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Responses of Canopy Growth and Yield of Potato Cultivars to Weather Dynamics in a Complex Topography: Belg Farming Seasons in the Gamo Highlands, Ethiopia

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Abstract: Potato is an increasingly important crop in Ethiopia. The Gamo Highlands are one of the large potential potato producing regions in Ethiopia. The growing conditions are different from those in the temperate regions, where most of the agronomical expertise on potato has been developed. The influence of environmental conditions on the crop in the Gamo Highlands is poorly understood. We conducted field trials with eight potato cultivars in six locations and during two seasons. The canopy cover (CC) and plant height (PH) were measured with high temporal resolution and tuber yields were assessed as well. The experiments were conducted near our newly installed weather stations at different elevations. CC and PH were strongly correlated with temperature sum (Tsum). Tuber yields differed among elevations and cultivars. Nevertheless, these differences were poorly explained by environmental variables. We also found that no single cultivar performed best at all elevations. The number of branches was a predictor of yield, suggesting that radiation interception was limiting tuber growth. Tuber yield was optimal when the number of days to crop maturity was around 100–110 days. We conclude that Tsum is a predictor of crop growth, but environmental variables poorly explain yield variations, which calls for further investigation.

Keywords: canopy cover; cumulative radiation; dry matter allocation; harvest index; temperature sum

1. Introduction

Potato (*Solanum tuberosum* L.) is an important and emerging crop in Ethiopia [1,2]. Drought, crop failure and food insecurity have been severe, as well as other related problems in the Horn of Africa in the recent past [3,4]. For instance, the years 1972–1973, 1982–1983, 1986–1987, 1987–1988, 1997–1998, and 2015–2016 are identified as strong El Niño episodes [3,5,6]. In Ethiopia, El Niño events are often excessively warm and dry and they often cause crop failure and famine in most parts of the country [6–8]. Potato is called the hunger breaker as it has a short crop cycle compared to cereals [9,10]. Therefore, it plays an important role in sustaining food security during difficult

periods [11,12]. However, because the crop is mainly grown by small farm holders with limited access to farming knowledge and technologies, the actual yield is much lower than the achievable and potential yields [13–16].

Over the last decade, potato production in the western world declined significantly, mainly because of a decline in acreage. Developing countries currently produce more than developed countries and their production has more than doubled in ten years, mainly due to increases in the area harvested and in some regions because of improvements achieved in seed technology, fertilizer use and fungicide application [17]. In Eastern Africa, however, the production quantity has grown exponentially since 1990 [13] primarily because of a significant increase in the acreage. The yield per hectare has hardly grown, because access to inorganic fertilizers [18] and pesticides [19] is limited and the farming has been conducted in nutrient depleted soils with insufficient moisture, particularly at the onset of the growing season [1,20]. As a result, the yield gap in the region is around 65%, which is much larger than the 35% in the western world [13,21]. Note that the yield gap is the difference between the potential yield and the actual yield [17,21]. Potential yield is the maximum yield attained when the crop is grown in non-limiting (i.e., with abundant water and nutrients) conditions, in which the abiotic and biotic stresses are controlled. The actual yield is the yield the farmer harvests.

Much of the knowledge of the relationship between potato growth and environmental conditions is based on western studies in temperate climates, for example [22–26], where the temperature is usually a limiting factor [27,28] during the early part of the growing season, soil moisture only becomes limiting during advanced stages of growth, and crop management is characterized by high levels of input. The Ethiopian climate and environmental conditions are rather different, temperature is moderate ($10\text{ }^{\circ}\text{C} < T_{\text{mean}} < 20\text{ }^{\circ}\text{C}$), soil moisture may be limiting, particularly during the early part of the growing season [20,29,30], and agronomic inputs are generally low [2,20]. Weather conditions are, in fact, variable too in space [31]. In Ethiopia, potato can only be grown in the mid- and highlands, because the lowlands are too warm ($T_{\text{max}} > 25\text{ }^{\circ}\text{C}$, [31]). Weather conditions in the mountains change along the slope [29,31], causing potato growth and yield to also change with elevation.

There are a number of articles related to potato agronomy in Ethiopia, e.g., [1,32–34]. However, much less is known about the relationship between environmental conditions and potato growth in tropical regions like Ethiopia than in the temperate climates. To this end, we collected crop growth and tuber yield data in the 2017 and 2018 growing seasons along two transects in the highlands, where we also have weather stations installed [29]. This study is an extension of our previous work described in [29,31]. In the current paper, environmental conditions, potato growth and tuber yield relations are investigated at a high temporal resolution and we identify where the growing conditions are optimal in the Gamo Highlands. Ultimately, this knowledge can help us estimate the potential yield and select and develop varieties, which are better capable of dealing with the environmental conditions [17,21].

The Gamo Highlands, a topographically pronounced region in southern Ethiopia, is a region with a high potato production potential [19,29,35]. The crop is best grown in a long growing season and with high incoming radiation, between ~ 12 and $24\text{ MJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, average daily temperature between 5 and $21\text{ }^{\circ}\text{C}$, precipitation between 600 and 1200 mm per annum depending on the climate of a location [36,37]; and in a soil with good water-holding capacity and sufficient nutrient availability [13,38,39]. These environmental conditions are available in the Gamo Highlands at elevations higher than 1600 m above sea level (a.s.l.) [29,31].

The National Meteorological Agency (NMA) classified the Ethiopian climatic seasons into three, namely *belg* (February to May), *kirmet* (June to September), and *bega* (October to January) [40,41]. *Kirmet* is the wettest season in most of the country, except the southern and southeastern parts of the country [42]. Southern Ethiopia receives its maximum precipitation during *belg*. The other regions of the country may also receive small amounts of rain in *belg* [40]. *Bega* is a dry season, but potato can grow if irrigated [16]. Note that only 5% of the total arable land is irrigated in the country [43]. In the Gamo Highlands, potato grows mainly during the *belg* season under rain-fed agriculture [29,31]. Farmers prefer the *belg* season for potato cropping because of the season's meteorological and agronomic

suitability for potato cropping, i.e., the moisture availability is optimal and disease risks are relatively low [29,32,38]. Late blight caused by *Phytophthora infestans* is the most important potato disease in Ethiopia, followed by bacterial wilt caused by *Ralstonia solanacearum* [32,44].

The potato crop growth is traditionally explained in terms of responses to environmental variables [13,22]. The major growth-influencing factors are temperature, photoperiod, soil moisture (in terms of precipitation and/or irrigation), the incoming shortwave radiation ($SW\downarrow$), and nitrogen supply [13,45]. These factors can explain the crop's canopy dynamics in terms of lateral or horizontal growth [e.g., estimated from canopy cover or Leaf Area Index (LAI) measurements and vertical growth (e.g., plant height)]. A summary of how meteorology influences potato growth closely related to this investigation is given below.

In a potato crop, many complex physiological processes are strongly affected by temperature [22]. Temperature can affect canopy development, tuber bulking and growth cycle duration [17]. The temperature is very different in the tropics than in temperate climates, regarding both mean and variability. A daily mean temperature of 15–18 °C is generally considered as an optimal temperature for potato growth in the tropical highlands [46]. The growth rate declines nearly linearly to zero when either the average temperature decreases to 5 °C or increases to 28 °C from this optimum. An average daily temperature (T_{mean}) of less than 5 °C gives low photosynthesis rate with a risk of frost and diseases, while a $T_{\text{mean}} > 28$ °C causes high respiration rates with a rapid foliage development, retarded tuberization, little partitioning of dry matter to the tubers, poor starch synthesis, resulting in a large number of small tubers per plant, and low dry matter concentration [13,23,39,46].

The potato crop is relatively sensitive to drought stress, which occurs regularly in the Horn of Africa [41]. It is only cultivated where precipitation is sufficient or where irrigation can be applied [46]. Water-stressed potato plants result in yield reduction because of reduced leaf area and/or reduced photosynthesis per unit of leaf area and often produce fewer and smaller tubers [39]. Of all growth stages of the crop growth period, the tuber bulking period is the most drought-sensitive stage [47].

Millard and Marshall [48] explained that the potato tuber yield is a product of four processes, namely (1) radiation interception, (2) conversion of intercepted radiation to dry matter, (3) partitioning of dry matter between tubers and other parts of the plant, and (4) regulation of tuber dry matter contents. Sibma [49] showed that the potato yield and the total $SW\downarrow$ during the entire growing season were positively correlated. The dry matter production of a crop is linearly related to the intercepted radiation. The produced dry matter is distributed over different parts of the potato plant [24]. Allen and Scott [50] showed that the potato tuber dry weight positively and linearly correlated with the total intercepted radiation during the growing season. The Harvest Index (HI), which is a function of the amount of cumulative radiation intercepted by the crop during the growing season, is dependent on the location and season and is specific to a given cultivar [13].

The canopy dynamics in the potato crop is explained based on three distinct growth phases (Figure 1). These growth stages include the canopy buildup phase (P1), the maximum canopy cover phase (P2), and the canopy decline phase (P3) [45]. P1 covers the time between emergence (when 50% of the plants have emerged) and the maximum canopy cover and is characterized by the appearance of stems, lateral branches and leaves, and growth of those organs. P2 is the period from the maximum canopy cover to the onset of canopy senescence; whereas the period from the onset of senescence to the end of the crop cycle is called P3 [45].

Crop growth at the early stages of development (emergence and initial foliar expansion) can be related and explained by the temperature sum (T_{sum}) rather than the number of calendar days as the crop's physiological processes depend on temperature [13,51]. T_{sum} is the cumulative sum of the daily average temperature above a base temperature (T_b) during the crop growth period. Studies considered T_{base} for potato crop between 0 and 5.5 °C [13,25,45,52]. T_{sum} is expressed in units of day-degrees (d °C or dd) [13]. Haverkort [13] discussed that the canopy growth during P1 can be described by a linear relation with T_{sum} . At the end of P1, the canopy cover is at its maximum and does not change anymore with T_{sum} in P2, while it decreases in P3.

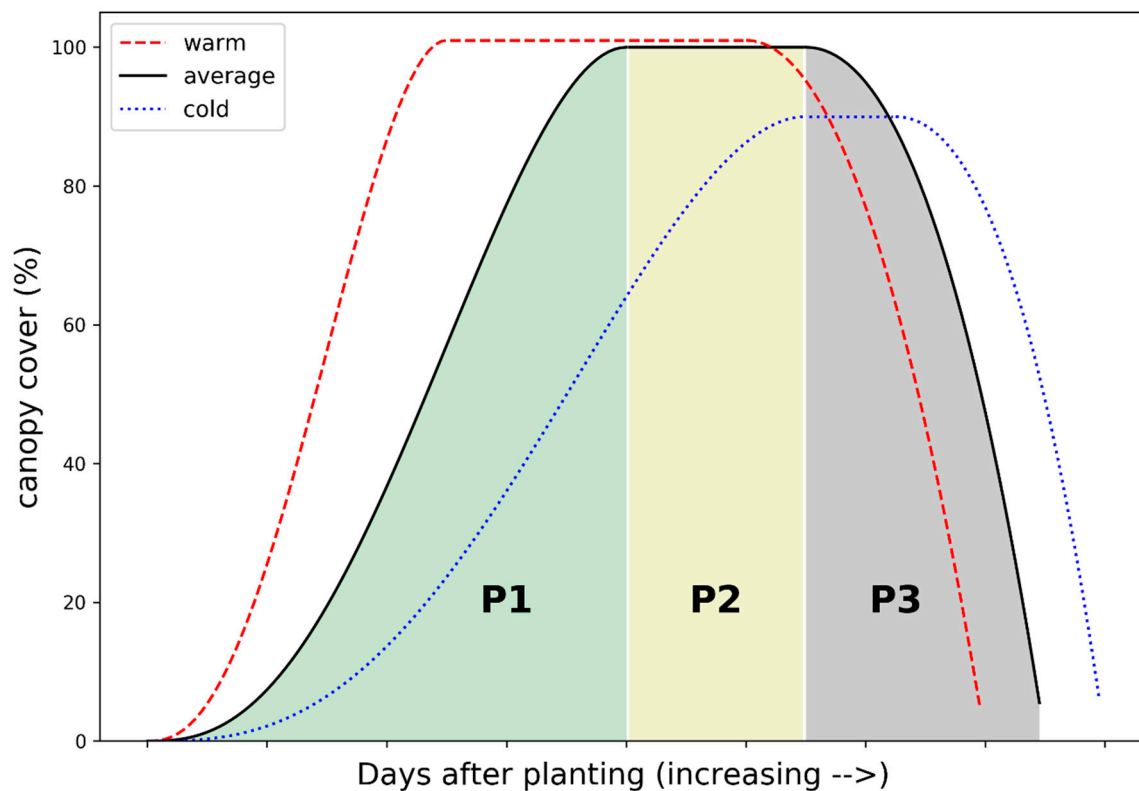


Figure 1. A hypothetical model-based representation of the canopy dynamics expressed in percent canopy cover as a function of days after planting (not scaled) based on the beta function to determinate growth for the canopy buildup phase (P1) [45,53], maximum cover phase (P2), and canopy decline phase (P3) [45], as shown. Note that the break-down into these three phases indicated is only applicable to the ‘average’ curve shown with the solid line. We assumed canopy growth for warm, mild, and cold temperatures scenarios to mimic meteorological conditions in lowlands, midlands, and highlands of potato growing regions in the Gamo Highlands, respectively.

To our knowledge, there are only a few studies focusing on the relationship between potato, weather and seasonal climate in Ethiopia. Haverkort et al. [16] used station observations to calculate the attainable and achievable potato yield for *belg*, *meher*, and *bega* agronomic seasons. Minda et al. [29,31] conducted studies about weather variability along the slopes of the Gamo Highlands in relation to potato growth. In Minda et al. [31], the potato crop growth and attainable yield are simulated using modelled weather data. The authors showed that precipitation positively influenced yield, and the minimum and maximum temperatures both negatively influenced it. Using weather observations and a potato crop model, Minda et al. [29] showed that the soil moisture is the most important variable that influenced crop yield.

The Gamo Ethiopian Meteorological Stations (GEMS) network (currently, eight automatic weather stations) is operational since April 2016. Details of the GEMS network are found in Minda et al. [29]. Close to the network, we planted and monitored eight potato cultivars in the *belg*-2017 (five locations) and *belg*-2018 (six locations) seasons to explain crop growth and yield variations among cultivars, across elevations, and seasons as influenced by environmental conditions. Therefore, the aim of this study was to study how the potato crop growth and yield vary with variations in the environmental variables during the crop growth phases (mainly in P1) in the Gamo Highlands, southern Ethiopia. To attain our aim, we formulated the following research questions.

1. How does canopy growth vary with environmental variables in P1 across elevations, among potato cultivars, and between seasons? Does this growth follow similar patterns as in temperate climates?

2. How does the yield depend on physiological crop characteristics, such as number of tubers, number of branches, days to maturity, cultivar, and on meteorologically dependent variables, such as intercepted radiation and temperature?

To answer these research questions, we collected high temporal resolution data (one-day or two-day intervals) on canopy cover and plant height for improved and local cultivars. We also collected data on the plant, yield and yield traits (e.g., branch numbers, tuber numbers and tuber weights per plant) at five to six farms (at different elevations) and for six improved (*Gudene*, *Belete*, *Horro*, *Hunde*, *Ararasa* and *Jalene*) and two local (*Suthalo* and *Kalsa*) cultivars in two *belg* seasons [2,54,55]. From the improved cultivars, *Gudene*, *Belete*, and *Jalene*, and the two local cultivars are commonly cultivated in the Gamo Highlands [56]. Note that the potato crop has been cultivated in Ethiopia for more than 150 years. In the country, improved varieties started to be released since 1987 [57]. In the Gamo Highlands, the crop has been cultivated for decades [58]. Although this represents a significant effort, the number of possible predictor variables is large and we are facing a mathematically underdetermined system. We therefore confront the data with existing theory, which is to a large extent developed for the potato crop in a temperate climate, to test if and where these theories deviate for the mountainous tropical climate in Ethiopia.

2. Materials and Methods

2.1. GEMS Weather Dataset during Belg 2017 and 2018

The weather data in this study were taken from the Gamo Ethiopian Meteorological Stations (GEMS) network. The GEMS network records weather (max/min/mean temperature— T_{\max} , T_{\min} , T_{mean} , precipitation—PPT, the incoming shortwave radiation— SW_{\downarrow} , wind, and relative humidity), edaphic (soil moisture tension— ψ and temperature— T_{soil}) and plant related (leaf wetness) variables with every 15-min (in *belg*-2017) or 30-min (in *belg*-2018) temporal resolution. The network is operational since April 2016. Eight automatic weather stations (AWS) have been installed in a complex topographic region in the Gamo Highlands, Southern Ethiopia. The Gamo Highlands form a heterogeneous landscape composed of complex topography extending from the narrowest portion of the Great East African Rift Valley at 1000 m a.s.l. to the summit of Mount Guge at 3600 m a.s.l., including Lake Abaya and Lake Chamo, forest, and agricultural lands. Descriptions of the study area and the GEMS network data are provided in detail in Minda et al. [29]. *Belg*-2017 was during a La Niña phase characterized by a warmer and drier season than the climatology in the Gamo Highlands [29,59,60]; whereas, *belg*-2018 was relatively cool and wet (Table 1). Table 1 presents the locations of the experimental farm sites with mean seasonal environmental (weather and edaphic) variables and descriptions of the potato cultivars and date of planting in the *belg* seasons.

Table 1. Descriptions of the crop experimental sites with the *belg* (Feb–May) average seasonal weather (mean T_{mean} , mean SW_{\downarrow} , and *belg* total PPT); edaphic (mean soil moisture (ψ) and mean soil temperature (T_{soil}); and some of the potato crop experimental descriptions in *belg*-2017 ('17) and *belg*-2018 ('18). Note that the GEMS location deviates a few meters from the farm sites. The soil sensors were placed at four depths: 5, 10, 20, and 40 cm, in which averages of the four depths were reported. Note that soil moisture sensors measure from 200 (dry soil) to 0 (fully saturated soil) kPa. Key: Lon—longitude, Lat—latitude, Elv—elevation.

Station	Lon (°)	Lat (°)	Elv (m)	Meteorology (<i>belg</i>)						Edaphic (<i>belg</i>)				Potato crop					
				T_{mean} (°C)		SW_{\downarrow} (MJ·m ^{−2} ·d ^{−1})		PPT (mm· <i>belg</i> ^{−1})		ψ (kPa)		T_{soil} (°C)		No of cultivars planted		Date of planting		Disease observations	
				'17	'18	'17	'18	'17	'18	'17	'18	'17	'18	'17	'18	'17	'18	'17 ^e	'18 ^e
Gircha	37.566	6.309	2985	13.0	12.2	17.3	15.7	443.8	476	60.6	43.5	16.4	13.8	8	2	07-Mar	12-Mar	No	Yes
Gazesso	37.333	6.132	2880	13.7	13.2	17.0	15.3	>475 ^d	462	52.2	45.5	17.6	16.4	8	8	02-Mar	03-Apr	No	Yes
Chencha ^{a,c}	37.566	6.258	2765	14.0	13.2	18.4	16.1	540.2							2		08-Mar		Yes
Zozo ^{a,c}	37.605	6.265	2695												2		12-Mar		Yes
Tegecha ^c	37.575	6.184	2383	20.3	18.3	18.6	14.0	458.8	564	130.7	140.0	22.7	21.7	8		05-Apr		Yes	
Geresse ^b	37.310	5.929	2298		16.6		14.1							8	8	10-Apr	05-Apr	No	Yes
Derashe	37.368	5.637	2122											8	8	01-Apr	27-Mar	No	Yes

^a Farm with no weather station nearby; ^b Weather data obtained from the National Meteorology Agency (NMA) manual stations, Ethiopia; ^c Field experiment was absent either in *belg*-2017 or *belg*-2018; ^d precipitation record with two-weeks missing data; ^e we observed that incidence and severity levels were different among farms, but these were not quantified.

2.2. The Potato Farm Experiments during Belg-2017 and Belg-2018

The potato field experiments in this study (*belg*-2018) are follow-up field experiments (*belg*-2017) from Minda et al. [29]. We planted the following six improved varieties (with their year of release): *Gudene* (2006), *Belete* (2009), *Horro* (2015), *Hunde* (2006), *Ararasa* (2006), *Jalene* (2002), and two local varieties: *Suthalo* (unknown) and *Kalsa* (unknown) [2,54,55]. During *belg*-2017, the seed tubers were collected from three research centers, and the seed tubers of the local cultivars were purchased from local markets. From the *belg*-2017 harvest, we selected seed tubers from Gircha and Gazesso farms and stored them in the diffused-light storage (DLS) facility at the Gircha site (mean temperature during storage was only 11.7 °C). The DLS facility allowed free ventilation and light diffusion; it suppressed elongation of sprouts and slowed down sprout ageing [15]. We kept the well-sprouted seed tubers stored in the cool environment for all the farms to be planted in the following *belg* season. Our planting material was of superior quality compared to the commonly planted seed material and our crops were healthier than farmers' plots in the region.

The experiments in *belg*-2017 and *belg*-2018 were done with different planting dates depending on moisture availability in the farm site (Table 1). A randomized complete block design—RCBD was applied with three replications [61]. The plot size was 3 m × 3 m and the planting pattern (between rows × between plants) was 0.75 m × 0.30 m resulting in a plant density of 4.4 plants per square meter of land. Spacing between plots and replications was 1 m and 1.5 m, respectively. Urea (144 kg·ha^{−1}), NPS (236 kg·ha^{−1}), and muriate of potash (125 kg·ha^{−1}) fertilizer doses were added at planting, but the urea was split into two dressings, in which the first half was applied at planting and the remaining half was added at the start of the flowering stage. Agronomic practices such as weeding, hoeing, and earthing-up were done as recommended. Data were taken from the middle two rows. This allowed us to avoid border effects [62].

2.3. Canopy Growth and Crop Yield Observations

Plant height (cm) and canopy cover (%) data were collected to estimate the canopy growth. The distance between the soil surface (basal end of stem) and the upper most tip (shoot apex) of the main stem was considered as plant height [63]. Decreases in plant height because of increases in ridge height during hoeing and earthing-up were estimated and data were corrected. The amount of intercepted radiation can be determined using canopy cover measurements [64,65]. The percentage of the canopy covered with green foliage was measured with a grid with dimensions that are a multiple of the planting pattern (0.75 m, between rows × 0.30 m, between plants) divided by 100 rectangles [13,66]. All rectangles at least half filled with green leaf were counted and the percentage canopy cover was determined [64,66,67]. The center of the grid was placed on top (at center) of a selected plant, so that the shorter side (0.30 m) of the grid was aligned with the ridge. In *belg*-2017, plant height measurements were taken six times per week for farms—Gircha and Gazesso, and for cultivars—*Gudene* and *Suthalo*. In *belg*-2018, those measurements were taken three times per week for farms—Gircha and Chench; and for cultivars - *Gudene* and *Belete*. Canopy cover data were taken three times per week in *belg*-2017 for Gircha, and for cultivars—*Gudene* and *Suthalo*. Five randomly selected plants per plot were measured for canopy cover and plant height observations and the means of 15 plants are reported.

Boyd et al. [64] provided a detailed analysis of the relation between canopy cover and LAI. They provided data that suggest that the slope of this relationship could be influenced by the way the crop was managed. These authors also showed that when the duration of ground cover was used (a parameter they coined ground cover duration), the variation in the tuber yield accounted for was equally large, or even higher, than when they used leaf area duration.

The following yield and yield traits observations were systematically collected at the harvest date: total number of lateral and apical branches per plant at crop maturity [68]; number of marketable tubers per plant (80–300 g in weight and 30–60 mm in diameter); number of non-marketable tubers per plant (< 80 g in weight and < 30 mm in diameter); weight of non-marketable tubers per plant (kg) [69]. These data were taken from five randomly selected plants from the central two rows and the averages

of the three plots are reported. The total yield per plot, i.e., the sum of the weight of marketable and non-marketable tubers, was calculated and the average of the three plots is reported. Note that in *belg-2017*, the Tegecha farm was strongly affected by diseases, mainly late blight. In the following year, however, all farms were affected by different intensities of diseases. We did not quantify or rate disease observations.

2.4. Statistical and Mathematical Data Analysis Approaches

2.4.1. Crop Growth and Environmental Variables Relations

For studying the correlations between the environmental and crop variables, we calculated and report the average weather and crop observations to daily, or five-daily, or sub-seasonal (e.g., during P1), or seasonal temporal scales. We selected the Gircha site for the following reasons. First, our weather station has been operational since April 2016 in this site. It is located in the newly established highland crops horticultural research centre run by Arba Minch University. Second, the Gircha region is one of the best-known potato producing areas in the Gamo Highlands. Third, Gircha is the coolest amongst our farms and is equipped with a DLS facility. For some data collection or analysis, we selected *Gudene* from the improved and *Suthalo* from the local cultivars as these are the most widely improved and local cultivars cultivated in the Gamo Highlands, respectively.

For studying the temporal variation of canopy growth as a function of environmental variables, we considered P1 as the period between that time that the crop attains 10% and 90% of the maximum plant height. However, continuous measurements of plant height data are not available for some cultivars and farms. Hence, for studying the correlation between weather and tuber number per plant, P1 was best estimated from other crop datasets. In these instances, we defined P1 as the period from crop emergence (50% of the plants emerged) to a week after the date of flowering (50% of the plants flowered). We also considered average weather in P2 and P3 to study relationships between weather and tuber weight per plant. The starting date for P2 was one day after the end of P1. The end time of P3 was considered as two weeks after the day of crop maturity. Maturity was defined as the onset of canopy senescence (when the vines started to become yellowish) [70]. We applied linear and quadratic statistical correlations to identify the relation between crop growth (plant height and canopy cover) and environmental variables.

2.4.2. The Daily Crop Growth and Temperature Sum

Temperature sum (Tsum) explains plant development for most crops [71]. Crop growth, mainly during the early stages of emergence and initial foliage expansion, is easiest related to the Tsum, i.e., the cumulative daily average temperature expressed in day-degrees (d °C). Tsum is calculated using Equation (1).

$$Tsum = \sum_{i=1}^{i=n} \left[\frac{(T_{max} + T_{min})}{2} \right] - T_b \quad (1)$$

Note that the Gamo Ethiopian Meteorological Stations (GEMS) data showed that the lowest daily average temperatures was 7 °C and the highest was 30 °C for all potato growing farms in both *belg-2017* and *belg-2018*. As a consequence, the mean daily temperature, estimated from the minimum and maximum temperatures on that day, in the potato growing locations in the Gamo Highlands was always above T_b [13,45,52].

2.4.3. Estimating Harvest Index using the Cumulative Incoming Shortwave Radiation

The plot of cumulative crop growth and measured canopy cover against cumulative incoming solar radiation ($SW\downarrow_{cum}$) may be used to estimate how efficiently the intercepted solar radiation is converted into crop dry matter [13,45,64]. The dry matter is produced by the potato crop with a Radiation Use Efficiency (RUE) of ~ 2.0 g·MJ⁻¹. The RUE is the amount of dry matter (in g) produced

per mega joule of global radiation intercepted. The intercepted radiation is allocated to different parts of the plant (leaves, stems, tubers, and roots), depending on the crop growth stage. The efficiency of a cultivar in allocating dry matter to the tubers can be estimated from the harvest index (HI), the ratio of tuber weight over total plant weight. We estimated total plant weight as a function of the intercepted radiation and the radiation use efficiency as shown in Equation (2) [13].

$$HI = \frac{Y \times DMC}{SW_{\downarrow, cum} \times RUE} \times 100 \quad (2)$$

here, Y is the tuber fresh yield at harvest in $g \cdot m^{-2}$; DMC is the dry matter concentration ($DMC = 20\%$); $SW_{\downarrow, cum}$ is the cumulative amount of SW_{\downarrow} intercepted by the canopy in $MJ \cdot m^{-2}$ and RUE can be from 1.07 to 2.24 g per MJ for potato crop [72–74], but here, we assumed RUE to be $2.0 g \cdot MJ^{-1}$. The total dry matter accumulation is directly proportional to the total amount of intercepted radiation in many crops including potato [50,75]. For the entire crop growth period, $SW_{\downarrow, cum}$ can be calculated as [13,76,77]:

$$SW_{\downarrow, cum} = \int (f_t \times SW_{\downarrow, t}) dt \quad (3)$$

where, f_t is the fraction of canopy cover observed on a daily base and $SW_{\downarrow, t}$ is the average incoming shortwave radiation in $MJ \cdot m^{-2}$ on that day.

3. Results

3.1. The Role of Environmental Variables on Canopy Growth in the Canopy Buildup Stage

In this section, we study how the potato crop grows during the canopy buildup phase (P1, see Figure 1) in terms of plant height and canopy cover as a function of environmental conditions. Previous studies have shown that $Tsum$ is a good predictor of canopy growth during P1 of the crop development stage in temperate climates [13,51,78].

3.1.1. Canopy Cover and Temperature Sum

Figure 1 presents a schematic overview of canopy growth in terms of calendar days for temperature regimes. Figure 2 presents the observed quadratic correlation between $Tsum$ ($d \cdot ^\circ C$) and canopy cover (%) for the *Gudene* (a) and *Suthalo* (b) cultivars in Gircha in *belg*-2017. The linear regression between the canopy cover and $Tsum$ in P1, has an r^2 of 0.98 for *Gudene* and an r^2 of 0.96 for *Suthalo*. Haverkort [13] also explained that the canopy cover showed a linear relation with $Tsum$ in P1. However, as Figure 2 shows, the relation is better described with a quadratic than linear relation, in which the r^2 is improved to greater than 0.99 for both cultivars. We also calculated the rate of increase in the canopy cover as a function of other environmental variables, but the correlations were poor (not shown here).

3.1.2. Plant Height and Temperature Sum

In Section 3.1.1, we showed the canopy cover described in a quadratic function of $Tsum$. Besides the canopy cover, $Tsum$ also explains the plant height. Here, we will study the relationship between the plant height and $Tsum$. Figure 3 shows how plant height relates to the cumulative temperatures during P1.

The plant height is strongly correlated with $Tsum$ (Figure 3). The linear correlation showed an $r^2 > 0.98$ for the improved and local cultivars. The correlation was large for the medium-high (Chencha, 2765 m) and high (Gazesso and Gircha > 2850 m) parts of the mountains, both in dry (*belg*-2017) and wet (*belg*-2018) seasons. The combined r^2 of *Gudene* in three farms and two *belg* seasons gave an r^2 value of 0.95 (f). Similarly, *Belete* in Gircha and Chencha showed an r^2 of 0.97 (i).

The slopes of the lines are in the order of $0.1 cm \cdot (d \cdot ^\circ C)^{-1}$ with variations of tens of percents between varieties and years. The *Belete* cultivar grew faster than the *Gudene* cultivar in Gircha in

belg-2018. For the other cultivars and locations, the data were too sparse to explain. The high correlation coefficients between Tsum and plant height indicate that the variability in growth rates within a growing season was small. Nevertheless, there are variations, which we will study in more detail in Section 3.1.3.

Our results indicate that Tsum did not exclusively explain growth in plant height in P1. The Tsum—plant height curve deviated from linearity for some periods in P1 for some cultivars and environments. The periods characterized by a slowdown in the growth rate are shaded in Figure 3a,c. These deviations need additional environmental variables to be explained. This will be presented in detail in the following section.

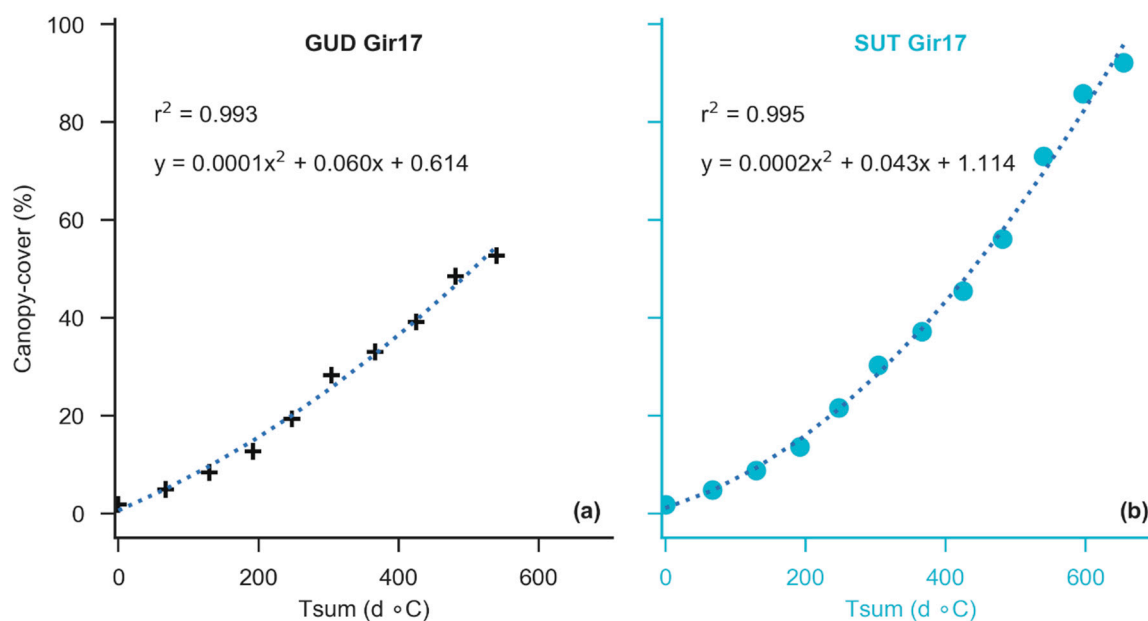


Figure 2. Measured canopy cover (%) as a function of Tsum (d °C) for improved cultivar *Gudene* (GUD) (a) and the local cultivar *Suthalo* (b) during belg-2017 in Gircha. The canopy cover—Tsum curve shows a quadratic relation. The lines in each plot show the quadratic function curve (canopy cover = slope1 \times Tsum² + slope2 \times Tsum + intercept) and the quadratic correlation coefficient (r^2) are shown.

3.1.3. A Further Look at the Plant Height—Temperature Sum Curve

Figure 4b shows a day-by-day data analysis to the dip in the rate of canopy increase marked by the yellow shaded region in Figure 3a for the improved and Figure 3c for the local cultivars.

In Figure 3a,c, we showed that the r^2 was 0.99 for *Gudene* and 0.98 for *Suthalo* cultivars. However, for those highlighted data points in the figures, the r^2 was slightly decreased for *Gudene*, 0.96 and *Suthalo*, 0.93, as shown in Figure 4a,b. In the figures, we marked periods with contrasting environmental features: R1 and R2 with gray and yellow shades, respectively.

We call R1—moisture and R2—radiation limited regimes that influenced the canopy growth during P1. R1 was a dry period without precipitation. In this period, the soil moisture tension increased from 30 kPa to 35 kPa. We also noted that the SW \downarrow was high. In this circumstance, the two potato cultivars responded differently. The growth rate of the improved cultivar—*Gudene*—dropped to 20% of the overall growth rate ($0.03 \text{ cm} \cdot (\text{d } ^\circ\text{C})^{-1}$ compared to $0.14 \text{ cm} \cdot (\text{d } ^\circ\text{C})^{-1}$), while the local cultivar—*Suthalo*—kept growing at 64% of the overall growth rate ($0.06 \text{ cm} \cdot (\text{d } ^\circ\text{C})^{-1}$ compared to $0.09 \text{ cm} \cdot (\text{d } ^\circ\text{C})^{-1}$). Apparently, the improved cultivar was more sensitive to soil moisture than the local cultivar as explained in R1.

In R2, the soil was sufficiently moist (soil water tension decreased to 5 kPa) after having 70 mm of total precipitation. In this period, however, SW \downarrow declined from 20 to nearly 10 $\text{MJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$, which indicated an increase in cloud cover. Interestingly, we found a faster growth in the plant height

per degree-day for *Gudene* ($0.13 \text{ cm} \cdot (\text{d } ^\circ\text{C})^{-1}$, i.e., close to overall) than for the *Suthalo* cultivar ($0.01 \text{ cm} \cdot (\text{d } ^\circ\text{C})^{-1}$, 15% of the overall). In other words, in R2, the *Gudene* cultivar was more efficient in converting the limited radiation to biomass (here, in terms of vertical growth) than the local *Suthalo* cultivar. Note that the local seeds are not renewed for decades, which could influence crop growth rates. Thus, we showed that the canopy growth was strongly correlated with Tsum, but other secondary factors such as moisture availability, radiation intensity and intrinsic factors related to seed quality may influence the canopy growth too.

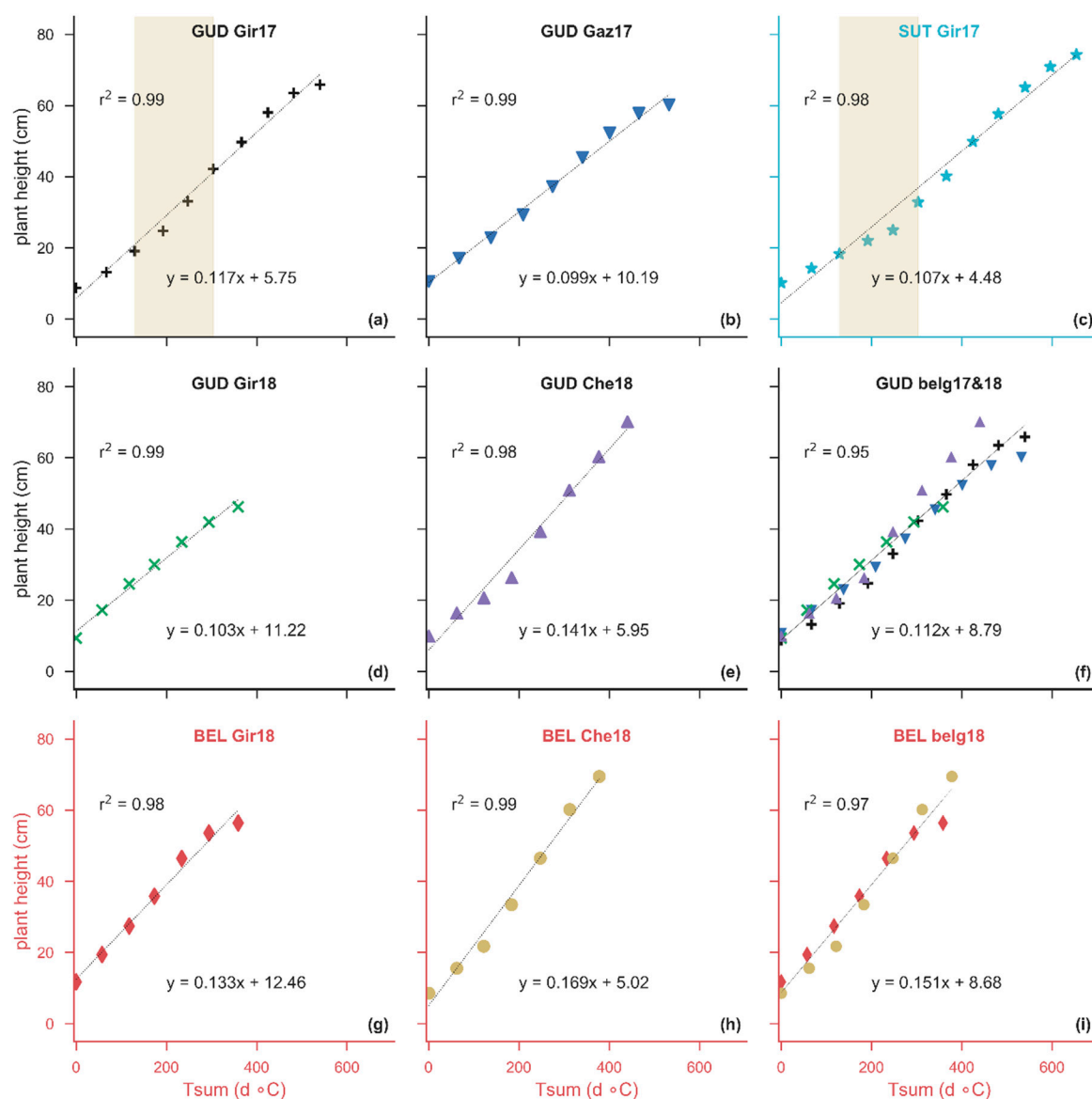


Figure 3. Measured plant height (cm) as a function of Tsum ($\text{d } ^\circ\text{C}$) for *Gudene* (GUD) (a,b,d,e) and *Belete* (BEL) (g,h) and *Suthalo* (SUT) (c) during belg-2017 and belg-2018 represented by suffix 17, and 18, respectively. The experimental farms are Gircha (Gir), Gazesso (Gaz) and Chench (Che). (f) and (i) show combinations (a series of data combinations for a cultivar for all sites and seasons for linear regression calculation only) of *Gudene* (black axes) and *Belete* (red axes) cultivars, respectively. The lines in each plot show the linear function line (plant height = slope \times Tsum + intercept); r^2 shows the linear correlation coefficient; and the yellow shades (a,c) show a period with dips in the rate of increase in plant height—Tsum curves, which will be discussed in the following section.

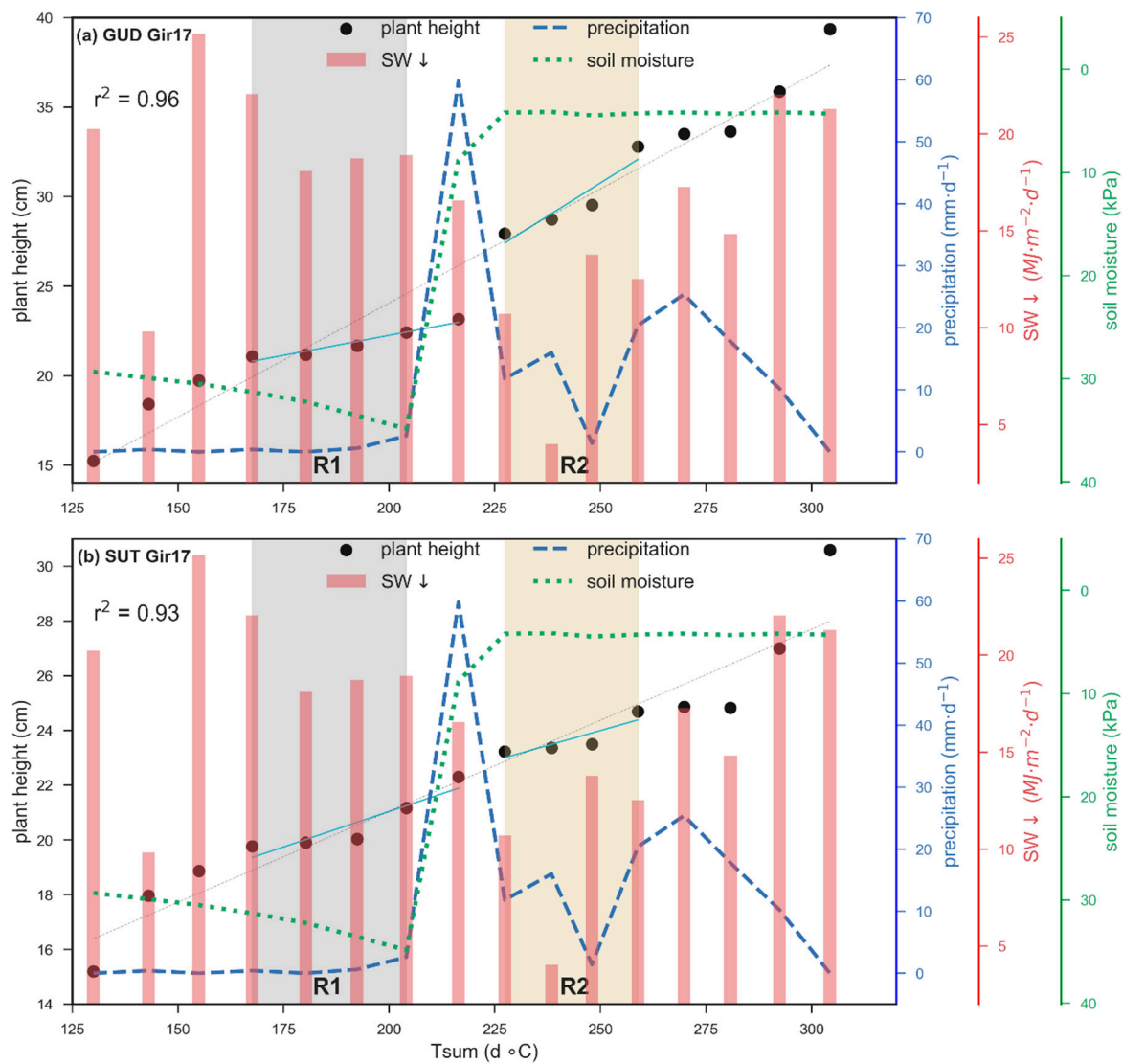


Figure 4. The correlation between Tsum ($d^{\circ}C$) and plant height (cm) for *Gudene* (a) and *Suthalo* (b) cultivars at the Gircha farm in belg-2017 at the times that the dips in the rate of increase in plant height occurred (we zoom into the highlighted spots using daily data) in Figure 3a,c. The daily total precipitation ($mm \cdot d^{-1}$) (blue y-axis), daily total $SW\downarrow$ ($MJ \cdot m^{-2} \cdot d^{-1}$) (red y-axis), and soil moisture tension (ψ) (kPa) (green and inverted y-axis) are shown on the right-side y-axis. The +/bar/line plots' colors correspond to the colors of the y-axis. (R1) shows moisture limited and (R2) radiation limited regimes during this part of P1. The thin gray line shows the linear correlation line. The cyan colored lines in the shaded regions show the linear trend for the moisture and radiation limited periods during P1. The ψ is an average of four records, which are measured at four soil depths (5, 10, 20, and 40 cm) and the averages of the four sensors are reported. Note that soil moisture sensors measure from 200 kPa (dry soil) to 0 kPa (fully saturated soil).

3.2. Response of Yield to Variations in Elevation, Cultivar and Environmental Variables

The previous section studied how the plant height and canopy cover developed during the canopy buildup phase (P1), mainly as a function of Tsum. In this section, we will study how yield and yield traits depended on variations in weather and edaphic variables in P1, P2, and P3 as influenced by topography and cultivar.

3.2.1. Yield Variations with Topography and Among Cultivars

Figure 5 shows how tuber yield varied across cultivars and elevations in the Gamo Highlands. The tuber yield ($\text{t}\cdot\text{ha}^{-1}$) varied significantly among cultivars, with elevation and between *belg* seasons. In *belg*-2018, yields were nearly 50% lower than those in the previous year. *Belg*-2018 was 0.5 to 2.0 °C cooler, $\text{SW}\downarrow$ was 1.7 to 4.6 $\text{MJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ lower, and precipitation was up to ~100 mm more than in *belg*-2017 depending on the location (Table 1). In addition, the soil was > 50% moister and > 1.0 °C cooler than in *belg*-2017 (data not shown). Besides the inter-seasonal differences in the environmental variables, agronomical conditions were different in those years. For instance, Tegecha (2383 m a.s.l.) was the only farm affected by late blight in *belg*-2017, whereas all farms were affected by the disease in *belg*-2018, although the level of the outbreaks differed (based on our observations, but not quantified). It is remarked that the yield variations among cultivars were larger for higher yield farms and that yield variations with elevation were larger for productive cultivars.

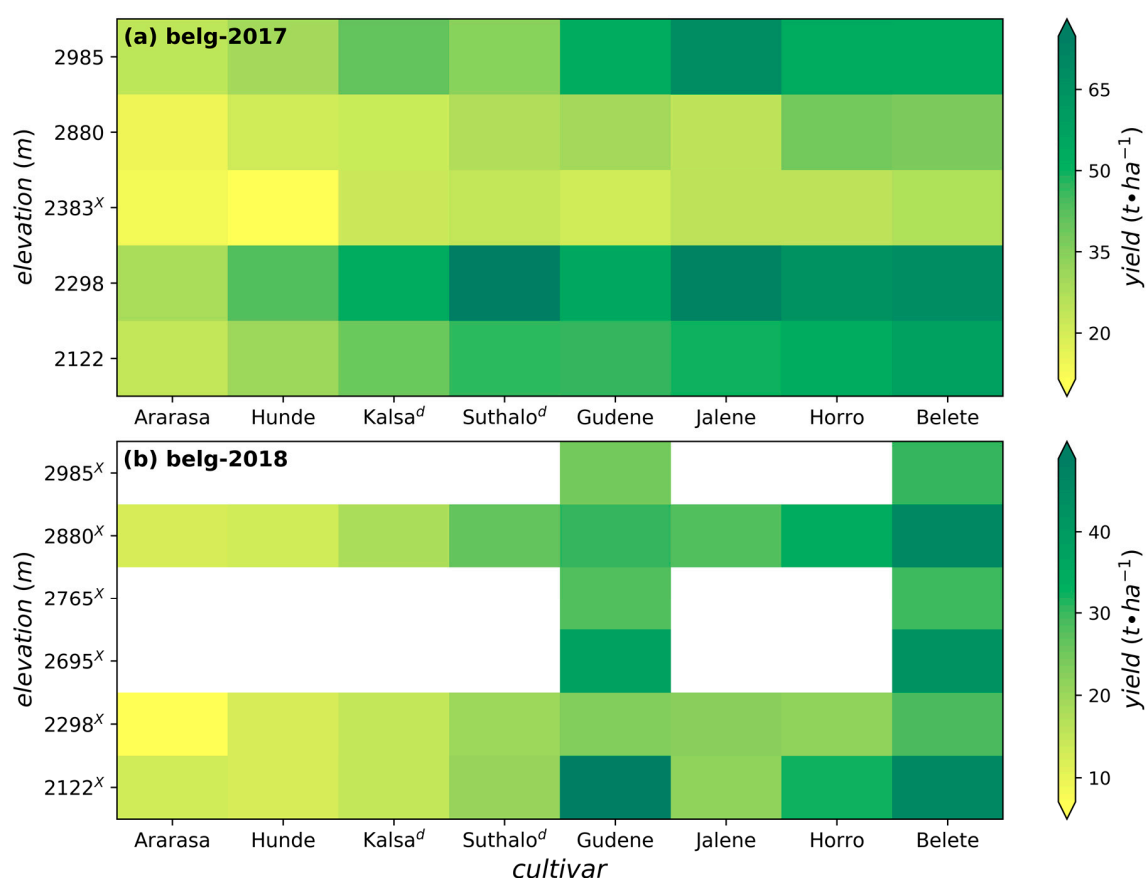


Figure 5. Yield ($\text{t}\cdot\text{ha}^{-1}$) variations as a function of elevation (m) associated with the five farms in *belg*-2017 (a) and six farms at different elevations in *belg*-2018 (b), as shown in Table 1. The x-axis shows the eight potato cultivars planted, in order of increasing mean yield (*belg*-2017). The white spaces in (b) represent missing data. Note that the y-axis are not scaled and each elevation point (not continuous in space) shows an experimental site mentioned in Table 1. Furthermore, the yields during the two *belg* seasons are so different that the scales of the color-bars are different. The x-axis names with a ‘d’ superscript are local cultivars. The ‘x’ superscript in the y-axis show farms affected by diseases.

The figure also shows that there was a large variation in yield among cultivars and among farms at different altitudes. Particularly the elevational variation was difficult to explain and it did not show a clear pattern. This might be associated with differences in soil quality, while variation in crop management and disease intensity may conceal the effects of meteorology on crop growth. Nevertheless, in the following sections, we will attempt to explain the variations in terms of environmental variables.

Figure 5 shows a substantial variation in the observed yield at five farms during *belg*-2017, and at six farms in *belg*-2018. In *belg*-2017, the cultivar mean yield varied from 25 t·ha⁻¹ for *Ararasa* to 60 t·ha⁻¹ for *Belete*. However, in *belg*-2018, the yield and the variation were smaller ranging with yields from 7 t·ha⁻¹ for *Ararasa* and 48 t·ha⁻¹ for *Belete*. It is interesting to note that the relative trend in yields among cultivars in *belg*-2017 was similar as in *belg*-2018. In both years, *Belete* performed best in terms of yield in the Gamo Highlands. However, comparing yields of the cultivars at a farm level showed that *Belete* was not everywhere the best performing cultivar. For example, in the *belg*-2017, *Jalene*, *Horro*, and *Suthalo* showed the highest yield in Gircha (2985 m), Gazesso (2880 m), and Geresse (2298 m), respectively. Thus, this shows that selecting the best performing cultivar, in terms of yield, needs to be location specific. In *belg*-2018, a wetter season, we observed (not quantified) that crop diseases such as late blight affected all farms to a variable extent.

Figure 6 presents the development of the canopy cover growth of the *Gudene* and *Suthalo* cultivars and the (cumulative) incoming radiation in MJ·m⁻² during *belg*-2017. The SW↓ was large during the first part of the growing season (P1), characterized by the absence of thick cloud covers and precipitation. The plant uses the radiation particularly for the canopy buildup and for initializing the tubers. After canopy closure typically at the end of May, the SW↓ decreased by 50%, although the intercepted radiation was larger because the canopy cover was now at its maximum. In this phase (P2 and P3), the plant used the majority of the intercepted light for growing the tubers. In the following sections, we will study how the tuber yield depends on environmental conditions in P2 and P3 and on the choice of cultivar. We hypothesize that radiation intensity and precipitation in P1 are important predictors of tuber number, realized at the end of P1. Subsequently, the harvested tuber fresh weight per plant depends on the environmental conditions in P2 and P3.

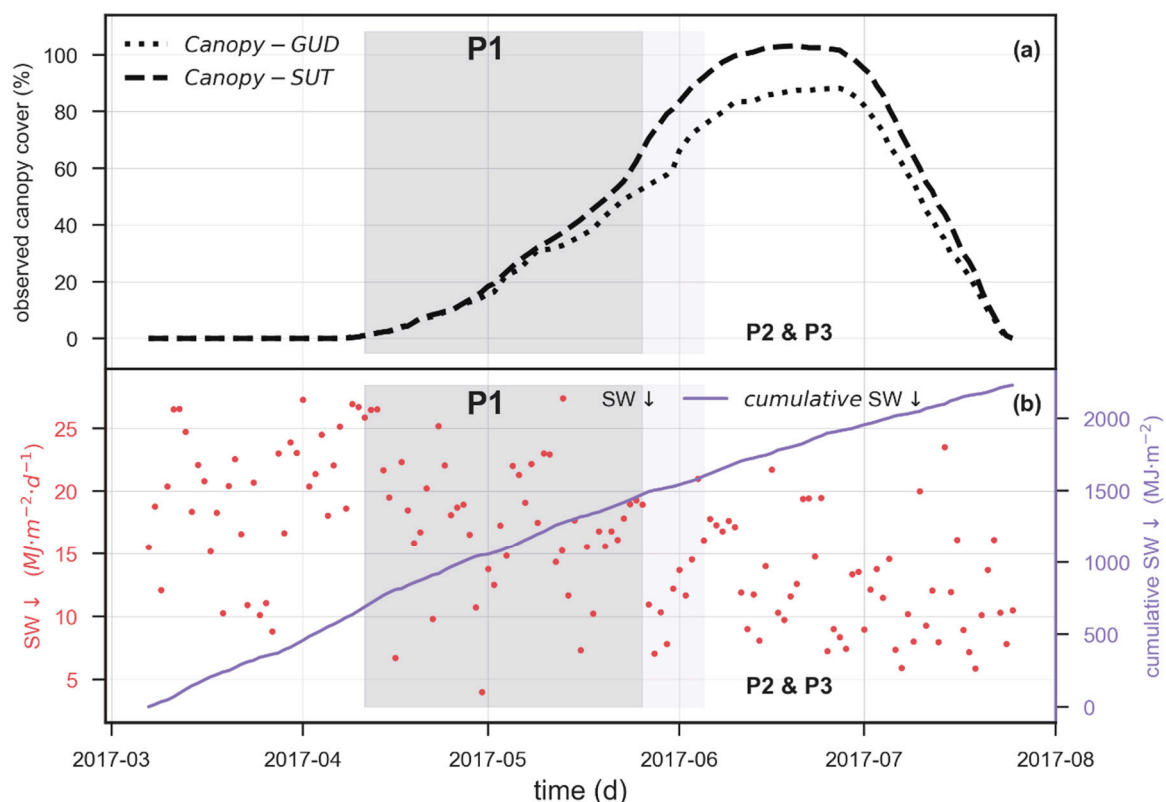


Figure 6. The observed canopy cover (%) (a) and the daily SW↓ (MJ·m⁻²·d⁻¹) (b) during the crop growth period in Gircha farm in *belg*-2017. In (b), the cumulative SW↓ (MJ·m⁻²) is shown on the right-side y-axis. The cultivars are *Gudene* (improved) and *Suthalo* (local). The crop growth phases P1–P3 are slightly different for the two cultivars.

3.2.2. Tuber Number as a Function of Radiation and Precipitation in P1

Figure 7 shows the impact of $SW\downarrow$ and precipitation in P1 on the number of tubers developed at the end of P1 for two cultivars in *belg-2017* and *belg-2018*. For the local (*Suthalo*) cultivar, the tuber number was quite constant at around 20 tubers per plant. From our data, we were unable to find a clear relationship with radiation intensity and precipitation. With around nine tubers per plant for the *Belete* cultivar, the number of tubers was lower than the *Suthalo*. The *Belete* tubers were 1.5 (2018)–1.8 (2017) times heavier than the ones of other cultivars. For the *Belete* cultivar, however, the tuber number decreased from 10.0 to 7.3 per plant with increasing $SW\downarrow$. The larger yield of the *Suthalo* cultivar, as compared to *Ararasa*, *Hunde* and *Kalsa*, was attributed to the larger number of tubers per plant.

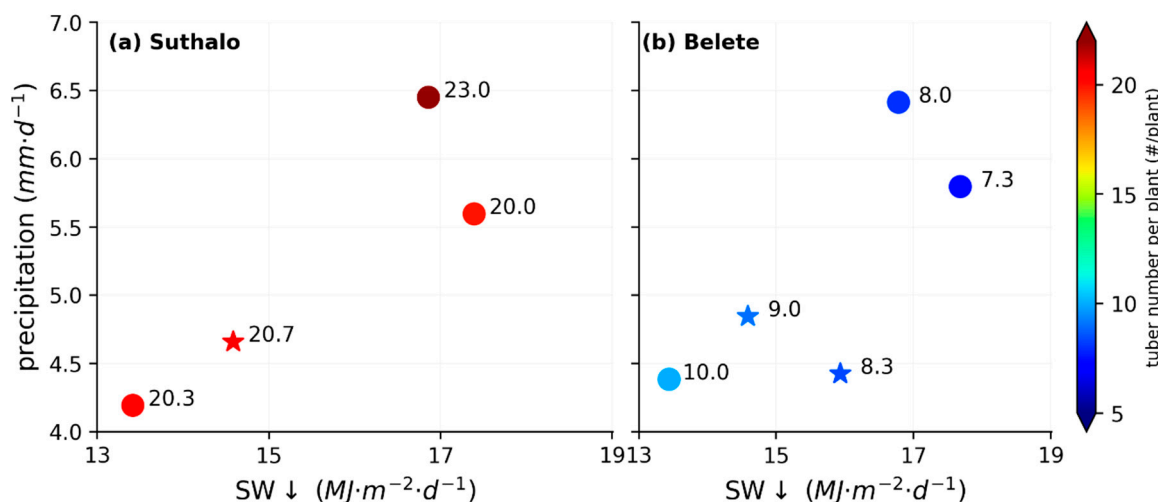


Figure 7. Tuber number per plant (color bar with values shown by the scattered points) at harvest as a function of $SW\downarrow$ (MJ·m⁻²·d⁻¹) and precipitation (mm·d⁻¹) for the local (a) and improved (b) cultivars during *belg-2017* (circles) and *belg-2018* (stars). The $SW\downarrow$ and PPT are mean values in P1.

The lack of a strong and physiologically expected relationship of the tuber number and radiation intensity may perhaps be explained by the high levels of radiation in the area. 10 MJ·m⁻²·d⁻¹ is the equivalent of 230 W·m⁻² or 530 μmol PAR m⁻²·s⁻¹ for 12 h. With a light saturation point near 400 to 500 μmol PAR m⁻²·s⁻¹ [79,80], the actual light intensity was larger than that most of the day, except during sunrise and sunset.

The tuber number per plant itself was generally poorly correlated ($r^2 = 0.11$) with yield, except for the *Suthalo* cultivar (all farms in *belg-2017* and *belg-2018*, $r^2 > 0.84$) (not shown here).

3.2.3. Number of Branches and Yield

Figure 8 shows that the number of branches had quite a strong relationship with total yield, across all cultivars, at least in *belg-2017*. In *belg-2017*, the number of branches had a wider range than in *belg-2018*, as did the yield. In all experiments, the number of plants per m² was the same (Section 2.2). The relationship may be explained by better light interception by the plant with more branches, suggesting that the number of plants per m² could be increased. In *belg-2018*, there were a number of plots with less than six branches per plant, which impaired the otherwise positive relationship. Note that, in Section 3.2.1, we showed that the seasonal climates are significantly different in both years, which can influence the branch numbers (Table 1). However, the number of branches might also be a reflection of physiological age of the seed tubers. The seed tubers in *belg-2017* were from different origins whereas the seed tubers in *belg-2018* were from the same origin.

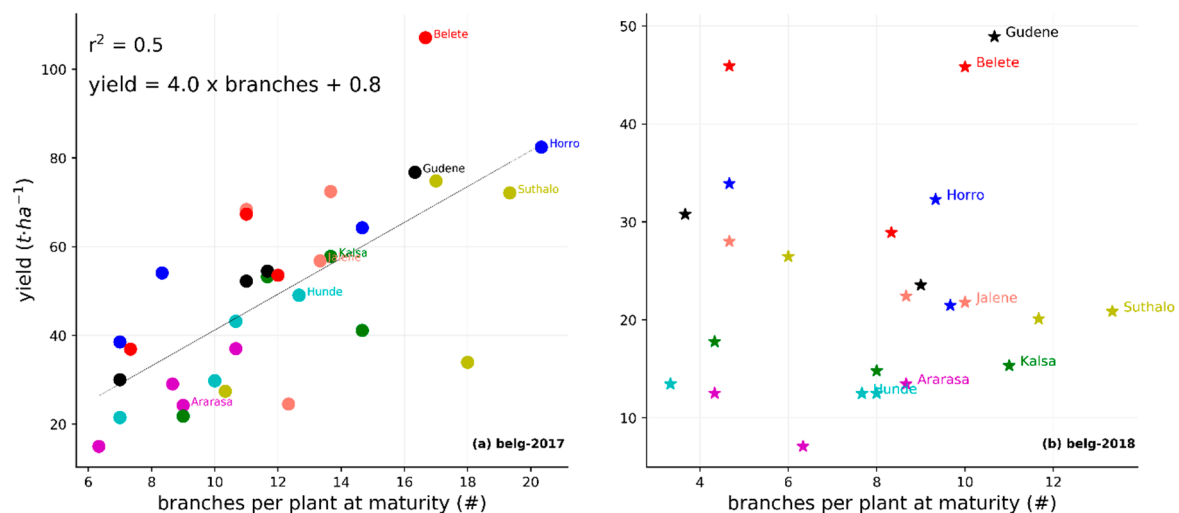


Figure 8. Variations in the observed yield ($\text{t}\cdot\text{ha}^{-1}$) for eight cultivars as a function of total number of branches at maturity (#). The colors represent cultivars in four locations in *belg*-2017 (a) and six locations in *belg*-2018 (b). The linear coefficient of correlation (r^2) and the linear regression equation are shown in (a); and no clear correlation is observed in (b). Note that scales along x and y-axes are different for both panels.

3.2.4. Days to Maturity and Yield

Figure 9 shows the yield as a function of days taken to crop maturity (Section 2.4.1). The figure shows a large variation in the number of days to maturity and tuber yield. In *belg*-2017 (Figure 9a), the results indicate an optimum yield (at around 100 days), which agrees with [76]. This trend was consistent for all cultivars. The highest yields were attained in the lower elevation areas (Gerese and Derashe), where the number of days to maturity was between 95 to 105 days (potato can be harvested in 90 days, and it can take up to 150 days in cooler climates such as northern Europe [28]). The Tegecha site was also in this range, but yields were affected by diseases in 2017. At lower elevations, the temperature was too high and the foliage grew fast, while it did not result in bulking [81]. At higher elevations, the growth was slower, the onset of tuber formation occurred later, which eventually increases yield [50]. In addition to the meteorology, soil moisture and nutrient availability can play key roles in determining the time to maturity and yield across farms, but we do not have these data available. In *belg*-2018 (Figure 9b), the yield and days to maturity data were less variable and would fit into the lower left part of Figure 9a. As such, the growing conditions in *belg*-2018 were much different from the ones in *belg*-2017, but the results did not contradict the results of *belg*-2017.

3.2.5. Tuber Fresh Weight as a Function of Environmental Variables in P2 and P3

Figure 10 presents the tuber fresh weight per plant as a function of $\text{SW}\downarrow$, T_{mean} and soil moisture tension (ψ) in *belg*-2017 and *belg*-2018. The environmental variables did not show a clear correlation with tuber fresh weight in *belg*-2018. However, in *belg*-2017, the tuber fresh weight at harvest showed an increasing trend with $\text{SW}\downarrow$ and ψ , and a decreasing trend with T_{mean} . The following explanation is about *belg*-2017.

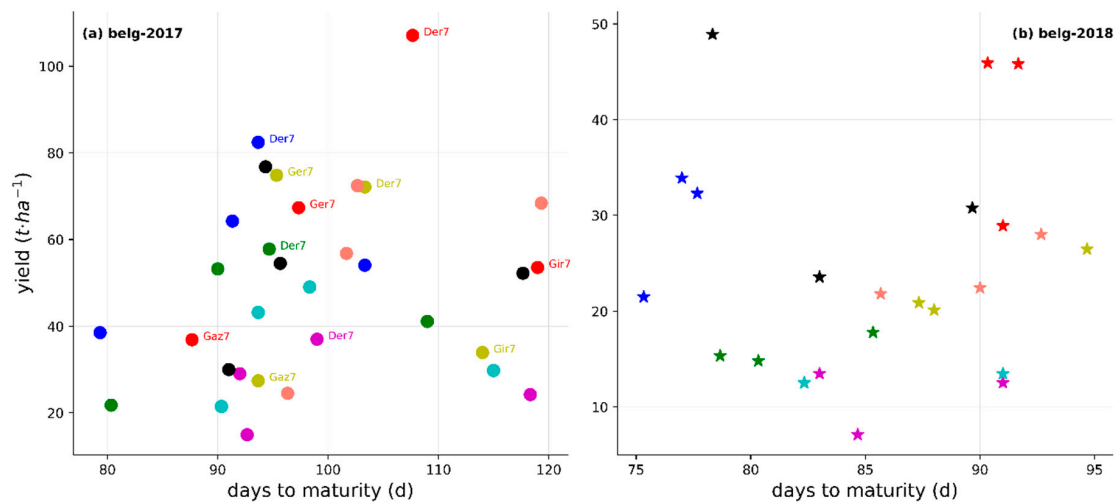


Figure 9. Variations in the observed yield ($\text{t}\cdot\text{ha}^{-1}$) for eight cultivars as a function of days to crop maturity (d). The colors represent cultivars in four locations (Gaz7—Gazesso, Ger7—Geresse, Der7—Derashe, and Gir7—Gircha) in *belg*-2017 (a) and six locations in *belg*-2018 (b). Note that x and y-axes ranges are different for both panels; and the colors (e.g., red dots and line—*Belete* and yellow dots and line—*Suthalo*) represent a cultivar in different farms.

The tuber fresh weight increased from 200–900 g/plant at $10.5 \text{ MJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ in Tegecha (*belg*-2017) to 800–2100 g/plant at $13 \text{ MJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ in Gircha in *belg*-2017. It is interesting to note that the variations (in terms of the standard deviations) in the tuber fresh weight per plant among cultivars increased significantly (from 500 to 1000 g/plant) as the $\text{SW}\downarrow$ increased. However, the 2–4 fold increase in tuber fresh weight seems large relative to the 30% increase in radiation. Therefore, we are careful at explaining the correlation as a causal relationship. The relation found may also be explained by warmer weather and decreased soil moisture in Tegecha [29]. It should also be noted that the Tegecha farm was affected by diseases (Figure 5).

Tuber fresh weight decreased from nearly 1400 g/plant with T_{mean} of $\sim 11.5^\circ\text{C}$ in Gircha to 500 g/plant with T_{mean} of 17°C in Tegecha in *belg*-2017. This is remarkable, because the optimal temperature for potato growth is often considered to be near 15 to 18°C [46]. However, the yield depends on rate and duration of growth, where temperature near the optimum mainly affects the rate of growth. Gazesso is only slightly warmer and wetter than Gircha in *belg*-2017 (Table 1). These are indications that $\text{SW}\downarrow$ and T_{mean} are probably not dominant drivers of the tuber fresh weight in the Gamo Highlands and the relationships are induced by other variables.

Tegecha also shapes the soil moisture—tuber fresh weight space. At the highest soil moisture tension (the driest soil), it has the lowest tuber fresh weight. Gircha, with the highest $\text{SW}\downarrow$, coolest temperature and moderate soil moisture (as compared to Tegecha and Gazesso) had the highest tuber fresh weight per plant. However, considering that the soil moisture and temperature are positively correlated and both are negatively correlated with temperature, it is difficult to attribute the variations in tuber fresh weight to the environmental variables. Interestingly, the difference in tuber weight among cultivars was consistent (*Belete* and *Ararasa* were the highest and lowest, respectively in both years) among *belg* seasons.

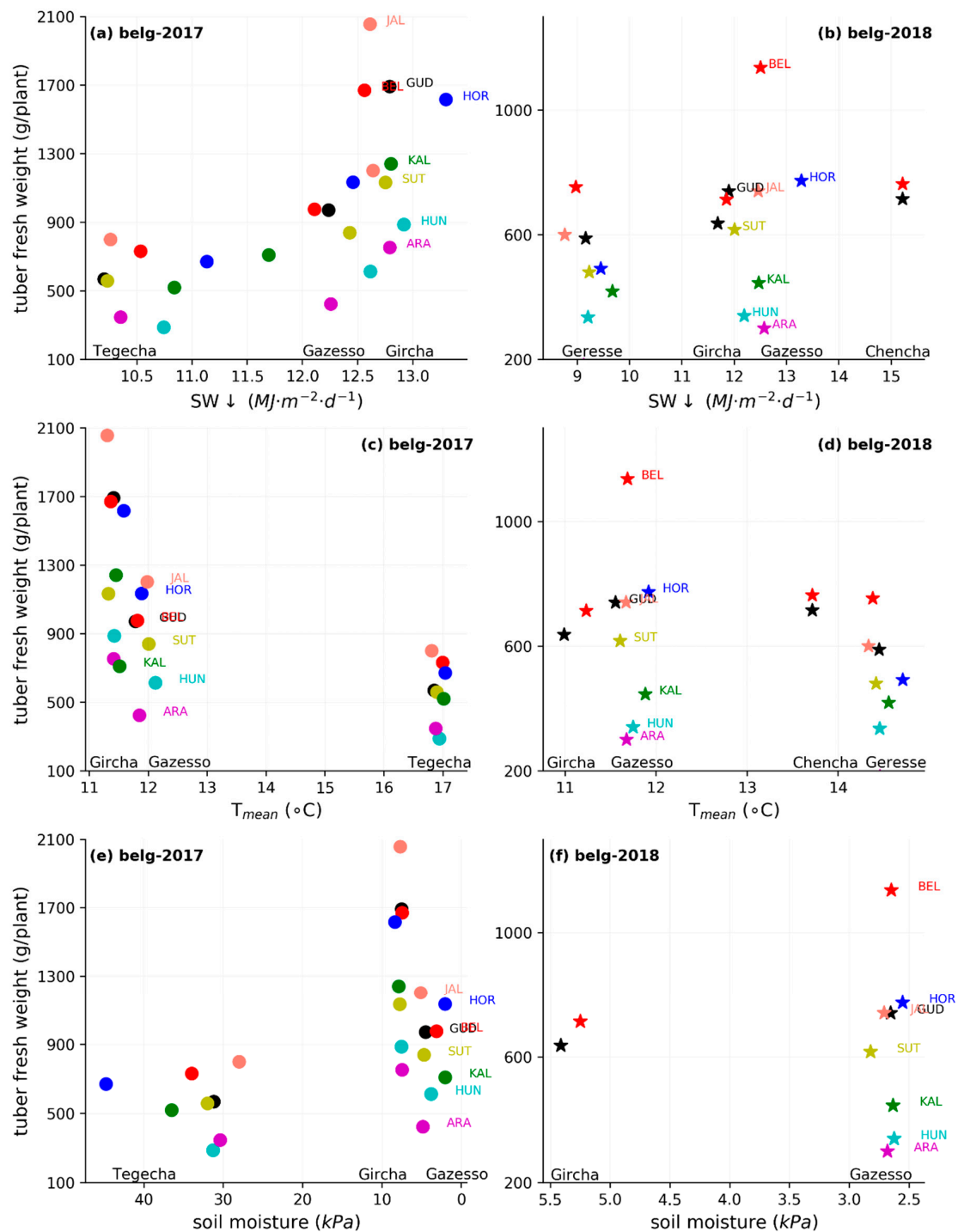


Figure 10. Tuber fresh weight gram per plant (g/plant) at harvest as a function of mean $SW \downarrow$ ($MJ \cdot m^{-2} \cdot d^{-1}$) (upper row—a, b), T_{mean} ($^{\circ}C$) (middle row—c, d), and soil moisture tension (ψ) (kPa) (lower row—e, f). The left panels show *belg-2017* and the right panels indicate *belg-2018*. The cultivars were *Ararasa*—ARA, *Hunde*—HUN, *Suthalo*—SUT, *Kalsa*—KAL, *Horro*—HOR, *Belete*—BEL, *Gudene*—GUD, and *Jalene*—JAL as marked in colors. The weather station/farm names are indicated below the corresponding dataset shown in the scattered dots. The $SW \downarrow$, T_{mean} and ψ are average values in the period from P2 to P3. Note that from farms in *belg-2017* and *belg-2018*, those farms with available $SW \downarrow$, T_{mean} , and ψ data records are included here. Note that the mean value of ψ at four soil depths (5, 10, 20, and 40 cm) are reported; and $\psi = 200$ kPa is a fully dry soil and $\psi = 0$ kPa means a fully saturated soil.

3.2.6. Partitioning of Dry Matter over Parts of the Plant

The harvest index (Section 2.4.3) indicates the percentage of the produced dry matter allocated to the tubers. In western countries, the HI is relatively constant at around 75% and depends on cultivar traits and growing conditions.

In our experiments, we estimated the total produced dry matter from the cumulative amount of intercepted radiation. Figure 6 shows that the canopy cover for the local cultivar and the improved one, both grown at Gircha, developed similarly. However, the yield was significantly different for the two cultivars, resulting in a harvest index of 44% for *Suthalo* and of 80% for *Gudene*. This shows that *Gudene* invested more of its dry matter in the tubers than the *Suthalo* cultivar, and that choosing the right cultivar has an important effect on the yield.

4. Discussion

In this paper, we analyzed a large number of observations of potato plant growth and yield for dependency on environmental conditions and physiological effects, aiming to find out if potato behaves similarly in Ethiopia as it does in temperate climate regions. Here, we will discuss the obtained results in relation to results from experiments in the western world, to highlight aspects that should be investigated in more detail in future experiments.

Research question 1: How does canopy growth vary with environmental variables in P1 across elevations, among potato cultivars, and between seasons?

The temperature sum turned out to be a strong predictor of canopy cover and plant height in the canopy buildup phase (P1, shown in Figure 1), with explained variances (r^2) > 0.90 and relatively similar slopes across cultivars and years (from Figure 2 to Figure 4). Haverkort [13] also explained canopy cover as a linear function of Tsum during P1.

However, the growth rates appeared to also depend on cultivar and growing conditions, specifically light intensity and soil moisture [29]. The local *Suthalo* cultivar appeared less sensitive to drought than the improved cultivar *Gudene* (Figure 4). Ethiopian farmers indeed mention that local cultivars are more drought resistant [12]; Kolech et al. [57] also mentioned that some of the local cultivars in Ethiopia are drought tolerant. In contrast, the canopy growth rate of *Gudene* was less sensitive to limited radiation. This suggests that the water and radiation use efficiency (RUE) of the two cultivars may be different. We cannot rule out that seed quality differed among experiments. The RUE of potato cultivars is between 1.07 and 2.24 g per MJ of intercepted radiation depending on cultivar and light intensity [72–74]. These findings are as expected [51,82] and we do not recommend further research in the field of response of canopy cover and plant height to meteorological conditions. However, we do recommend further research into the performance of different cultivars under meteorologically or nutrient-limiting conditions with experiments under field conditions or in controlled chambers, and with controlled seed quality. It is also worthwhile to investigate the RUE of the local and improved cultivars for a better understanding of the Tsum and canopy growth relations.

Research question 2: How does yield depend on physiological crop characteristics, such as number of tubers, number of branches, days to maturity, cultivar, and on meteorologically dependent variables, such as intercepted radiation and temperature?

Yield and yield traits showed significant variations among farms, cultivars and *belg* seasons. There were consistent differences (Figure 2) between the average yields at farms located at different elevations. Elevation itself, however, did not seem a strong predictor (Figure 5). We anticipate that soil fertility, management or climate may explain the differences between farms.

Cultivar was an important predictor of yield variation (Figure 3) across all farms and years. Even though some farms and cultivars had a higher overall yield, there was no single farm that performed best with all cultivars and there was no single cultivar, which performed best at all farms. Apparently, a cultivar's performance is specific for the conditions at a farm.

The number of tubers per plant did not vary logically with radiation intensity and precipitation (Figure 7). However, the range of those variables was small and the variables were probably not

limiting plant growth. The average number of tubers per plant across all farms and cultivars was 14 in *belg*-2017 and 10 in *belg*-2018. Most cultivars had tuber numbers close to the average, except *Ararasa* and *Hunde* in *belg*-2018 (about half) and *Suthalo* (about double in both years). The tuber number was not a predictor of yield for most cultivars, because the weight of individual tubers varied among cultivars. Consequently, the number of tubers per plant does not seem to be a variable of interest for further research. Similarly, Onder et al. [83] showed that the tuber number per plant was not affected by irrigation, but the mean tuber weight and tuber yield increased quite strongly with the irrigation level. Haverkort et al. [84] found that the tuber number per plant increased from 9 to 21 per plant when precipitation increased from 0.5 to 3 mm·d⁻¹ during the first 40 days after planting. The authors also showed that a further increase in precipitation did not lead to an additional increase in the number of tubers per plant. As the lower range of precipitation in our study was 4.0 mm·d⁻¹ (Figure 7), it appears that our results are in line with those of Haverkort et al. [84].

The number of branches per plant appeared to be a medium strong predictor of tuber yield ($r^2 = 0.5$), while the plant density was identical in all experiments (Figure 8a). In irrigation experiments, Yuan et al. [85] showed that increases in irrigation are associated with a larger number of branches ($r^2 > 0.8$) and ultimately increased tuber yield. Taye et al. [65] also found that the number of branches positively affected light absorption; and tuber yield for a tuber crop (*Plectranthus edulis*, a crop comparable to potato, *Solanum tuberosum* L.) in Ethiopia. The result suggests that radiation interception was an important constraint and that light interception was not maximal yet in the conditions during the experiment.

In *belg*-2017, the yield was optimal at around 100 days to maturity of the plant (Figure 9) [28]. This occurred predominantly at the somewhat lower farms (~2200 m a.s.l.). The highest yields in Derashe can be associated with early tuberization, resulting in an extended period of tuber growth and/or increased rate of tuber bulking [86]. At higher elevation (e.g., at Gircha), the growth was slower. This can be related to a delay in the onset of tuber formation, which extended the crop maturation period, but decreased yield [50]. The more humid conditions also make the crop susceptible to diseases [38]. At farms at even lower elevations, the temperatures were so high that the crop grew very fast, but with decreased tuberization rate [81]. These results are very similar to the ones we found in Minda et al. [31], where we explained the optimum yield at mid-levels in terms of radiation and soil moisture. With increasing elevation, the temperature becomes closer to the optimum temperature for potato, and the soil becomes moister. The lower temperatures and moister conditions increase the duration of leaf wetness, which is an important predictor for the occurrence of diseases like late blight. At mid-levels, the potato crop finds an optimum between those effects. It is interesting to note that cultivars have different responses to radiation and soil moisture limitations in P1 (Section 3.1.3). Although this may be an interesting explanation, we need to be careful of being too resolute, since the physiological age and size of the seed tubers may also cause differences in growth and yield. We also observed that the optimal number of days to maturity was different for each cultivar. We do not have detailed, cultivar-specific data about the growth of the tubers during P2 and P3, but this would definitely be worth further research.

Additionally, we may have found evidence that an increase in radiation intensity from 10 to 13 MJ·m⁻²·d⁻¹ in P2 and P3 increased yield from ~500 to ~1300 g/plant (Figure 10). However, these data were sparse and the range in radiation intensity was small. The suggestion that radiation interception was not saturated is remarkable, because Figure 6 shows that the canopy cover was near 100% at the end of P1. However, the radiation intensities are strong enough in this tropical environment for lower leaf levels to still intercept significant amounts of radiation. This suggests that LAI may be a better variable to express radiation interception and photosynthesis rates. Allen and Scott [50] also showed that the tuber dry weight increased nearly linearly from ~500 to 1000 g/plant as the total intercepted radiation increased from 500 to 1500 MJ·m⁻²·season⁻¹. In their experiment, the total radiation interception depended on the canopy cover or the LAI [50]. Figure 10 also showed that tuber weight per plant increased with soil moisture tension.

Curiously, we found that the yield decreases with temperature from 11 to 18 °C, which is often mentioned as the optimal temperature for potato growth. Haverkort et al. [13] explained that the optimal daily T_{mean} for tuber production is 18 °C and that tuber fresh weight decreases nearly linearly below and above that temperature. Van Dam et al. [23] found that the tuber dry weight was the highest at 15 °C for both Spunta and Désirée cultivars. Timlin et al. [87] explained that the tuber dry weight and temperature showed a quadratic relation, in which the optimal tuber weight is attained at different temperatures (17–22 °C), depending on the number of harvest days taken. Figure 10 shows that in our situation, the fresh tuber weight (g/plant) was the highest when $T_{\text{mean}} < 14$ °C and $\text{SW}\downarrow > 16 \text{ MJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ as opposed to Van Dam et al. [23] and Timlin et al. [87]. This contrasting result gives us the impression that temperature is not the real limiting factor determining the tuber fresh weight in our experiments. This underlines the importance of explaining the results carefully and designing a new field campaign, which enables us to disentangle soil, potato physiology, and meteorological factors.

With the available data, we could quantify the harvest index for two cultivars at Gircha. They appeared to be very different, 44% and 80%. This again shows that cultivars can behave very differently even though they are exposed to the same environmental and management conditions.

We did not find evidence that potato is behaving differently in Ethiopia than in the temperate climates. However, the temperature is rather constant in time and relatively close to the optimal temperature. Close to the equator and in the *belg* season, radiation intensities are large and probably only limiting early in the morning and late in the afternoon. LAI, however, may affect the radiation absorption.

We have collected abundant potato growth data, distributed over farms and cultivars. Only plant height and canopy cover were monitored during the growing season. The yield, tuber number and tuber weight were only measured at the end of the growing season. Thus, during P2 and P3, we had more predictor variables than response variables. In the future, we advise to use a simpler experimental structure, to better control seed quality, but to increase the frequency of the measurements during P2 and P3, particularly with respect to the below ground growth variables. Furthermore, we recommend to investigate the sensitivities of each cultivar to radiation, soil moisture and temperature and these variables should be monitored in detail during the entire growing season and different climatological years. Above/below ground yield traits (total dry matter, tuber number and tuber weight) should be measured frequently during the growing season. Because these require a large effort, the number of cultivars used should be reduced in favor of the number of replications.

5. Conclusions

Based on the analysis of field trials with eight potato cultivars in six locations and during two seasons, our conclusions on the relationships of environmental variables and potato dynamics at different phases are the following.

During the canopy buildup phase (P1), the temperature sum is a strong predictor of plant height and canopy cover of potato in Ethiopia. There are only small variations in growth rate among cultivars, but cultivars appear to have diverging sensitivities to soil moisture and radiation limitations.

Tuber yield is largely determined by growing conditions in the maximum cover phase (P2), and the canopy decline phase (P3), because the tuber number (initiated in P1) is not a predictor of total yield. The yield is quite variable between farms at different elevations and between cultivars. The number of branches and radiation intensity appear to positively affect the yield, but the underlying processes remain to be quantified and understood. Possibly, light interception and photosynthesis rates are enhanced in plants with more branches. Leaf Area Index may be an important constraint and it should be measured in future experiments.

The choice of cultivar has a large effect on yield. Still no single cultivar had the largest yield at all farms. This suggests that cultivars have different sensitivities to environmental conditions. It may follow that cultivars have a specific optimal elevation zone to grow in.

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