Received: 29 March 2023 | Revised: 1 October 2023 | Accepted: 5 October 2023

DOI: 10.1111/jac.12675

Journal of Agronomy and Crop Science WILEY

DROUGHT STRESS

Drought affects the synchrony of aboveground and belowground phenology in tropical potato

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Funding information
Deutsche Gesellschaft für Internationale Zusammenarbeit, Grant/Award Number: GIZ No. 11.7860.9-001.00

Abstract

The literature describes the belowground and aboveground phenology of potato to be linearly related. Bud formation is synchronous with tuber initiation and flowering with tuber filling. Many agronomic and breeding studies on potato use non-destructive aboveground phenology to assess belowground development. No information is currently available on the influence of water deficit on the synchrony of above- and belowground development in potato. Five contrasting potato genotypes were subjected to four irrigation treatments on two different soil types. The irrigation treatments were as follows: fully watered, early drought, intermediate drought, and late drought. In 5-day intervals after withholding water, detailed belowground and aboveground development was recorded. Results showed that the synchrony between aboveground and belowground development is strongly influenced by both water deficit and development stage at drought initiation. Under early drought, the aboveground development was hastened and belowground development was delayed. The opposite was found in later development stages. The earlier the drought was initiated, the longer the tuber filling phase was, while the bulking phase was shortened. We concluded that under terminal drought conditions aboveground development and belowground development need to be evaluated separately and cannot follow the standard evaluation system that uses aboveground phenology as a proxy for tuber formation belowground development rates.

KEYWORDS
abiotic stress, above- and belowground development, asynchrony phenology, growing cycle, *Solanum tuberosum*, water deficit

Key points

- Studies conclude from the aboveground development of potato plants to the belowground development stage, as potato development is linearly described under well-watered conditions.
- Different potato genotypes were investigated with staggered dates of withholding irrigation to analyse the changes in phenology under drought. The non-destructive evaluation was done aboveground and belowground separately.

- Under early drought, the synchrony changed in favour of longer belowground development and shorter aboveground development. Reverse development was analysed for potatoes grown under drought initiated at later development stages.
- This paper shows the importance to evaluate the above- and belowground development separately from each other for each potato genotype. Especially under drought conditions, it cannot be concluded from the aboveground to the belowground development.

1 | INTRODUCTION

1.1 | Phenology of potato

The belowground and aboveground development of potato (*Solanum tuberosum* L.) has been described as closely and linearly related (Meier, 2001; Obidiegwu, 2015). The first principal growth stage, the formation of sprouts and roots from the tuber, ends with emergence, when the sprouts become visible above the soil surface. Aboveground increasing leaf area and shoot branching coincide with belowground root growth, the formation of basal side shoots, and stolon initiation. Main stem elongation and further leaf area increase occur in parallel with tuber initiation. At flowering, in varieties that flower, and at maximum aboveground biomass, tuber formation and tuber filling take place. Finally, during the aboveground senescence process, development and ripening of the fruits, the skin of the tubers sets (=bulking phase). Tubers are physiologically mature and tuber dry matter reaches its maximum when the skin at the apical end of the tuber cannot be removed by thumb. When combining the above- and belowground development stages, the potato cycle can be described in a linear way: (1) growth initiation (sprouting, root formation, and emergence); (2) vegetative stage (leaf development with flowering paired with stolon and tuber initiation); (3) reproductive stage with tuber filling and fruit development; and (4) tuber bulking process with aboveground senescence (Figure 1).

1.2 | Influence of drought on phenology

The main climatic limitation of potato production under rainfed conditions is drought stress due to inadequate irrigation or erratic rainfall. Drought shortens growth duration (Minhas & Bansal, 1991) and reduces tuber number and size (Hughes, 1974), leaf area (Jefferies, 1993), harvest index (Lizana et al., 2017), and final tuber yield (Deblonde & Ledent, 2001). The effect of water deficit on yield depends strongly on the combination of stress severity and phenological stage. For example, severe water deficit during tuber filling hastened aboveground senescence, which resulted in severe yield reductions (Kuppinger et al., 2014). On the other hand, drought during tuber bulking resulted in longer bulking periods under drought and increased yields (Hoelle et al., 2020).

Many agronomic and breeding studies on drought effects in potato use aboveground phenological observations to conclude on belowground development. Yields are often evaluated with a single harvest at the end of the growing cycle (e.g. Deblonde & Ledent, 2001; Lahlou & Ledent, 2005) even when plants were subjected to water deficits during specific phenological stages, such as stolon initiation (Minhas & Bansal, 1991), tuberization (Rodríguez et al., 2016), or bud formation (Li et al., 2019).

Studies on long-term effects of drought on above- and belowground phenological development are not available, and no information is currently available on whether water deficit affects the synchrony of aboveground and belowground development in

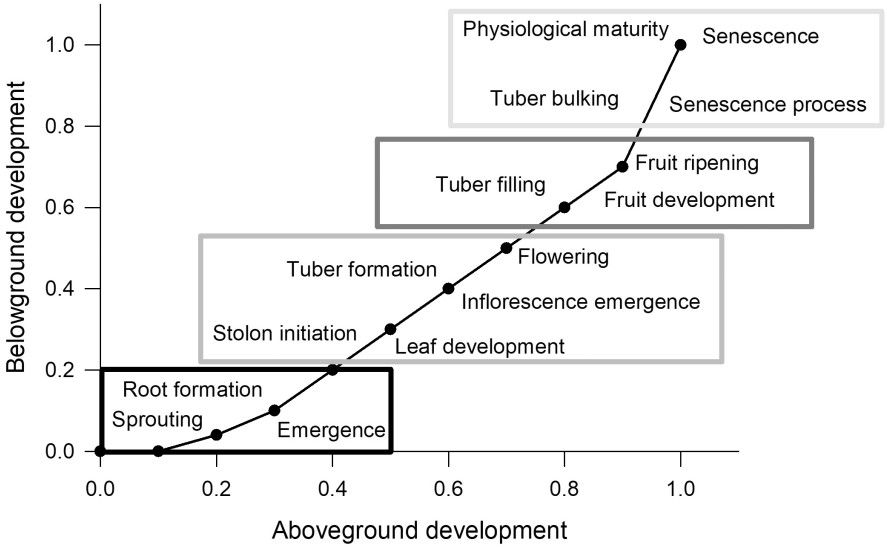

FIGURE 1 Macro-BBCH scale of the aboveground and belowground phenological development according to Meier (2001).

potato. In addition to continuous observations of the below- and aboveground phenology, water deficits initiated at and thus affecting different phenological stages are lacking. In this study, we investigated the synchrony of above- and belowground phenological development of 5 potato genotypes subjected to different levels of drought stress at different phenological stages. Additionally, we investigated the genotype-specific phenological responses to drought and identified corresponding adaptation and/or escape strategies.

2 | MATERIALS AND METHODS

2.1 | Site description

Field trials were conducted over two seasons at an experimental station of the "Instituto Nacional de Innovacion Agraria" in St. Rita de Siguas (16°28′35″ S; 72°6′18″ W), Peru. The photoperiod in Majes is 13 h in December and 11 h in July.

Meteorological data were recorded with a HOBO® Weather Station close to the experimental plots. Air temperature, air humidity, wind and gust speed, and photosynthetically active *radiation* at 2 m height were recorded in 15-min intervals. No rainfall occurred during the field trials. Climate data for the two experimental periods are shown in Figure 2. Fields chosen for the field experiments, although classified as arenosol according to the IUSS Working Group (WRB, 2006), contrasted in soil texture. In the first season, the soil was characterized by a loamy sand texture, whereas in the second season a neighbouring field with sandy soil was selected (Table 1). For each field, 5 soil samples were taken in a diagonal transect for two depths (0 to 15 and 15 to 30 cm) before planting. Soil pH, texture, bulk density, field capacity, and permanent wilting point were determined at the soil testing laboratory at the Universidad Agraria La Molina, Lima, Peru.

2.2 | Genotypes, experimental design, and crop management

In both years, the same drought-tolerant and susceptible genotypes were used. The five potato genotypes (G1–G5; *Solanum tuberosum)* were obtained from the International Potato Center (CIP). CIP's codes, maturity group, heat tolerance level, and virus resistance level are presented in Table A1. The five genotypes were planted by hand in a randomized split-plot design with three replications.

Each experimental plot was 3 m long and 2.7 m wide (8 m^2) per genotype and replication. Each plot consisted of 3 rows with row distance of 0.9 m and 0.3 m of space within the row. Each row contained 11 plants of the same genotype, and 9 plants of the middle row were used for sampling, whereas the outer rows were treated as border rows. Before planting, 1000 kg ha^{-1} Guano was applied

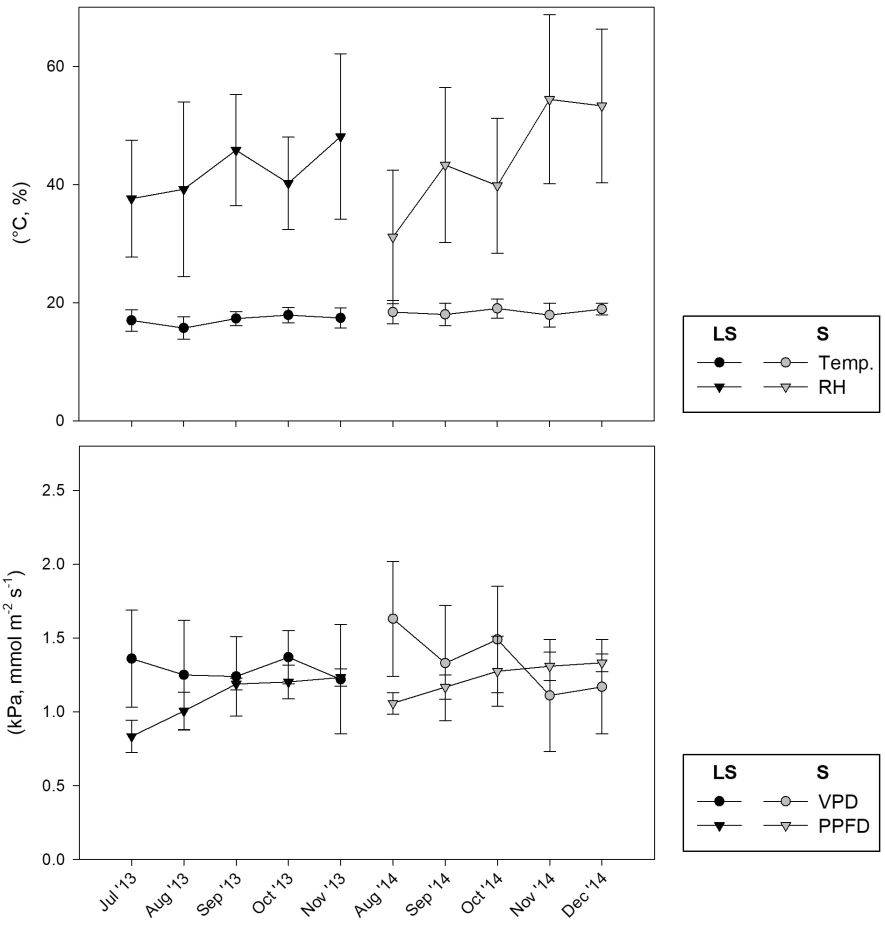

FIGURE 2 Weather conditions during the experimental periods in 2013 and 2014 in St. Rita de Siguas, Arequipa, Peru. Data are shown as monthly averages of daily mean values in loamy sand (LS) and sand (S). PPFD, photosynthetic photon flux density; RH, relative air humidity; Temp, temperature; VPD, vapour pressure deficit. The error bars represent the standard deviation.

TABLE 1 Means of soil parameter (± standard deviation) and water relations for the two experimental fields with S, sand; LS, loamy sand; OM, organic matter; BD, bulk density; FC, field capacity (pF 1.8); PW, permanent wilting point (pF 4.2); and PASW, plant-available soil water (mm).

		Soil texture			
Soil type	Depth (cm)	Sand (%)	Clay (%)	Silt (%)	OM (%)
LS	0–15	80.8 ± 1.79	11.2 ± 1.79	8.0 ± 1.41	1.5 ± 0.49
	15–30	81.6 ± 1.67	10.0 ± 1.41	8.4 ± 1.67	1.0 ± 0.25
S	0–15	94.0 ± 3.46	4.4 ± 0.89	0.4 ± 0.89	0.9 ± 0.18
	15–30	96.0 ± 1.41	4.0 ± 1.41	0.0 ± 0.00	0.7 ± 0.13

			BD	Soil water		
Soil type	Depth (cm)	pH	g cm^{-3}	FC (vol %)	PW (vol %)	PASW (mm)
LS	0–15	8.1 ± 0.18	1.18	23.2	8.5	58.8
	15–30	7.9 ± 0.19				
S	0–15	7.4 ± 0.24	1.15	20.8	5.0	63.2
	15–30	7.5 ± 0.41				

into the furrows and pre-sprouted seed tubers were placed by hand with the sprouts upside. Mineral fertilizer was applied manually as 162 kg ha^{-1} potassium sulphate (50% K_2O, 18% S, INTI), 81 kg ha^{-1} ammonium nitrate (33% N—3% P_2O_5–0% K_2O, MISTI S.A.), and 244 kg ha^{-1} Fertiphos®-Plus (20% P_2O_5; 36% CaO; 6% S, 17% SiO_2; 1.08% Fe_2O^3; 0.9% MgO; micronutrients: Zn, Mn, Cu, and B). An additional top dressing of 120 kg ha^{-1} ammonium nitrate followed during hilling. Seed tubers were disinfected with Homai (BASF) and afterwards with Decis (Bayer) against potato beetle (*Leptinotarsa decemlineata*). Fungicides and insecticides were applied in approximately 20-day intervals according to the instructions of the suppliers. The following products were used: Sorba 50 EC (Syngenta), Ultra Pegasol (Farmagro S.A.), Rover (Sipcam Pacific), Pentacloro Farmex, Cipermex (Farmex), Confidor 350 SC Fitoraz (Bayer), and Evisect 50 SP (Arysta). Insecticides with changing functional groups were applied to avoid build-up of resistances in the field. Manual weeding was done in 14-day intervals.

2.3 | Assessment of phenology and soil moisture

In both years, four irrigation treatments were implemented: fully irrigated plants (T1), early drought (T2) with withholding irrigation at 50 days after planting (DAP), intermediate drought (T3) with irrigation withheld after 65 DAP, and at 80 DAP named late drought (T4) (Table 2). Fifty days after planting, most genotypes started tuber filling or were at early tuber filling stage. The second treatment started during tuber filling and the last drought at tuber bulking. All three development stages are described to be drought-sensitive.

Detailed observations of plant growth and growth responses to environmental changes, as well as timing of fertilizer application or plant protection measures, are commonly related to specific development stages of the plants. The BBCH scale has been developed to describe the phenology of various mono- and dicotyl crops (Meier, 2001). In this scale, the penology of potato is divided into

TABLE 2 Water supply (l plant^{-1}) for the fully irrigated control (T1) to individual plants, respectively, for the drought treatments, T2, T3, and T4 in % water supply per plant of fully irrigated control with LS, loamy sand; S, sand.

	LS	S
(L plant^{-1})		
T1	152	83
% of control		
T2	32	45
T3	47	51
T4	59	57

Note: Water was withheld after 50 days after planting (DAP) in the early drought (T2), at 65 DAP in the intermediate drought (T3), and at 80 DAP in the late drought treatment (T4).

10 macro-stages and within each stage 10 related micro-stages. For each aboveground development step, a corresponding belowground process has been defined, which is linearly related (Figure 1). The macro-stages of the BBCH scale are defined as 0–0.9—sprouting/germination; 1.0–1.9—leaf development; 2.0–2.9—formation of basal side shoots below and above soil surface; 3.0–3.9—main stem elongation; 4.0–4.9—tuber formation; 5.0–5.9—inflorescence emergence; 6.0–6.9—flowering; 7.0–7.9—development of fruit; 8.0–8.9—ripening of fruit and seed; and 9.0–9.9—senescence. For the purpose of this study, we adapted the stages to a linearly incrementing aboveground macro-development: 50% of the plants germinated (=0.1), 50% with flowers (=0.5), 50% of the plants with wilting symptoms (=0.75), and 50% of the plants senescent (=1). The aboveground development was evaluated in 7-day intervals.

The belowground phenology was evaluated in 10-day intervals at one plant per genotype and replication ($n = 33$). For each development stage, following codes were used: 50% of the plants germinated (=0.1), 50% of the plants at stolon initiation (=0.25), 50% of the plants at tuber initiation (=0.5), 50% of the plants at the tuber

filling stage (=0.75), and 50% of the tubers were physiologically mature (=1). Physiological maturity/end of tuber bulking was defined as tuber skin is connected to tuber flesh and the skin cannot be easily removed by peeling. The tuber filling duration was defined as the time of tuber initiation until end tuber filling, by measuring by tuber size. The tuber bulking duration describes the time between tuber end filling and the physiological maturity.

The daily above- and belowground development was calculated as follows:

$$\text{Daily development} = \frac{\text{difference between developement code}}{\text{days to next development stage}}$$

For example, genotype X needed 15 days between stolon initiation (=0.25) and tuber initiation (=0.5). Therefore, daily development rate was calculated as follows:

$$\frac{0.5 - 0.25}{15} = 0.016 \text{ daily development rate}$$

In 3- to 5-day intervals, depending on irrigation schedule, soil moisture was assessed via frequency domain reflectometry (FDR, PR2 Soil Moisture Profile Probe, Delta T-Devices). The profile probe measures soil moisture from 0 to 40 cm depth, in 10 cm increments, through glass fibre access tubes that were installed for each genotype and replication. Soil moisture was measured 3–4 h after irrigation. The water loss in comparison with the irrigated control ranged in the early drought from 10% after 10 days without water up to 33% in the first season in loamy sand and 55% in the second season on sand after 30 days without water (Figure 3). In the intermediate and late droughts, water loss was up to 20%–30% of the full irrigated control.

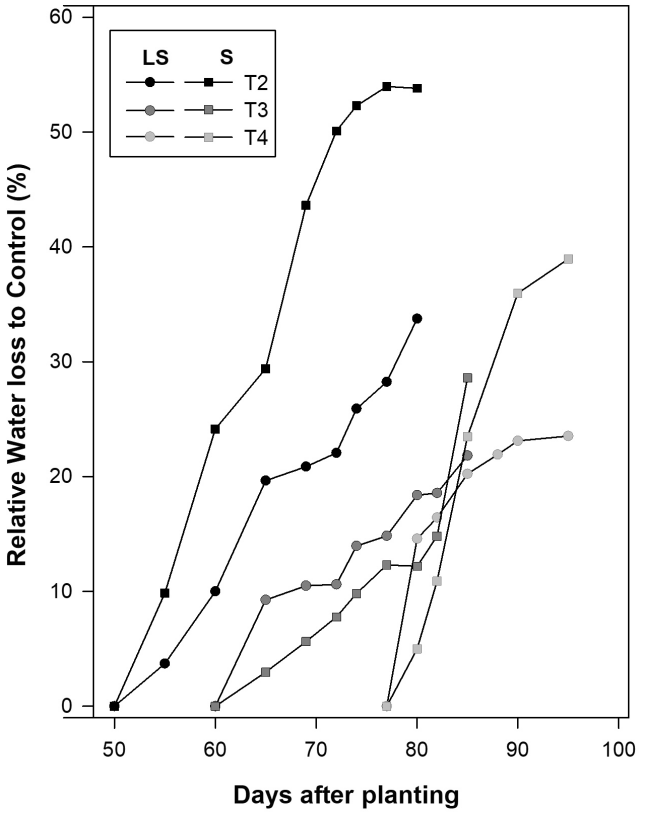

FIGURE 3 Development of soil moisture in vol. % at days after planting for the four irrigation treatments (T1–T4) in loamy sand (LS) and sand (S). Measurements were taken in 5-day intervals per genotype, treatment, and replication. Each data point represents a mean of 15 measurements of the average soil moisture from 10 to 40 cm depth. Error bars have been omitted for readability.

2.4 | Calculation of percentage of development cycle

For each genotype and replication, above ground and below ground were evaluated separately. The total number of days to maturity was set as 100, and percentage share of each development stage was calculated relative to the total duration. The time to emergence was taken out of the total duration as it was the same for all genotypes and treatments. All graphs were created with SigmaPlot 12.5, Systat Software, Inc., Erkrath, Germany.

3 | RESULTS

3.1 | Genotypic phenological responses to drought

Soil type and irrigation treatment affected the aboveground and belowground phenology of the five potato genotypes included in this study, except for emergence, which was affected by soil type. Differences in emergence, with G5 being the slowest to emerge (19 DAP) and G4 the fastest (12 DAP), were not significant. Soil type strongly affected time to flowering and tuber filling; however, only in plants grown on sand, significant effects of the drought treatments on the duration of tuber filling were found. Grown on sand, flowering was observed about 14 days earlier on average across genotypes and drought treatments, whereas tuber filling was delayed by 12 days on average across genotypes and drought treatments with the exception of G5 where tuber filling occurred about 4 days earlier on sand than on loamy sand. Since irrigation treatments were initiated as a function of DAP and not executed by phenological stages of the individual varieties, water deficit was introduced during earlier development stages on sand (flowering observed between 40 and 46 DAP on average across treatments) than on loamy sand (flowering between 56 and 59 DAP across treatments). Late drought treatments significantly increased the period of tuber filling in plants grown on sand but had no effect on plants grown on loamy sand.

In general, drought treatments did neither affect the period of tuber bulking nor the onset of senescence significantly; however, in plants grown on sand, onset of aboveground senescence was hastened as compared to plants grown on loamy sand and occurred on average about 5 days earlier across treatments and genotypes with the strongest effect in G5 with an average of 18 days earlier. A

similar effect was observed for the tuber bulking period for plants grown on sand; however, genotypic differences in the belowground development were less pronounced.

Late drought (T4) in plants grown on sand significantly delayed physiological maturity on average by 18 days when compared to plants subjected to late drought on loamy sand and 15 days when compared to fully watered plants grown on sand, respectively. The strongest effects in this regard were observed in G1 and G4 with a delay of about 30 days each (Tables 3 and 4).

3.2 | Environmental factors shift the synchrony between below- and aboveground development

Due to large genotypic differences in the overall duration from planting to physiological maturity, comparing phenological responses based on absolute numbers of days does not allow analysing the environmental effect on the genotypic phenology. Since in potato the desired product is not a seed but a storage organ, the relative time the plant invests in building up the storage (sink) and filling it (source) makes the differences in genotypic yields. Genotypes varying in duration can be compared regarding the effects of environmental factors on critical phenological stages across using values representing the share of the individual phenological stage in the overall duration. Figure 4 compares the relative shares of above- and belowground development stages within the overall duration for genotypic responses to soil type and drought. On both soils, the relative share of all above- and belowground phenological stages after withholding irrigation was influenced by drought. In general, drought increased the relative tuber filling phase and senescence while the relative time to flowering was shortened. It can be expected from the data presented in Figure 1 that 50% of the belowground development constitutes the sink filling phase (tuber filling, bulking, and maturity). The filling phase started after sink dimensioning (tuber formation) and after full source development (flowering), which concludes 70% of the aboveground development. In the current study, under full irrigation, the sink filling phase constituted 70% of belowground development on loamy sand, whereas on sand the sink filling phase accounted for 75%. Flowering accounted for 70% and 65% of aboveground development in loamy sand and sand, respectively. Early drought treatments shifted this relationship by reducing the remaining aboveground development after flowering to 18% and 25% of the total cycle on loamy sand and sand, respectively, during which 70% and 75% of the sink filling occurred on loamy sand and sand, respectively. The largest share of the later tuber development was attributed to tuber filling, whereas the share of tuber bulking was strongly shortened under drought. The earlier irrigation was withheld, the larger was the deviation between above- and belowground phenology. Accelerated aboveground development combined with slower belowground development led to a large disparity between belowground and aboveground development. As a result, aboveground development is no longer indicative for belowground development.

TABLE 3 Mean aboveground development (± standard deviation) in days after planting (DAP) in the four irrigation treatments T1–T4 of the 5 genotypes. The first treatment (T1) represents the fully irrigated control; LS, loamy sand; S, sand.

		Flowering (DAP)		Senescence (DAP)	
	T	LS	S	LS	S
	1	57 ± 5*ab*	45 ± 8*a*	104 ± 12*a*	98 ± 12*a*
	2	56 ± 5*ab*	45 ± 4*a*	89 ± 6*b*	83 ± 5*c*
	3	56 ± 4*b*	42 ± 3*a*	88 ± 8*b*	85 ± 3*bc*
	4	59 ± 3*a*	42 ± 4*a*	92 ± 11*b*	92 ± 7*ab*
LSD		*4.7*	*5.3*	*10.3*	*9.5*

Note: Water was withheld after 50 DAP in the early drought (T2), at 65 DAP in the intermediate drought (T3), and at 80 DAP in the late drought treatment (T4). ANOVA analysis with *Fisher's least significant difference test* and Bonferroni's correction at significant level $p = .05$ ($n = 15$). Model used: Phenological stage = G + T + Replication + G*T, Genotypes (G) 1–5; see Table A1.

4 | DISCUSSION

Aboveground phenology and belowground phenology were adversely affected by soil type and stress intensity. In general, aboveground phenology was hastened, whereas belowground phenology was delayed. The earlier the drought was initiated, the longer the tuber filling phase was, while the bulking phase was shortened. This effect resulted in significant differences in stress intensity during specific growth stages for the various drought treatments on the two

TABLE 4 Mean belowground development in days after planting (DAP) in the four irrigation treatments T1–T4 of the 5 genotypes.

		Tuber filling duration (days)		Tuber bulking duration (days)		Physiological maturity (DAP)	
	T	LS	S	LS	S	LS	S
	1	39 ± 5*b*	51 ± 5*b*	25 ± 10*a*	17 ± 17*a*	90 ± 11*a*	95 ± 2*b*
	2	47 ± 10*ab*	51 ± 6*b*	20 ± 14*ab*	15 ± 16*a*	93 ± 22*a*	94 ± 20*b*
	3	47 ± 9*ab*	47 ± 9*b*	10 ± 4*c*	9 ± 1*a*	80 ± 9*a*	80 ± 9*b*
	4	51 ± 16*a*	71 ± #*a*	14 ± 5*bc*	13 ± 1*a*	91 ± 11*a*	113 ± 9*a*
LSD		*10*	*11*	*9*	*10*	*15*	*16*

Note: The first treatment (T1) represents the fully irrigated control; LS = loamy sand; S = sand. Water was withheld after 50 DAP in the early drought (T2), at 65 DAP in the intermediate drought (T3), and at 80 DAP in the late drought treatment (T4). Model used: Phenological stage = G + T + Replication + G*T, Genotypes (G) 1–5; see Table A1.

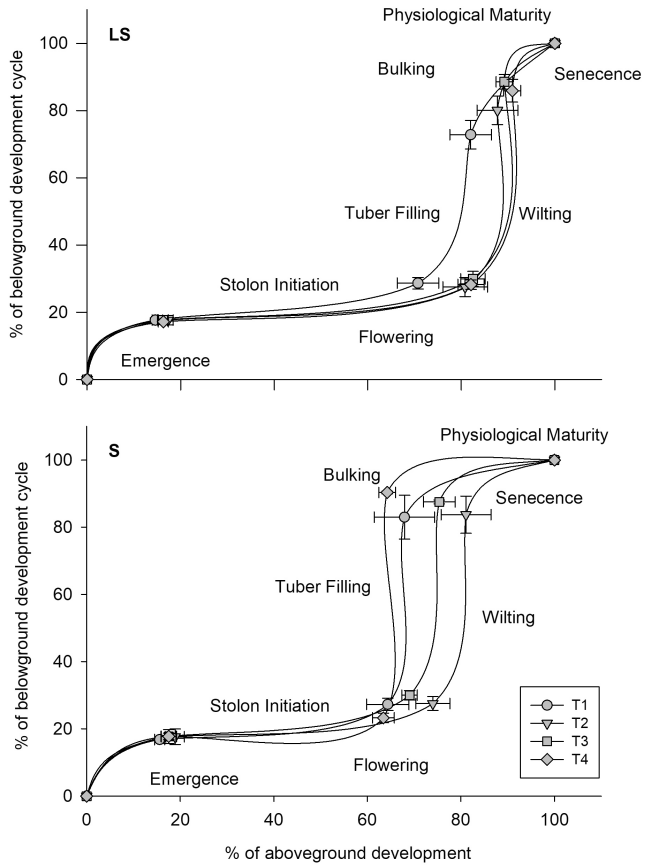

FIGURE 4 The synchrony of above- and belowground phenology averaged over all 5 potato genotypes grown in loamy sand (LS) and sand (S). The first treatment (T1) represents the fully irrigated control. Water was withheld after 50 days after planting (DAP) in the early drought (T2), at 65 DAP in the intermediate drought (T3), and at 80 DAP in the late drought treatment (T4).

soil types. In addition, these effects were strongly altered by genotypic responses to these factors, increasing the disparity of treatment effects created by the different soil types on a genotypic level.

4.1 | Phenology and environmental factors

In order to exclude confounding effects of water availability, soil type by genotype interactions are best studied under full irrigation. Genotypes varied significantly in the length of their respective phenological cycles due to late (Genotype 5) or early maturity (Genotype 1). Genotypes with delayed germination showed early tuberization and flowering (Wurr et al., 1992). Since in potato the desired product is not a seed but a storage organ, the relative time the plant invests in building up the storage (sink) and filling it (source) makes the differences in genotypic yields and not flowering time. To evaluate treatment effects on phenology in genotypes differing in overall duration, the duration of individual phenological stages needs to be standardized as the share in the respective overall duration, making it possible to compare soil type effects on duration among different genotypes. Both soil types, sandy loam and sand, had optimal physical growing conditions for potato. Aboveground, the date of flowering differed significantly between the two soil types in the fully irrigated control. On average in plants grown on sandy soil, genotypes flowered 10 days earlier than in plants grown on loamy sand. Belowground under full irrigation, stolon initiation, bulking duration, senescence, and day of maturity were not affected by soil type, but differences in soil type resulted in differences in the duration of tuber filling. In plants grown on sand, tuber filling duration was 12 days longer than in plants grown on sandy loam. Most studies evaluate tuber development by tuber yield, size, dry matter partitioning, and starch content (Geremew et al., 2007) since repeated measurements of stolon and tuber development to evaluate tuber filling period are difficult to perform, as digging up and measuring the same plant several times during the growing period may negatively influence stolon and mini tuber development. In addition, several phenological stages are present simultaneously as new tubers develop while others approach physiological maturity (Ewing & Struik, 1992). This circumstance renders the exact determination of a belowground phenological stage, and thus the period of tuber filling, difficult. Since tuber initiation is independent from stolon initiation, flowering, and the duration of the whole cycle (Celis-Gamboa et al., 2003), we evaluated genotypic stolon initiation and tuber filling over the entire vegetation period.

4.2 | Phenology and drought stress

Withholding irrigation in staggered intervals resulted in different drought severities, which in turn affected genotypic phenology differently, resulting in competition for assimilates between foliage and tubers (Ivins & Bremner, 1965). In general, drought hastened aboveground phenology and delayed belowground phenology, which resulted in significant genotypic differences in stress intensity during specific growth stages (Hoelle et al., 2020).

Drought shortened the duration of tuber bulking, reduced canopy growth, and induced early foliage senescence, which is in line with earlier observations by Spitters and Schapendonk (1990), who reported the strongest effects on tuber yields for early drought, which induced early tuber bulking while leaf area was still small. In the present study, drought advanced foliage senescence by up to 15 days, with genotypic differences most pronounced in early drought in plants grown on loamy sand and late drought in plants grown on sand.

However, drought significantly affected belowground development, particularly late drought prolonged the duration of tuber filling. Earlier studies related canopy size at tuber initiation with tuber growth and foliage senescence (Ivins & Bremner, 1965; Slater, 1963); however, in the experiment reported here irrigation was withheld when the canopy was already fully developed and potential tubers already initiated. The extended duration of tuber filling effectively decoupled belowground development rates from aboveground development rates. Thus, drought broke the synchrony between above- and belowground phenology by prolonging the duration of

tuber filling while shortening the time to flowering and senescence. Smaller amounts of plant-available water and thus a faster drying of the soil for plants grown on sand shifted the severeness of the drought into earlier phenological stages with an even stronger effect on the synchrony. This way, the tubers developed into a more severe water deficit than the aboveground biomass, indicating a shift in source—sink relationship in favour of storage organ formation. In contrast, under fully irrigated conditions, development rates of above- and belowground biomass showed no shift in partitioning preferences.

Many agronomic studies use the aboveground phenology as a proxy for the belowground development, although, even under optimal growing conditions, there is no physiological link between flowering and tuber development, as some genotypes do not flower per se or abort buds (Jefferies & Lawson, 1991). The observed, drought-induced shift in phenological synchrony in favour of faster aboveground development clearly supports the findings of Celis-Gamboa et al. (2003) and indicates that the system of linear development from Meier (2001) cannot be applied to potato grown under water deficit conditions. However, the interaction between drought, phenological stages, and tuber yield still needs more systematic research as we could not confirm the findings of van Loon (1981) that the tuber bulking period is the most drought-sensitive stage with regard to final tuber yield.

5 | CONCLUSION

Aboveground phenology and belowground phenology were adversely affected by environmental factors, such as soil type and water deficit. In general, aboveground phenology was hastened, whereas belowground phenology was delayed, leading to significant differences in stress intensity during specific growth stages for the various drought treatments on the two soil types. In addition, these effects were strongly modified by genotypic responses to these factors, increasing the disparity of treatment effects created by the different soil types on a genotypic level. We concluded that under terminal drought conditions aboveground development and belowground development need to be evaluated separately and cannot follow the standard evaluation system that uses aboveground phenology as a proxy for tuber formation belowground development rates.

AUTHOR CONTRIBUTIONS

Julia Hoelle: Investigation; validation; conceptualization; writing – original draft; methodology. **Awais Khan:** Project administration. **Folkard Asch:** Supervision; writing – review and editing; methodology.

ACKNOWLEDGEMENTS

The authors gratefully acknowledge financial support by the German Ministry for Collaboration and Development (Deutsche Gesellschaft für Internationale Zusammenarbeit; GIZ No. 11.7860.9-001.00). The authors thank INIA-Arequipa for providing facilities. The authors are grateful to Jesus Zumaran and Leah Kuppinger for their support during the field trials. The authors gratefully acknowledge excellent technical assistance by Jorge Vega, Anthony Quello, Elisabeth Torreblanca, and Trinidad. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

We have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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How to cite this article: Hoelle, J., Khan, A., & Asch, F. (2024). Drought affects the synchrony of aboveground and belowground phenology in tropical potato. *Journal of Agronomy and Crop Science*, *210*, e12675. https://doi.org/10.1111/jac.12675

APPENDIX A

TABLE A1 Breeders code, virus resistance group, growing duration, and variety name of the five genotypes. Early maturing genotypes mature within 70 days after planting (DAP). Intermediate genotypes are mature after 80–90 DAP and late maturing genotypes later than 90 DAP under growing conditions in Majes.

No.	CIP number	Group	Duration—Majes	Variety name
G1	CIP 392797.22	Lowland tropic virus-resistant	Early	Unica
G2	CIP 397078.12	Lowland tropic virus-resistant	Intermediate	
G3	CIP 392025.7	Lowland tropic virus-resistant	Intermediate	
G4	CIP 397073.16		Early	
G5	CIP 301040.63	Lowland tropic virus- and late blight-resistant	Late	