When the primary inflorescence (inflorescence of the primary level of the main stem) is first observed, the first

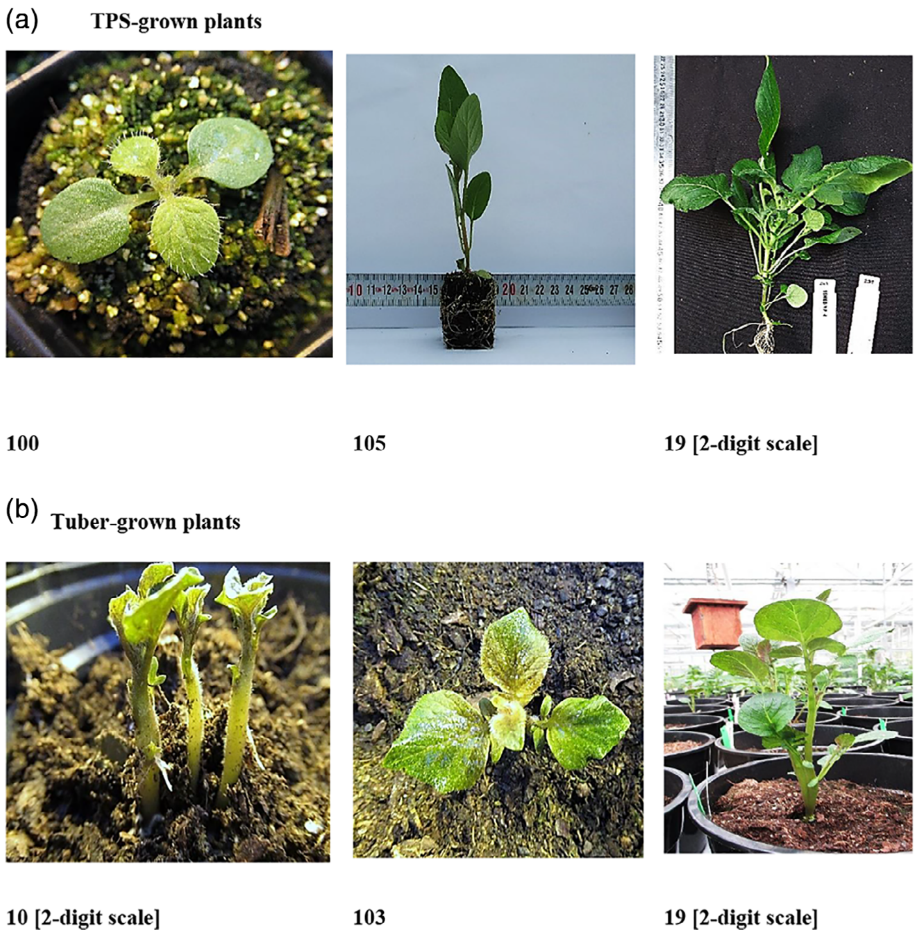


FIGURE 3 Depiction of leaf development and stem elongation of true potato seeds (TPS)-grown and tuber-grown plants in the Principal Stage 1 of the potato Biologische Bundesanstalt, Bundessortenamt and CHemical Industry (BBCH) scale, with corresponding codes for each stage. Pictures were taken from different hybrids at different moments in the greenhouse during the course of observation of growth stages of diploid hybrid potato. (a) Represents TPS-grown plants and (b) represents tuber-grown plants

Stage 501 is determined. Hack et al. (1993) describes three stages for each level of sympodial branching: 51/501, 55/505 and 59/509 for the primary level of the main stem, 521, 522 and 529 for the second level and so forth to describe the development of the inflorescence (Table 7). In addition to the original description, new augmented descriptions that further detail the stages have been added to highlight the development especially of the levels of sympodial growth in more detail. Stages 511 to 519 provide augmented descriptions that highlight the clear rules of sympodial branching in potato plants. The stages provide descriptions of individual buds on the primary inflorescence (main stem). Additionally, alternative codes for 521-5N9 have been provided to further detail the augmented stages by indicating the development of one or more buds developing on one or more inflorescences in a particular level of sympodial branching (Table 7; Figure 5). These stages have been added to avoid redefining the original BBCH scales and to provide alternative methods of defining the development stages.

4.2.2 | Principal Growth Stage 6: Flower development

Flower development is Stage 600 on the scale, and it describes the percentage of flowers observed in an inflorescence. Considering that potato inflorescences might undergo abortion of buds and flowers, and that the expected number of flowers per bud is not fixed, description using the percentage of observed flowers is complex. In many other crops, Stage 600 in the BBCH scale is described as the number of flowers open at a given time. This is informative in crop species with a few inflorescences, however, because of sympodial branching patterns in potato, the description of the stage using counts of flowers proves to be limiting as well because new inflorescences develop with each successive level of branching. As such new flowers develop on the plant with each successive observation rendering the results of the previous observation erroneous. To address this without redefining the original scale, stages 610 to 619 are used to describe proposed alternative methods to define the development stages (Table 8; Figure 6).

4.2.3 | Principal Growth Stage 7: Berry growth

In the original scale, berry growth is determined using the percentage of berries in fructification to have reached full size at time of observation. The original description (Hack et al., 1993) has been maintained for description as possible changes do not comply with the basic rules of the BBCH scales.

4.2.4 | Principal Growth Stage 8: Berry ripening

Principal Stage 8 describes ripening of berries. The stages are detailed from when berries are mature and still green (Stage 801), to their discolouration (Stage 805) and to shrivelling and potentially falling off the plant in the order of sympodial branching in the plant in the original scale (Hack et al., 1993) (Table 9). Additional description of berries falling off the plant has been added to indicate that this is a normal and highly likely occurrence in potato plants (Table 9). Figure 7 depicts some development stages in berry ripening as observed on potato plants.

4.2.5 | Principal Growth Stage 9: Senescence

Senescence is the last stage of plant development on the BBCH scale and is detailed in Principal Growth Stage 9. As plants mature, plant parts begin to senesce which is shown by discolouration and drying out of the plant parts. Hack et al. (1993) describes the changes in the plants using colour: yellow and brown. Change in colour however does not conform only to senescence because of maturity but may also be observed when plants suffer environmental stress among

TABLE 4 Description of the phenological growth stages of true potato seeds (TPS)-grown and tuber-grown F1 diploid hybrid plants grown from true seeds and tubers during Principal Stage 2 according to the basic (two-digit) and extended (three-digit) Biologische Bundesanstalt, Bundessortenamt and CHemical Industry (BBCH) scale. To distinguish between above- and below-ground basal branches, augmented descriptions using codes 220/229 have been added to describe below ground basal branches

Two-digit code	Three-digit code	Description of formation of basal branches in both TPS- and tuber-grown plants
		For all planting material types
20	200	Onset of development of above-ground basal branches
21	201	First basal branch visible (>5 cm) from above-ground node
22	202	Second basal branch visible (>5 cm)
23	203	Third basal branch visible (>5 cm)
2n	20n	Stages continue until…
29	209	Nine or more basal branches visible (>5 cm)
		For seed tuber- and seedling tuber-grown plants
	220	Onset of development of below-ground basal branches
	221	First basal branch visible (>5 cm) from below-ground node
	222	Second basal branch visible (>5 cm)
	223	Third basal branch visible (>5 cm)
	22n	Stages continue until…
	229	Nine or more basal branch visible (>5 cm)

TABLE 5 Description of the phenological growth stages of true potato seeds (TPS)-grown and tuber-grown F1 diploid hybrid plants grown from true seeds and tubers during Principal Stage 3 according to the basic (two-digit) and extended (three-digit) Biologische Bundesanstalt, Bundessortenamt and CHemical Industry (BBCH) scale. Stage 30/300 to 39/309 maintains original descriptions outlined by Hack et al. (1993) by using percentage of canopy cover in describing the stages

Two-digit code	Three-digit code	Description of main stem elongation (above ground)
30	300	Beginning of canopy cover
		Onset of main (1st level/primary stem) stem elongation
31	301	10% canopy cover
32	302	20% canopy cover
33	303	30% canopy cover
34	304	40% canopy cover
35	305	50% canopy cover
36	306	60% canopy cover
37	307	70% canopy cover
38	308	80% canopy cover
39	309	Crop cover complete: about 90% canopy cover

FIGURE 4 Depiction of above-ground basal branches in the Principal Stage 2 of the proposed augmented Biologische Bundesanstalt, Bundessortenamt and CHemical Industry (BBCH) scale with corresponding codes for each stage. White arrows indicate all above-ground basal branches developing on the primary stems and >5 cm

TABLE 6 Description of phenological stages describing tuber bulking of F1 diploid hybrid potato plants derived from any type of planting material during Principal Growth Stage 4. Harvestable plant parts in potato are mainly tubers and thus this stage describes tuber growth and development. Codes 400 to 409 define the stages in the original scale and 410 to 419 provide alternative descriptions using the harvest index (HI)

Two-digit code	Three-digit code	Description of tuber bulking in TPS- and tuber-grown plants
40	400	Tuber initiation: swelling of first stolon tips to twice the diameter of subtending stolons
41	401	10% of total tuber final mass reached
42	402	20% of total tuber final mass reached
43	403	30% of total tuber final mass reached
44	404	40% of total tuber final mass reached
45	405	50% of total tuber final mass reached
46	406	60% of total tuber final mass reached
47	407	70% of total tuber final mass reached
48	408	Maximum of total tuber mass reached, tubers detach easily from stolons, skin set not yet complete
		(Skin easily removable with thumb)
49	409	Skin set complete: (skin at apical end of tuber not removable with thumb) 95% of tubers in this stage
	410[a]	Tuber initiation: swelling of 1 or more stolon tips in tuber bearing stolons
	411	HI of 0.1
	412	HI of 0.2
	413	HI of 0.3
	414	HI of 0.4
	415	HI of 0.5
	416	HI of 0.6
	417	HI of 0.7–0.8
	418	HI >0.8: maximum of total tuber mass reached
		Tubers detach easily from stolons
		Skin set not yet complete, skin easily removable with thumb
	419	Skin set complete
		Skin at apical end of tuber not removable with thumb
		95% of tubers in this stage

[a]Proposed augmented descriptions of Principal Stage 4 of the potato BBCH scale. Applicable for use in the absence of a final tuber mass that is used to describe tuber development in the original BBCH scale (see Meier, 1997).

other factors. Additionally, colour changes may be uneven and depending on cultivar or genotype, differences in the hue of the same colour are observed. A proposed description (Table 10) is to use discolouration without defining the specific colour to be observed. This

TABLE 7 Description of phenological growth stages of true potato seeds (TPS)-grown and seed tuber-grown F1 diploid hybrid potato plants during Principal Growth Stage 5 according to original Biologische Bundesanstalt, Bundessortenamt and CHemical Industry (BBCH) scale and the augmented BBCH scale for potato using a basic (two-digit) and extended (three-digit) BBCH scale. The augmented descriptions adds codes 511–519 and provides alternatives for 521-5N9 (see table footnote)

Two-digit code	Three-digit code	Description of inflorescence emergence in TPS- and tuber-grown plants
51	501	First individual buds (1–2 mm) of first inflorescence visible (main stem)
55	505	Buds of first inflorescence extended to 5 mm
59	509	First flower petals of first inflorescence visible
	511	First individual bud(s) (<1 mm) of first inflorescence (primary level of main stem) visible
	513	Individual bud(s) (2–4 mm) begin to swell (primary order of main stem)
	515	Individual bud(s) (5 mm) swell and extend (primary level of main stem)
	517	Individual bud(s) (7 mm) swell and extend (primary level of main stem)
		Sepals begin to open
	519	First flower petals (<5 mm)of first inflorescence visible (primary level of main stem)
		Flower petal colour still greenish
	521[a]	First individual bud(s) (<1 mm) in one or more inflorescence(s) visible (2nd level)
	523	Individual bud(s) (2–4 mm) in one or more inflorescence(s) begin to swell (2nd level)
	525	Individual bud(s) (5 mm) in one or more inflorescence(s) swell and extend (2nd level)
	527	Individual bud(s) (7 mm) in one or more inflorescence(s) swell and extend (2nd level)
		Sepals begin to open
	529	First flower petals (<5 mm) in one or more inflorescence(s) visible
		(2nd level)
	531	First individual bud(s) (<1 mm) in one or more inflorescence(s) visible (3rd level)
	53n	Stages continue until…
	5 N9	First flower petals (<5 mm) in one or more inflorescence(s) visible

(Continues)

TABLE 7 (Continued)

Two-digit code	Three-digit code	Description of inflorescence emergence in TPS- and tuber-grown plants
		(N^{th} level)

[a]The original BBCH scale defines codes 51–59/501–509 and 521–5N9, see Meier (1997). The augmented BBCH scale defines additional codes 511–519 and alternative descriptions for 521–5N9. Citations should be given to indicate which version of the BBCH scale for potato has been used.

removes subjectivity and conserves the intended meaning of the description in the original BBCH scale.

4.3 | Harvest index (HI), dry matter partitioning to the tubers and fraction of final tuber yield

In the original BBCH scale, tuber development stages can only be described in relation to the final tuber mass of the plant (Hack et al., 1993). The augmented BBCH scale proposes the use of a HI of

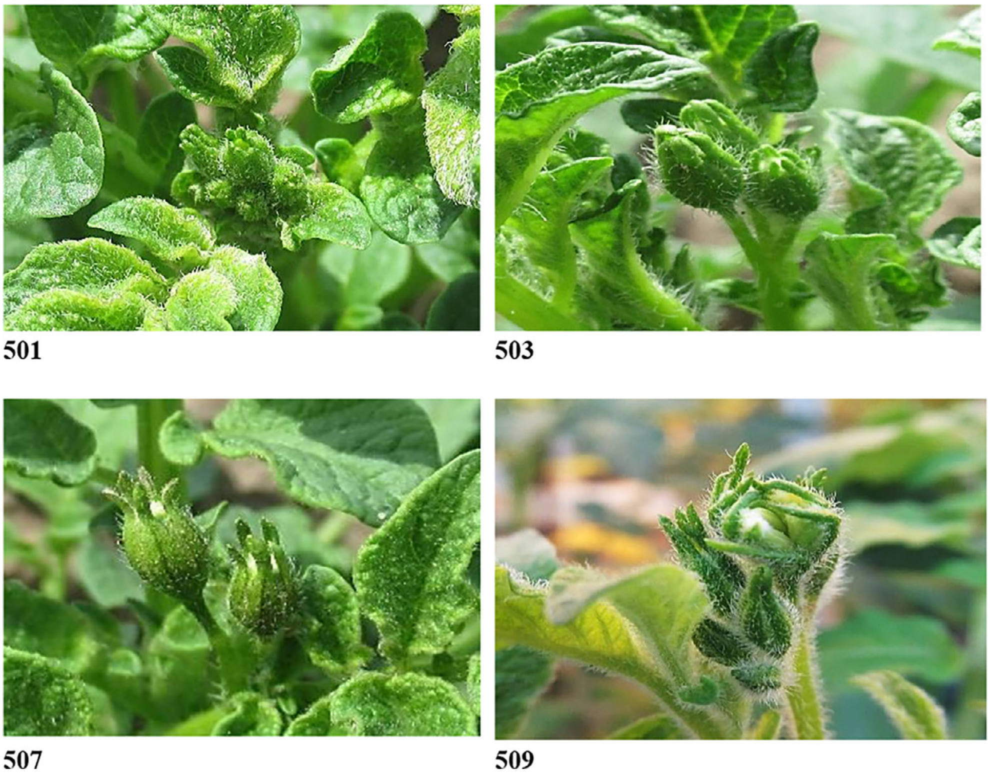


FIGURE 5 Depiction of inflorescence development of true potato seeds (TPS)-grown and tuber-grown plants in the Principal Stage 5 of the potato Biologische Bundesanstalt, Bundessortenamt and CHemical Industry (BBCH) scale with corresponding codes for each stage

TABLE 8 Description of phenological growth stages of true potato seeds (TPS)-grown and seed tuber-grown F1 diploid hybrid potato plants during Principal Growth Stage 6 according to the original Biologische Bundesanstalt, Bundessortenamt and CHemical Industry (BBCH) scale and the augmented BBCH scale for potato using (two-digit) and (three-digit) codes. The augmented descriptions adds codes 610–619 and provides alternatives for 620–6N9 (see table footnote)

Two-digit code	Three-digit code	Description of flower development in TPS- and tuber-grown plants
60	600	First open flowers in population
61	601	Beginning of flowering: 10% of flowers in the first inflorescence open (main stem)
62	602	20% of flowers in the first inflorescence open
63	603	30% of flowers in the first inflorescence open
64	604	40% of flowers in the first inflorescence open
65	605	Full flowering: 50% of flowers in the first inflorescence open
66	606	60% of flowers in the first inflorescence open
67	607	70% of flowers in the first inflorescence open
68	608	80% of flowers in the first inflorescence open
69	609	End of flowering in the first inflorescence

TABLE 8 (Continued)

Two-digit code	Three-digit code	Description of flower development in TPS- and tuber-grown plants
	610	Beginning of flowering
		Flower petals visible on one or more flower bud(s) (<5 mm) (main stem)
	611	Flower petal extends (>5 mm) (main stem)
		Flower colour begins to change
	613	Flower petals partially reflexed (main stem)
	615	Flower petals open (main stem)
		Flower fully mature: bright full flower colour
	617	Flower senescing (main stem)
		Flower petals begin to shrivel and close: petals dry out
	619	Flower senescent (main stem)
	620[a]	Beginning of flowering
		Flower petals (<5 mm) of flower buds in one or more inflorescence(s) visible (2nd level)
	621	Flower petal (>5 mm) of flower buds in one or more inflorescence(s) extends (2nd level)
		Flower petals still green
	629	Flowers in one or more inflorescences senescent (2nd level)
	63n	Stages continue until…
	6N9	Flowers in one or more inflorescences senescent (N^{th} level)
		End of flowering

[a]The original BBCH scale defines codes 60–69/600–609 and 620–6N9, see Meier (1997). The augmented BBCH scale defines additional codes 610–619 and alternative descriptions for 620–6N9. Citations should be given to indicate which version of the BBCH scale for potato has been used.

FIGURE 6 Depiction of augmented flower development stages of true potato seeds (TPS)-grown and tuber-grown plants in the Principal Stage 6 of the potato Biologische Bundesanstalt, Bundessortenamt and CHemical Industry (BBCH) scale with corresponding codes for each stage. Images represent stages of flower development based on proposed alternative descriptions from stage 610 to 619. Pictures of flowers were taken from different plants in both the greenhouse and field under different conditions to depict the various stages in the Principal Growth Stage 600

the plant at the time of harvest to allow determination of the stages in the absence of final tuber mass.

In a potato crop, dry matter initially partitions into stems and leaves until the point of tuber initiation in a standard potato crop. Tuber development results from daily allocation of dry matter to the tubers by the crop after tuber initiation. According to Kooman, Fahem, Tegera, & Haverkort (1996), from tuber initiation, an increasing part of dry matter is partitioned into the tubers with less amounts partitioned into above ground vegetative parts such as stems and leaves. A 90% point is attained when 90% of dry matter has been allocated to tubers (Figure 8). Eventually, all assimilates are concentrated in the tubers and no allocations are given to other plant parts causing cease in leaf growth and later senescence.

Figure 8 also describes the progress in the growth and developmental stages in Principal Stage 400 in potato plants. From tuber initiation to a HI of 0.6, advancement of the growth and development stages takes less time in the earlier phase of the Principal Stage 4 than in later phases. When growing conditions are optimal, relative plant growth rates are assumed to be maximum and associated with rapid tuber bulking. The shift in dry matter partitioning from the shoots to the tubers is gradual and depending on maturity type of the cultivar (Struik, 2007b). Bulking is most rapid when a maximum number of tubers growing rapidly is reached (Struik, Haverkort, Vreugdenhil, Bus, & Dankert, 1990; Struik, Vreugdenhil, Haverkort, Bus, & Dankert, 1991). In cases where conditions are unfavourable for the plant to support all growing tubers, tuber resorption may

TABLE 9 Description of phenological growth stages of true potato seeds (TPS)-grown and seed tuber-grown F1 diploid hybrid potato plants during Principal Growth Stage 8 according to the basic (two-digit) and extended (three-digit) Biologische Bundesanstalt, Bundessortenamt and CHemical Industry (BBCH) scales

Two-digit code	Three-digit code	Description of berry maturity in TPS- and tuber-grown plants
81	801	Berries in the first fructification still green, seed light-coloured (main stem)
85	805	Berries in the first fructification ochre-coloured or brownish
89	809	Berries in the first fructification shrivelled, seed dark
		Berries may fall off the plant
	821	Berries in one or more fructifications still green, seeds light-coloured (2nd level)
	829	Berries in one or more fructifications shrivelled, seeds dark coloured (2nd level)
	83n	Stages continue until…
	8N9	Berries in one or more fructifications shrivelled, seeds dark coloured (N^{th} level) Berries may fall off the plant

TABLE 10 Description of phenological growth stages of true potato seeds (TPS)-grown and seed tuber-grown F1 diploid hybrid potato plants in Principal Growth Stage 9 according to the basic (two-digit) and extended (three-digit) Biologische Bundesanstalt, Bundessortenamt and CHemical Industry (BBCH) scales. Descriptions in bold are original descriptions from Meier (1997)

Two-digit code	Three-digit code	Description of senescence of above-ground plant parts in TPS- and tuber-grown plants
91	901	**Beginning of leaf yellowing** About 10% of above ground parts start to desiccate
93	903	**Most of the leaves yellowish** 30% of above-ground parts discoloured and dry
		Dry leaves and ripen berries begin to fall
95	905	**50% of the leaves brownish** 50% of the above-ground parts discoloured and dry
97	907	**All leaves and stems dead, stems discoloured and dry**
99	909	**Harvested product**

FIGURE 7 Depiction of berry ripening on true potato seeds (TPS)-grown and tuber-grown plants in the Principal Stage 8 of the potato Biologische Bundesanstalt, Bundessortenamt and CHemical Industry (BBCH) scale with corresponding codes for each stage

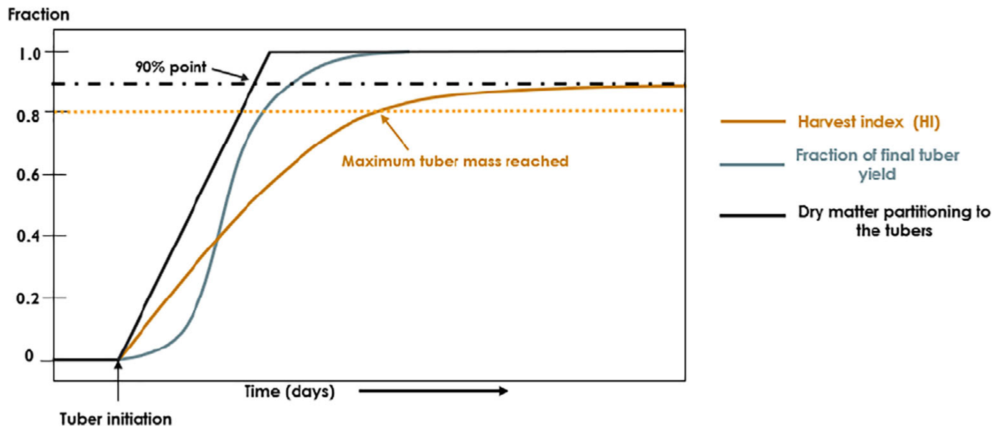
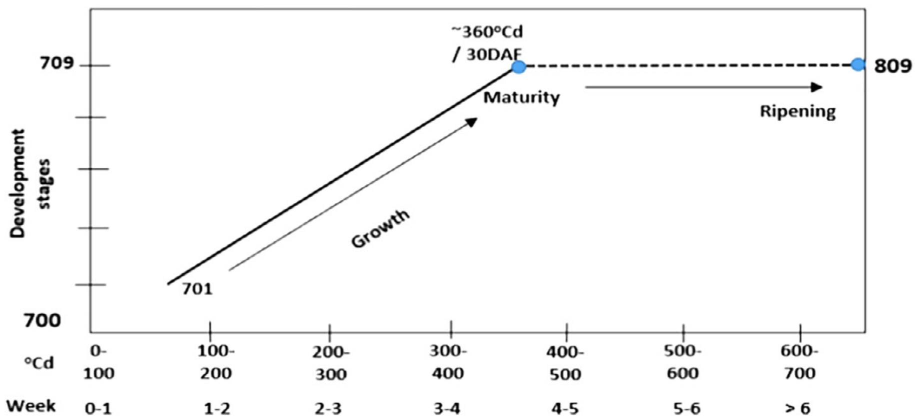


FIGURE 8 Schematic representation of the development of tuber yield, dry matter partitioning to the tubers and harvest index (HI) over time, partly adapted from Struik & Wiersema (1999) and Kooman et al. (1996). The scheme strongly depends on cultivar, environmental conditions and their interactions and therefore the curvature of the graphs may vary depending on these factors. The fraction of final tuber yield is shown by a sigmoid curve and has a close association with the development over time of the proportion of dry matter partitioned to the tubers and the HI. The dry matter partitioning to the tubers over time is portrayed by a black line and indicates the change in proportion of the dry matter produced on a certain day that is allocated to the tubers. The 90% point in the graph indicates the point where 90% of newly produced assimilates are partitioned to the tubers (Kooman et al., 1996), after which—at 100%—no dry biomass is located to other vegetative plant parts and leaf growth ceases and crop senescence starts (Kooman et al., 1996; Struik & Wiersema, 1999). The HI continues to increase beyond that moment until the crop is completely senesced. Fast development of the haulm and early onset of tuberisation are required for a high HI. However, the highest HI is not necessarily associated with the highest yields

FIGURE 9 Conceptual graph of berry growth over degree days (°Cd)



occur thereby declining the number of tubers on the plant. When maximum tuber mass is reached (Figure 8), tuber bulking ceases and the tuber skin starts to set (Struik & Wiersema, 1999; Wohleb et al., 2014).

Final tuber yield (Figure 8) is mainly affected by accumulated intercepted radiation, the HI as well as the concentration of dry matter in the tubers (Kooman et al., 1996; Struik & Wiersema, 1999). Final tuber yield is therefore highly affected by cultivar and environmental conditions during the growing period. The total plant biomass and HI largely determine the tuber yield ha^{-1}. A higher HI indicates a higher yield ha^{-1}. Similarly, the higher the proportion of dry matter concentrated in the tubers, the higher the fraction of final tuber yield attained by the crop (Kooman et al., 1996). The 90% point in the fraction of final tuber yield is attained later than that of dry matter partitioned to the tubers.

4.4 | Berry growth and development

As berries develop on a single inflorescence at different times and berry size is very variable even at inflorescence level, the use of final berry size in description of Principal Stage 700 is highly limiting in application of the scale as final size cannot be determined for each individual berry. Similarly, the use of colour, tenderness or firmness to determine berry development stages is limiting as definition is quite subjective because of differences between and within cultivars. FAO (2004) recommends the combination of such indices with other practices such as the use of accumulation of heat units or number of days from flowering. An alternative method of description of berry development would therefore be the use of accumulated heat units to describe berry setting. Berry development begins after fertilisation and various studies on flowering and berry growth in potato indicate

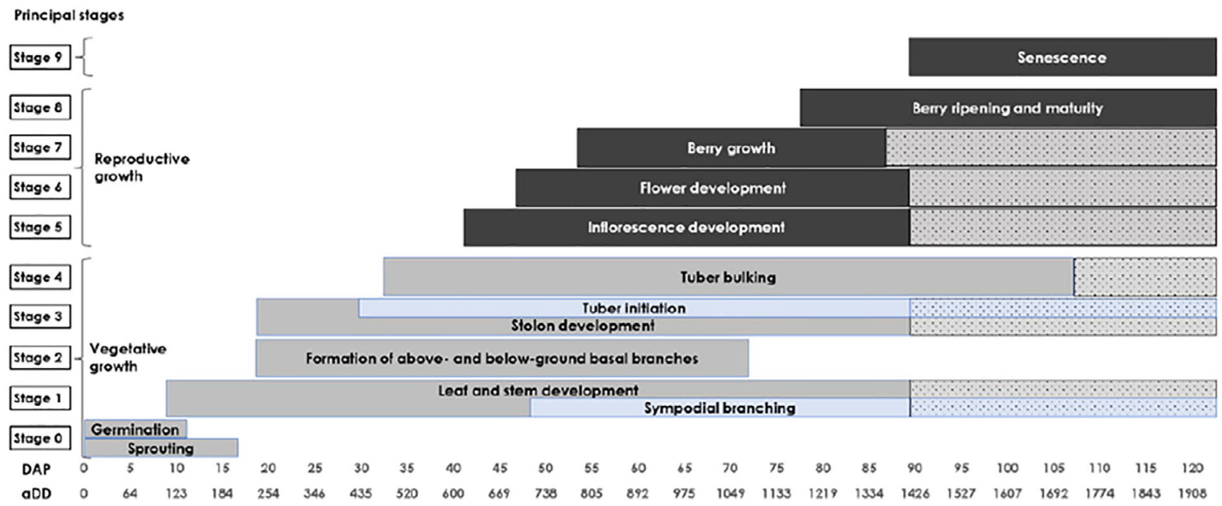


FIGURE 10 Timeline of onset of principal growth and development stages of the Biologische Bundesanstalt, Bundessortenamt and CHemical Industry (BBCH) scale from germination or sprouting (depending on planting material type) to senescence with additional stages of onset of stolon branching and tuber initiation as well as beginning of sympodial growth of the potato main stem. Scheme is based on diploid experimental hybrid 19H07 during the 2018 and 2019 growing period. The dotted regions on the timelines indicate the possibility of continuous development of a particular stage. Additional timelines of occurrence of sympodial branching and tuber initiation have been added to indicate the occurrence of the stages and how they coincide with the Principal Growth Stages. DAP describes the time after planting in days and aDD describes the accumulated growing degree days from planting to harvest

that berry set to full ripening takes about 40 to 42 days from flowering. Almekinders (1995) describes berries as mature at 30 days from flowering and according to Struik & Wiersema (1999), berries mature 30 to 50 days after pollination, and this may also depend on genotype and temperature.

Temperatures ranging from 16 to 18°C are optimal for berry growth and based on this data a conceptual graph (Figure 9) of required thermal time (°Cd) was developed to show the progress in growth and development from Principal Stage 7 to complete berry ripening at completion of Stage 8. The stages will therefore be described when the ovary begins to swell occurring between 0 and 100°Cd and an increase in berry size over time until about 30 days after flowering to full size and maturity on the main stem (Figure 9). This applies to each individual berry in an inflorescence, because it is known that a single inflorescence can house various reproductive stages at a single point in time in potato plants. Further development in the stage will be shown by growth of berries in the inflorescence of one or more branches in other levels of sympodial branching following the sequence of flower bud and flower development.

4.5 | Timeline of occurrence of principal growth and development stages

Figure 10 shows a sequential timeline of principal growth and development stages in potato plants. In potato, different principal growth stages occur concurrently throughout the life cycle of the plant. The BBCH scales allows for description of two or more coinciding principal growth stages as occurring at the same point in time (Lopez-Bellido, Lopez-Bellido, Muñoz-Romero, Fernandez-Garcia, & Lopez-Bellido, 2016). This is important in applying the scale to potato as multiple stages of development run concurrently throughout the lifetime of the plant. The sympodial branching in potato causes multiple stages of vegetative and reproductive growth to run simultaneously causing the plant to attain one or more stages at the same time (Figure 10). Additionally, the figure shows the sequence of steps in the tuberisation process following a precise order of development from stolon development to tuber bulking and maturity. It should be noted that stolon development starts earlier (Figure 10) than reproductive development, as stolons are known to appear even during tuber storage or in earlier stages of plant development in greenhouse nurseries, especially under environmental conditions that cause stress during plant growth (Struik & Wiersema, 1999).

Additionally, because of sympodial branching, which strongly affects the reproductive growth stages, different inflorescences can attain various reproductive stages at the same time. The augmented descriptions of the BBCH scale for potato addresses this by progressing the stages of development when one or more flower buds, flowers, or berries attain a particular stage in either the main stem or in the multiple branches of a particular level of sympodial branching.

5 | CONCLUSIONS

Augmented descriptions to the original BBCH scale for potato (Hack et al., 1993) have been proposed in this paper to allow application to hybrid potato planting materials as well as application to its use in hybrid breeding. In vegetative growth stages, descriptions of leaf development and progress in plant height through stem elongation have been clearly extrapolated. Additionally, descriptions of differences in types of basal branches between planting materials have been included. For underground growth and development, a HI has been proposed as a measure for tuber bulking to allow for description of the scale in the absence of a final tuber mass, especially during intermediate harvests prior to final harvests. Stolon development, a precursor of tuberisation, could not be clearly described as detailed descriptions and coding would alter the basic integrity of the BBCH scale. However, description of stages of stolon development are important and its lack of is suboptimal as they precede tuber development and show progress in below ground development of the potato plant.

For reproductive growth stages, which are of importance in hybrid breeding, alternative descriptions of flower development in addition to the original descriptions have been added. Similarly, berry growth and development have been articulated. Sympodial branching patterns in potato, which influence development of both vegetative and reproductive growth stages have been clearly defined to give clear descriptions of each level of branching and its associated growth and development. Additional photographs depicting the various stages have been provided to enable easy identification of stages and association of codes and the respective outlook on the plants.

These augmented descriptions of the original scale will help in applying the BBCH scale for potato without limitations caused by type of planting material or stage of plant growth at time of use as well as the purpose of description as both the original and alternative descriptions can be applied where appropriate.

ACKNOWLEDGEMENTS

This study was part of the Potarei project funded by the Responsible Research and Innovation programme of the Netherlands Organisation for Scientific Research (NWO; 313-99-301). Additional funding came from Solynta. The authors would like to thank Unifarm for conducting the experiments professionally. The authors also thank Priscilla Gandha, Julia Stockem, Ernst-Jan Eggers and Emmy de Lange for providing detailed comments, which helped improve the definition of the augmented BBCH scales.

ORCID

Olivia Cynthia Kacheyo https://orcid.org/0000-0002-2567-332X
Luuk Christiaan Maria van Dijk https://orcid.org/0000-0001-8625-5247
Michiel Erik de Vries https://orcid.org/0000-0002-1453-7672
Paul Christiaan Struik https://orcid.org/0000-0003-2196-547X

REFERENCES

Acosta-Quezada, P. G., Riofrío-Cuenca, T., Rojas, J., Vilanova, S., Plazas, M., & Prohens, J. (2016). Phenological growth stages of tree tomato (*Solanum betaceum* Cav.), an emerging fruit crop, according to the basic and extended BBCH scales. *Scientia Horticulturae*, *199*, 216–223.

Almekinders, C. J. M. (1991). Flowering and true seed production in potato (*Solanum tuberosum* L.) 2. Effects of stem density and pruning of lateral stems. *Potato Research*, *34*(4), 379–388.

Almekinders, C. J. M. (1995). *On flowering and botanical seed production in potato* (*Solanum tuberosum* L.). (Doctoral thesis). Wageningen Agricultural University, Wageningen, the Netherlands.

Almekinders, C. J. M., & Struik, P. C. (1996). Shoot development and flowering in potato (*Solanum tuberosum* L.). *Potato Research*, *39*(4), 581–607.

Almekinders, C. J. M., & Wiersema, S. G. (1991). Flowering and true seed production in potato (*Solanum tuberosum* L.) 1. Effects of inflorescence position, nitrogen treatment, and harvest date of berries. *Potato Research*, *34*, 365–377.

Almekinders, C. J. M., Chilver, A. S., & Renia, H. M. (1996). Current status of the TPS technology in the world. *Potato Research*, *39*, 289–303.

Almekinders, C. J. M., Chujoy, E., & Thiele, G. (2009). The use of true potato seed as pro-poor technology: The efforts of an international agricultural research institute to innovating potato production. *Potato Research*, *52*(4), 275–293.

Anon. (1987). EPPO crop growth stage keys. No. 12. Potato. *EPPO Bulletin*, *17*, 497–502.

Celis-Gamboa, B.C. (2002). *The life cycle of the potato* (*Solanum tuberosum* L.)*: From crop physiology to genetics*. (Doctoral thesis). Wageningen University.

Feller, C., Bleiholder, H., Buhr, L., Hack, H., Hess, M., Klose, R., … Weber, E. (1995a). Phänologische Entwicklungsstadien von Gemüsepflanzen. II. Fruchtgemüse und Hülsenfrüchte. *Das Nachrichtenblatt des Deutschen Pflanzenschutzdienstes*, *47*(8), 193–206.

Feller, C., Bleiholder, H., Buhr, L., Hack, H., Hess, M., Klose, R., … Weber, E. (1995b). Phänologische Entwicklungsstadien von Gemüsepflanzen. I. Zwiebel-, Wurzel-, Knollen- und Blattgemüse. *Das Nachrichtenblatt des Deutschen Pflanzenschutzdienstes*, *47*(9), 217–232.

Griess, H. (1987). *Code zur Kennzeichnung von Entwicklungsstadien und -phasen der Kartoffel (Anleitung)*. Berlin, Germany: Akademie der Landwirtschaftswissenschaften der DDR.

Griess, H. (1989). Code of developmental stages for potato. In *Summaries of EAPR section physiology meeting*. *Gross Lüsewitz, German Democratic Republic* (pp. 54–55). Gross Lüsewitz, Germany: Institute for Potato Research of the Academy for Agricultural Sciences of the GDR.

Hack, H., Gall, H., Klemke, T., Klose, R., Meier, U., Stauss, R., & Witzenberger, A. (1993). Phänologische Entwicklungsstadien der Kartoffel (*Solanum tuberosum* L.). Codierung und Beschreibung nach der erweiterten BBCH-Skala mit Abbildungen. *Das Nachrichtenblatt des Deutschen Pflanzenschutzdienstes*, *45*(1), 11–19.

Hack, H., Bleiholder, H., Buhr, L., Meier, U., Schnock-fricke, U., Stauss, R., … Witzenberger, A. (1992). Einheitliche Codierung der phänologischen Entwicklungsstadien mono- und dikotyler Pflanzen. – Erweiterte BBCH-Skala, Allgemein. *Das Nachrichtenblatt des Deutschen Pflanzenschutzdienstes*, *44*(12), 265–270.

Haverkort, A. J. (2018). *Potato handbook: Crop of the future*. Den Haag, the Netherlands: Aardappelwereld BV.

Jansky, S. H., Charkowski, A. O., Douches, D. S., Gusmini, G., Richael, C., Bethke, P. C., … Jiang, J. (2016). Reinventing potato as a diploid inbred line-based crop. *Crop Science*, *56*(4), 1412–1422.

Jefferies, R. A., & Lawson, H. M. (1991). A key for the stages of development of potato (*Solanum tuberosum* L.). *Annals of Applied Biology*, *119* (2), 387–399.

Kooman, P. L., Fahem, M., Tegera, P., & Haverkort, A. J. (1996). Effects of climate on different potato genotypes 2. Dry matter allocation and duration of the growth cycle. *European Journal of Agronomy*, *5*(3–4), 207–217.

Lindhout, P., de Vries, M., ter Maat, M., Ying, S., Víquez-Zamora, M., & van Heusden, S. (2018). Hybrid potato breeding for improved varieties. *Achieving Sustainable Cultivation of Potatoes*, *1*(1), 1–24.

Lindhout, P., Meijer, D., Schotte, T., Hutten, R. C. B., Visser, R. G. F., & van Eck, H. J. (2011). Towards F1 hybrid seed potato breeding. *Potato Research*, *54*(4), 301–312.

Lopez-Bellido, F. J., Lopez-Bellido, R. J., Muñoz-Romero, V., Fernandez-Garcia, P., & Lopez-Bellido, L. (2016). New phenological growth stages of garlic (*Allium sativum*). *Annals of Applied Biology*, *169*(3), 423–439.

Meier, U. (1997). *BBCH-Monograph. Growth stages of plants. Entwicklungsstadien von Pflanzen. Estadios de las plantas. Stades de développement des plantes*. Wissenschafts-Verlag Berlin, Wien: Blackwell. 622 pp.

Meier, U., Bleiholder, H., Buhr, L., Feller, C., Hack, H., Heß, M., … Zwerger, P. (2009). The BBCH system to coding the phenological growth stages of plants. *Journal für Kulturpflanzen*, *61*, 41–52.

Moreno, C., Quiñones, J. R., & Jiménez, P. (2016). Phenological growth stages of *Solanum sessiliflorum* according to the BBCH scale. *Annals of Applied Biology*, *168*(1), 151–157.

Murashige, T., & Skoog, F. (1962). A revised medium for rapid growth and bioassays with tobacco tissue cultures. *Physiologia Plantarum*, *15*(3), 473–497.

Muthoni, J., Shimelis, H., & Melis, R. (2013). Alleviating potato seed tuber shortage in developing countries: Potential of true potato seeds. *Australian Journal of Crop Science*, *7*(12), 1946.

Stockem, J., de Vries, M., van Nieuwenhuizen, E., Lindhout, P., & Struik, P. C. (2020). Contribution and stability of yield components of diploid hybrid potato. *Potato Research*, *63*, 417–432.

Struik, P. C. (2007a). Above-ground and below-ground plant development. In D. Vreughenhil, J. Bradshaw, C. Gebhardt, F. Govers, D. K. L. Mackerron, M. A. Taylor, & H. A. Ross (Eds.), *Potato biology and biotechnology: Advances and perspectives* (pp. 219–236). Amsterdam, the Netherlands: Elsevier Science BV.

Struik, P. C. (2007b). Responses of the potato plant to temperature. In D. Vreughenhil, J. Bradshaw, C. Gebhardt, F. Govers, D. K. L. Mackerron, M.A. Taylor & H. A. Ross (Eds.), *Potato biology and biotechnology: Advances and perspectives* (pp. 367–393). Amsterdam, the Netherlands: Elsevier Science BV.

Struik, P. C., & Wiersema, S. G. (1999). *Seed potato technology*. Wageningen, the Netherlands: Wageningen Academic Publishers.

Struik, P. C., Haverkort, A. J., Vreugdenhil, D., Bus, C. B., & Dankert, R. (1990). Manipulation of tuber-size distribution of a potato crop. *Potato Research*, *33*(4), 417–432.

Struik, P. C., Vreugdenhil, D., Haverkort, A. J., Bus, C. B., & Dankert, R. (1991). Possible mechanisms of size hierarchy among tubers on one stem of a potato (*Solanum tuberosum* L.) plant. *Potato Research*, *34*(2), 187–203.

Vos, J. (1995). Foliar development of the potato plant and modulations by environmental factor. In P. Kabat, B. J. van den Broek, B. Marshall, & J. Vos (Eds.), *Modelling and parameterization of the soil-plant-atmosphere system. A comparison of potato growth models* (pp. 21–38). Wageningen, the Netherlands: Wageningen Pers.

Vos, J. (1999). Potato. In D. L. Smith & C. Hamel (Eds.), *Crop yield, physiology and processes* (pp. 333–354). Berlin, Germany: Springer.

Wohleb, C. H., Knowles, N. R., & Pavek, M. J. (2014). Chapter 5: Plant growth and development. In R. Navarre & M. J. Pavek (Eds.), *The potato: Botany, production and uses*, (64–82). Boston, MA: CABI.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Kacheyo OC, van Dijk LCM, de Vries ME, Struik PC. Augmented descriptions of growth and development stages of potato (*Solanum tuberosum* L.) grown from different types of planting material. *Ann Appl Biol*. 2020; 1–18. https://doi.org/10.1111/aab.12661