



A growth scale for the phasic development of common buckwheat

Journal:	<i>Acta Agriculturae Scandinavica, Section B - Plant Soil Science</i>
Manuscript ID:	SAGB-2015-0166.R2
Manuscript Type:	Original Article
Keywords:	coordinated development, <i>Fagopyrum esculentum</i> , growth stage, sowing date, thermal time

SCHOLARONE™
Manuscripts

A growth scale for the phasic development of common buckwheat

Iduna Arduini^{1*}, Alessandro Masoni¹ and Marco Mariotti²

Department of Agriculture, Food and Environment, University of Pisa, Via del Borghetto 80, I-56124 PISA, Italy

Department of Veterinary Sciences, University of Pisa, Viale delle Piagge 2, I-56124 PISA, Italy

*Corresponding author. E-mail: iduna.arduini@unipi.it; Tel: +390502218902

For Peer Review Only

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

For Peer Review Only

A growth scale for the phasic development of common buckwheat

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25

For Peer Review Only

1 Growth scales give a standardized definition of crop development and increase the understanding
2 among researchers and growers. In the present research we defined a growth scale for the phasic
3 development of common buckwheat that was mainly based on a sequence of easily recognizable
4 changes occurring on the first and the terminal cluster of inflorescences formed on the main stem.
5 Observations were carried out on plants grown in two years throughout spring. In an attempt to
6 uniform the duration of phasic development across sowing dates, the length of phases and sub-
7 phases was calculated in days and in thermal time using nine combinations of cardinal
8 temperatures. A sequence of stages and various patterns of coordinated development were
9 maintained throughout all sowings and years. In specific: i) the first inflorescence became visible
10 after three true leaves had fully expanded on the main stem; ii) flowering reached the terminal
11 inflorescence cluster before full-sized green fruits became visible in the first inflorescence, and iii)
12 fruit ripening in the whole plant ended within two weeks of the end of ripening in the oldest
13 inflorescence. Plant size was increased with the delay of sowing, and the length of the growth cycle
14 was by approximately 400°Cd longer when plants experienced a day length longer than 15 h. This
15 changed the correspondence between flowering and ripening stages, so that full flowering was
16 associated with the development of green fruits in the first inflorescence when the cycle was short,
17 but with their development in the terminal cluster when it was long. Trends in grain yield did not
18 correspond to those in plant size and phase length. ~~It is our belief~~We are confident that this growth
19 scale will be a valuable tool for following the progress of buckwheat development and to predict
20 growth patterns and harvest time in response to temperature and photoperiod.

21
22 **Keywords:** coordinated development; *Fagopyrum esculentum*; growth stage; sowing date; thermal
23 time

24
25 **Abbreviations:** SD, sowing date; +INF, first inflorescence; TINF, terminal cluster of
26 inflorescences at the main stem apex; GDD, growing degree days.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
601
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Introduction

Common buckwheat (*Fagopyrum esculentum* Moench.), hereafter buckwheat, is a dicotyledonous annual herb of the family *Polygonaceae*. It is an ancient crop from Asia that was widely cultivated throughout Europe and North America up to the 19th century, but was later abandoned, especially in western Europe (Campbell 1997). Today there is a renewed interest in this crop worldwide, due to its nutritional quality for humans and livestock. Buckwheat plants contain proteins with a high biological value, the flavonoid rutin, polysaccharides, dietary fibres, lipids, polyphenols, and micronutrients (minerals and vitamins) (Ahmed et al. 2014). In agroecosystems, this species has an additional value, as it requires very low fertiliser inputs, it helps to suppress weeds, and it also offers a substantial late summer feed source for insects and honeybees (Amelchanka et al. 2010).

In most buckwheat ecotypes and cultivars, growth is indeterminate and the main stem consists of a highly variable number of metamers, 5-30 according to Cawoy et al. (2009), each giving one leaf and one axillary bud per node. Plants produce a lot of flowers, but only a low proportion develop into dark-hulled triangular achenes (Halbrecq et al. 2005). Flower and fruit development are sequential, both within and between inflorescences, and the duration of corresponding phases is highly variable depending on the number of reproductive structures produced by the plant, which, in turn, is greatly influenced by environmental conditions (Taylor & Obendorf 2001; Michiyama et al. 2005). The morphology of buckwheat plants and the progress of flower development and achene ripening have been described in detail (Marshall & Pomeranz 1982; Funatsuki et al. 2000; Quinet et al. 2004; Halbrecq et al. 2005; Cawoy et al. 2009). However, to the best of our knowledge, the definition of a growth scale that describes buckwheat phasic development through a sequence of stable and easily recognizable growth stages is lacking (Meier 2001). A primary reason is the great morphological plasticity in response to growth conditions, which is increased by the high level of genetic heterogeneity in most cultivars (Funatsuki et al. 2000; Michiyama et al. 2007).

1 Moreover, the timing of buckwheat phasic development has mainly been described in days or
2 weeks after sowing (Campbell 1997; Funatsuki et al. 2000; Taylor & Obendorf 2001; Quinet et al.
3 2004; Halbrech et al. 2005; Cawoy et al. 2009; Baumgertel et al. 2010; Gupta et al. 2011; Ahmed et
4 al. 2014), which does not take into account the well-known influence of temperature and day length
5 on this crop. Only a few attempts have related phasic development with thermal time and none with
6 day length. Seed maturation required approximately 1200°Cd in USA at 47° north latitude, with a
7 base temperature of 5°C (Edwardson 1995), and 700°Cd in Slovenia, with a base temperature of
8 10°C (Kajfež-Bogataj 1988). According to Cha et al. (1989), Korean buckwheat required
9 approximately 1100°Cd to reach optimum seed harvest when planted on July 11, but only 950-
10 1000°Cd when planted 10 to 20 days later.

11 The spread of buckwheat cultivation in different climatic regions entails substantial shifts from
12 conventional sowing dates, thus exposing plants to novel combinations of day length and
13 temperature. Therefore, an unambiguous definition of growth stages and an estimate of the duration
14 of development phases, as much as possible independent of local conditions, are of crucial interest.

15 The aim of the present study is to give a standardized definition of the chronological sequence of
16 growth stages that occur in buckwheat independently of sowing date. The influence of sowing date
17 on growth habit was evaluated through changes in plant height, number of inflorescences and grain
18 yield. In addition, in order to define a general model for the timing of phasic development, the
19 duration of phases was calculated in days and in thermal time, by testing several combinations of
20 cardinal temperatures.

21 **Material and methods**

22 *Environmental conditions*

23 The research was carried out in 2013 and 2014 at the Department of Agriculture, Food and
24 Environment of the University of Pisa (Italy, 43°40'N, 10°19'E), at a distance of approximately 4
25 km from the sea and 6 m above sea level. Photoperiod ranges from 8 h 46' to 15 h 14' and the day
26 length exceeds 15 h from 1st June to 13 July. Mean annual maximum and minimum daily air

1 temperatures calculated from 1878 to 2012 are 20.2 and 9.5°C, respectively, and mean rainfall is
2 989 mm per year. According to Köppen (1936), the climate is classified as Csa, humid temperate
3 with dry and hot summers. Over the research seasons (21 March – 21 September) of the two years,
4 the mean maximum and minimum daily air temperatures were approximately 25.5 and 12.5°C,
5 respectively, and were both by 0.5°C lower in 2014 than in 2013. Rainfall over the same period was
6 markedly higher in 2014, 434 mm compared to 316 mm.

7 *Treatments*

8 The European buckwheat variety ‘Lileja’ was used, because of its stabile yield, and its
9 widespread cultivation throughout Europe (Brunori et al. 2006; Goeritz et al. 2009; Kälber et al.
10 2012). Plants were collected from field trials and, in 2014, also from PVC pots (30 cm diameter, 35
11 cm height) that were filled with the same soil of the field trial. The pot experiment was established
12 to follow more frequently and precisely the progress of phenological development on distinct
13 tagged plants. Main soil physical and chemical properties were 51.1% sand (2 mm > Ø > 0.05 mm),
14 38.6% silt (0.05 mm > Ø > 0.002 mm), 10.3% clay (Ø < 0.002 mm), 8.2 pH (H₂O), 22.6 g kg⁻¹
15 organic matter (Walkley and Black method); 14.2 g kg⁻¹ total CaCO₃ (Scheibler method), 0.91 g kg⁻¹
16 total nitrogen (Kjeldhal method), 10.2 mg kg⁻¹ available P (Olsen method), 162.4 mg kg⁻¹
17 available K (ammonium acetate test method). Before tillage and at pot filling, phosphorous fertilizer
18 was applied at a rate of 44 kg P ha⁻¹ as triple superphosphate, and potassium fertilizer at a rate of 83
19 kg K ha⁻¹ as K₂SO₄. Nitrogen fertilizer was applied as urea, at a rate of 30 kg N ha⁻¹, just before
20 seeding. Pots were placed in the open air and, throughout the entire experiment, they were regularly
21 watered and kept free of weeds by hand hoeing.

22 In the field, 200 viable seeds m⁻² were sown at 15-cm row spacing in 3x5 m plots in both years.
23 In pots, 20 seeds were sown and then thinned to 10 seedlings at the cotyledon stage, which
24 corresponded to a final density of approximately 140 plants m⁻². In 2013 sowing dates (SD) were 8
25 April (SD IIa) and 27 May (SD IVa), while in 2014 five sowing dates were performed at 20-day

1 intervals throughout spring: SD I, 24 March; SD II, 14 April; SD III, 5 May; SD IV, 26 May, and
2 SD V, 17 June. For each sowing date five pots and a total of 50 plants were arranged.

3 *Data collection*

4 Weather data, daily minimum and maximum temperatures and rainfall, were collected from a
5 weather station located close to the experimental site.

6 In the field, the phasic development and the timing of the growth stages were recorded on 10
7 plants, collected at one-week intervals after the complete emission of the first true leaf. In pots, all
8 plants were observed at one to three-day intervals starting from emergence. A stage was considered
9 achieved when at least six out of ten plants had reached the specific stage in question. When
10 existing, the terminology previously reported for buckwheat was used for plant descriptions
11 (Funatsuki et al. 2000; Quinet et al. 2004; Halbrech et al. 2005; Michiyama et al. 2007). The main
12 stem nodes were numbered acropetally (N1, N2, etc.), starting from the node producing the first
13 true leaf (Figure 1). The cotyledon node was indicated as N0. Leaves were numbered according to
14 corresponding nodes, as L1, L2 and so on. The first inflorescence was indicated as +INF.
15 Uppermost racemes, whose subtending leaves were shorter than 1 cm, were considered together as a
16 terminal inflorescence cluster (TINF), and the most basal node of this cluster was taken as the
17 origin.

18 In the scale, we included only growth stages that were clearly recognizable in all plants and were
19 independent of sowing date. Thus, lateral branching was not reported. Whenever possible, codes
20 assigned to growth stages and their definition followed the general scheme of the subdivision of
21 plant developmental cycles reported in the extended BBCH-scale (Hess et al. 1997; Meier 2001).

22 At maturity, five replicates each consisting of 10 plants, were collected both from the field trials
23 and from pots, and the position of the nodes corresponding to +INF and TINF, the length of the
24 main stem, the total number of inflorescences and grain yield were determined.

25 *Calculation and statistics*

1 Thermal time was calculated as the sum of heat units measured in growing degree-days (GDD,
2 °Cd), as $GDD = ((T_{max} + T_{min})/2) - T_b$. In the formula, T_{max} and T_{min} are the daily maximum
3 and minimum air temperatures, and T_b is the base temperature below which no significant crop
4 development occurs. If $T_{min} < T_b$ then $T_{min} = T_b$ was also incorporated into the equation. An
5 upper threshold temperature (T_{ut}), above which crop development is negatively affected, was also
6 incorporated, i.e. if $T_{max} > T_{ut}$ then $T_{max} = T_{ut}$ (McMaster & Wilhelm 1997).

7 Since cardinal threshold temperatures are not well defined for buckwheat, we used several
8 combinations of T_b and T_{ut} , in order to find the one that minimized the variation in the duration of
9 phases over the sowing dates. Tested base temperatures were 0, 5 and 10°C (Kajfež-Bogataj 1988;
10 Edwardson 1995; Campbell 1997), the latter generally indicated as T_b for summer crops in the
11 Mediterranean region. For the upper threshold temperature, we tested 20, 25 and 30°C which are
12 reported to be critical for flower fertilization by several authors (Marshall & Pomeranz 1982; Tahir
13 & Farouk 1988; Cawoy et al. 2009). In summary, nine temperature combinations were tested: 0-
14 20°C, 0-25°C, 0-30°C, 5-20°C, 5-25°C, 5-30°C, 10-20°C, 10-25°C and 10-30°C.

15 The average growth rate of metamers during the vegetative phase was calculated as the ratio of
16 the thermal time from sowing to the stage 1st flowers open (0-60) and the position of the node
17 corresponding to +INF. The average growth rate of metamers, or inflorescences, during the
18 reproductive phase was calculated as the ratio of the thermal time from the stage 1st flowers open to
19 the end of fruit ripening (60-88) and the difference between the positions of nodes TINF and +INF,
20 or the number of inflorescences, respectively.

21 The effect of sowing date on biometric parameters and on the duration of phases, calculated both
22 in days and thermal time, was analysed by means of simple ANOVA with five replicates. Means
23 were separated by the least significant difference (LSD) test, when the F test indicated factorial
24 effects on the significance level of $p < 0.05$ (Steel et al. 1997).

25 **Results**

26 *Definition of growth stages*

1 Following the decimal code and the definitions of growth stages of the extended BBCH scale, we
2 elaborated a growth scale for buckwheat, choosing the ordered sequence of growth stages that was
3 observed in plants, independently of their size, year of cultivation and sowing date (Table 1).

4 In buckwheat, germination is epigeal and, therefore, emergence (stage 09) is closely followed by
5 the unfolding of cotyledon leaflets (stage 10). From our observations seedlings are established with
6 the complete emission of the first true leaf (stage 11), after which the shoot apical meristem
7 produces a sequence of main stem metamers, each consisting of one internode and one node with
8 one leaf and one axillary bud. Since we found that plants produced approximately seven main stem
9 metamers when they were sown between 24 March and 5 May (SD I, II, IIa and III), but
10 approximately 12 when they were sown after 20 May (SD IV, IVa and V) a three-digit code was
11 introduced to describe leaf development. Accordingly, the stage 1st leaf unfolded is indicated both
12 with the two-digit code 11 and the three-digit code 101, while the stages of leaf 10, 11 and 12
13 correspond to the codes 110, 111 and 112, respectively. The principal growth stage 2, describing the
14 progress of lateral branching, was not detailed in this scale, because branching was highly variable
15 among plants and in response to sowing dates, both in terms of first branch position, which varied
16 from the cotyledon node to that immediately below the first formed inflorescence, and in terms of
17 rate and duration of branch development (Figure 2).

18 Similar to branching, in the present research, the number of inflorescences per plant varied
19 greatly in response to sowing date. However, the first (+INF) and the terminal clusters (TINF) of
20 inflorescences formed on the main stem were easy to detect and to follow in their progress in all
21 plants and, therefore, we based reproductive stages on the changes occurring on them. In addition,
22 because of the long-lasting and widely overlapping flowering and ripening phases, we defined
23 different stages and sub-phases for each, and, after the appearance of the first green fruits at the
24 base of +INF (stage 70), the growth scale proceeds with two parallel sequences of stages, each with
25 distinct codes.

1 In buckwheat, the shift to reproduction is signalled by the appearance of a blossom bundle
2 through the upper unfolding leaf at the main stem apex (stage 50). In our research this varied from
3 L4 to L5, and the reproductive phase always started with the opening of the most basal flower in the
4 1st main stem inflorescence +INF (stage 60). Despite this, in the growth scale, we set beginning of
5 flowering (stage 62) when 1-2 flowers were open in the terminal cluster of inflorescences TINF,
6 because this stage is easier to record in field conditions. The percentage of flowers open in the plant
7 is highly variable in buckwheat in response to branching and was not reported. Nevertheless, we
8 observed that at full flowering (stage 65), at least 1-2 flowers were open in each of the main stem
9 inflorescences and in most inflorescences of the lateral branches. Advanced flowering (stage 66)
10 corresponds to the end of flowering in +INF. It is followed by late main stem flowering (stage 67)
11 when most main stem inflorescences have no more open flowers and only 1-2 flowers are open at
12 the same time in TINF. The end of flowering on the main stem (stage 68) and throughout the whole
13 plant (stage 69) were hard to identify, because blossoms and flowers were still present in senescent
14 plants, especially in later sowing dates (Figure 3a).

15 In line with the flowering phase, the first full-developed green achenes appeared at the base of
16 +INF (stage 70), but we set the beginning of fruit development (stage 71) when full-sized green
17 achenes became visible in TINF, and the beginning of fruit ripening (stage 80) when angles of these
18 achenes turned brownish red. In contrast, ripening stages were defined on the oldest inflorescence,
19 because the sequence of ripening was more ordered in +INF than in TINF. Accordingly, the
20 appearance of the first brown fruits (stage 85) was recorded in +INF, and advanced ripening (stage
21 86) corresponds to the stage all achenes in this inflorescence are brown. In sequence, late fruit
22 ripening (stage 87) indicates the complete ripening or abortion of all achenes of the main stem
23 inflorescences, and the end of fruit ripening (stage 88) when this occurs on the whole plant.

24 At last, we indicated the yellowing and withering of leaf margins as the beginning of plant
25 senescence (stage 90), whereas plants were considered dead (stage 97) when the stem was entirely

1 brown and fragile. It is worth noting that the senescence phase was always rather long, ranging
2 approximately from 20 to 30 days.

3 Observations performed on plants of the pot experiment, showed that, the correspondence
4 between various flowering and ripening stages was maintained throughout all the sowing dates
5 (Table 2). Specifically: i) the first inflorescence became visible (stage 50) when at least three true
6 leaves had fully expanded on the main stem (stage 13); ii) flowering reached the terminal
7 inflorescence cluster (stage 62) always before full-sized green fruits became visible in +INF (stage
8 70), and iii) fruit ripening in the whole plant ended within two weeks of the end of ripening in the
9 oldest inflorescence.. Otherwise, the sowing date changed the chronological sequence of some
10 stages, thus affecting their correspondence. In particular, 1st brown fruits visible in +INF (stage 85)
11 occurred when no more flowers were open in this inflorescence (stage 66) in SD I and II, but not in
12 the later sowings, where flowers and fruits at all developmental stages coexisted in the
13 inflorescence (Figure 3b). Accordingly: i) stage 85 was associated with the beginning of plant
14 senescence (stage 90) in SD I and II, whereas it followed closely full flowering (stage 65) and the
15 appearance of green fruits in TINF (stage 71) in SD III, IV and V. In turn, ii) stage 65 was
16 associated with the development of 1st green fruits in +INF (stage 70) in SD I and II, but with their
17 development in TINF (stage 71) in SD III, IV and V. Finally, the progress of lateral branching did
18 not match the main stem stages, except that the first lateral branch primordium became visible
19 approximately after three leaves had expanded on the main stem (stage 13) and around blossoming
20 (stage 50).

21 ***Growth parameters***

22 Sowing date influenced the growth habit of buckwheat plants. In both years, the first
23 inflorescence developed at the fourth node of the main stem (N4) in plants sown up to beginning
24 May (SD I, II, IIa and III), and at the fifth node (N5) in later sowings (SD IV, IVa and V), while the
25 terminal cluster developed approximately at N7 in the four earlier SD and at N12 in the later three.

1 Note that the node of the terminal cluster also indicated the total number of main stem metamers
2 formed by the apical meristem.

3 Measured growth parameters did not differ statistically between pot or field conditions and,
4 therefore, we reported field data from 2013 and the average of field and pot data for 2014.
5 Moreover, also between year differences in the April (SD II and IIa) and end of May (SD IV and
6 IVa) sowings were not significant, probably because temperatures did not differ markedly in 2013
7 and 2014 and irrigation nullified differences in rainfall. In plants sown from 24 March to 5 May
8 (SD I, II, IIa and III) the main stem height and the number of inflorescences per plant did not differ
9 statistically and were approximately 62 cm and 8.7, respectively (Figure 4). When sowing was
10 delayed (SD IV, IVa and V), the average stem height increased to 93 cm, while the number of
11 inflorescences per plant was approximately 22 in sowings performed at the end of May (SD IV,
12 IVa), and 38 in that of mid June (SD V). Grain yield was greatly affected by sowing date: it
13 decreased progressively from 1.9 to 0.1 g plant⁻¹ with its delay from March (SD I) to beginning
14 May (SD III) and increased again in later sowings, reaching 3.6 g plant⁻¹ with the mid June one (SD
15 V). Between year differences were approximately 0.5 g plant⁻¹, but were not statistically significant.

16 *Length of growth phases*

17 In buckwheat plants sown in spring, the length of the entire growth cycle, from sowing to the end of
18 fruit ripening (stages 0-88), was not markedly affected by year and sowing date, and was 80 and 87
19 days in 2013, and ranged from 80 to 91 days in 2014 (Table 3). In the second year, the duration of
20 the vegetative phase (stages 0-60) decreased by approximately 21% with the delay of sowing up to
21 SD III, and then remained unchanged, while that of the reproductive phase (stages 60-88) increased
22 by approximately 28% from SD I and II to SD III, and then decreased by 13% in SD IV and V.

23 With all combinations of cardinal temperatures, the amount of GDD needed to complete both the
24 vegetative and the reproductive phases differed significantly in response to sowing date (Table 3).
25 In contrast, between year differences in the amount of accumulated GDD at corresponding sowing
26 dates, II-IIa and IV-IVa, were always lower than 10°Cd and were not reported. In 2014, the thermal

1 time to complete the growth cycle was lower in plants sown in March-April (SD I and II) compared
2 to those sown after mid May (SD IV and V). In plants sown at the beginning of May (SD III) the
3 thermal time of the vegetative phase equalled that of the earlier SD, and the reproductive phase, that
4 of later SD. Accordingly, two types of growth cycle length were found in response to sowing date:
5 short thermal time in sowings performed in March and April (SD I, II and IIa), and long thermal
6 time in sowings performed in May and June (SD III, IV, IVa and V).

7 The combination of cardinal temperatures 0-25°C uniformed best the thermal time of the entire
8 growth cycle within each group of SD. Differences were only 13°Cd within early sowings (SD I, II
9 and IIa) and 10°Cd within later ones (SD III, IV, IVa and V), corresponding to a variation of less
10 than 1%. With the interval 5-25°C, differences were slightly higher, approximately 3% (Table 3).

11 The higher amount of GDD accumulated during the vegetative phase in SD IV, IVa and V
12 depended on the higher position of +INF on the main stem, which was N5 compared to N4. We
13 observed, indeed, that up to the stage of 1st flowers open, the average thermal time needed by
14 buckwheat to produce main stem complete metamers (internode+leaf+lateral branch primordium)
15 was constant across all tested SD and was 117°Cd metamer⁻¹ (± 2.4 SE) with the cardinal interval 0-
16 25°C. In contrast, we did not find a constant ratio between the thermal time of the reproductive
17 phase and the number of main stem metamers, or the number of inflorescences produced during that
18 period.

19 Since reproductive sub-phases overlap widely in buckwheat, in 2014, we calculated the thermal
20 time of each separately, in order to assess whether their duration was affected differently by
21 temperature and sowing date. The thermal time of main stem flowering (60-68) was approximately
22 twice as long in SD III, IV and V compared to earlier sowings, and differences within these two
23 groups of SD were lowest with the cardinal intervals 5-25°C and 5-30°C (Table 4). Similar patterns
24 were observed for the amount of GDD required by first flowers to develop into full-sized green
25 achenes (60-70), but differences within groups were lowest with 0-25°C. The additional amount of
26 GDD needed by green achenes to reach full maturity (70-85) was higher than that needed to reach

1 full size (60-70), and was quite uniform throughout sowing dates. Differences were lowest with the
2 interval 5-30°C and with all combinations including a base temperature of 10°C. Finally, late
3 flowering (68-69) and main stem fruits ripening (85-87) lasted significantly more in SD III than in
4 other sowings, and no significant differences were detected between SD I and II and between SD IV
5 and V, irrespectively of the temperature interval tested. However, differences in the length of phase
6 68-69 were lowest with the intervals 5-25°C, while those of phase 85-87 with 10-25°C.

7 **Discussion**

8 Despite the well known heterogeneity of buckwheat plants and the marked influence of sowing date
9 on growth habit and phase length (Funatsuki et al. 2000; Michiyama et al. 2007), the ordered
10 sequence of development stages reported in the growth scale was recorded in all examined plants.
11 Accordingly, up to the start of flowering, the phasic development of buckwheat can be described as
12 a sequence of metamers produced acropetally, each consisting in one internode, one leaf and one
13 lateral branch primordium. Thereafter, plants grow further by developing acropetally, main stem
14 metamers, consisting in one internode, one leaf and one inflorescence, and, basipetally, lateral
15 branches, in general one or two per node.

16 The differences in temperature and day length, experienced by buckwheat plants with the delay
17 of sowing from the beginning to the end of spring, increased the number of main stem metamers
18 and the growth of lateral branches, which caused a marked increase in plant height and in the
19 number of inflorescences per plant. This affected the length of phases during the entire cycle, but
20 changes were more pronounced after the start of flowering. Differences in the duration of phases
21 and sub-phases were never reduced, and even increased when they were expressed in thermal time,
22 highlighting that temperature was not the primary factor driving buckwheat development.

23 Though the thermal time of the vegetative phase was significantly higher in SD IV and SD V
24 compared with earlier SD, the amount of GDD required for the development of one complete
25 metamer was constant across sowing dates up to the stage 1st flowers open (stage 60). This confirms
26 that the duration of the vegetative phase is regulated by both temperature and photoperiod and, in

1 specific, that the former determines the growth rate of metamers, and the latter the number of
2 metamers produced below the first inflorescence. The cardinal temperature interval 0-25°C
3 uniformed best the length of the vegetative phase, suggesting that temperatures between 0 and 5°C
4 were not detrimental to early growth, in contrast to findings in the literature (Kajfež-Bogataj 1988;
5 Edwardson 1995).

6 Present results were obtained with the European variety Lileja in a the temperate Mediterranean
7 environment, but similar to our findings, Edwardson (1995), with the varieties Mancan and Manor
8 in USA, and Cha et al. (1989) in Korea with local varieties, reported that the length of the phase
9 from sowing to the beginning of flowering depended strongly on mean temperature, while this did
10 not occur for the reproductive phase. In Japan, Michiyama et al. (2005), found that plants exposed
11 to long days before the start of anthesis prolonged the vegetative phase and elevated the first
12 flowering node, and also indicated that a 14-h day length was critical for the summer ecotype
13 Shinanonatsusoba and 13-h for the autumn one Miyazakizairai. In the variety Lileja, we found that
14 the position of the first inflorescence increased from N4 to N5 when plants reached floral transition,
15 corresponding to the expansion of the first true leaf (Quinet et al. 2004), after 1st June (SD IV, IVa
16 and V) and, therefore, only when they experienced a day length longer than 15 h.

17 In line with findings of Michiyama et al. (2003), in the present research, only plants exposed to
18 the long days during the vegetative phase increased main stem height and the number of metamers
19 produced during the reproductive phase, suggesting that both parameters are determined in
20 buckwheat at initial growth stages. In contrast, the number of inflorescences per plant showed a
21 progressive trend with the increase of day length, and was by far higher in plants sown on 17 June
22 compared to those sown on 26 May. Since the number of main stem metamers equalled in the two
23 SD, the different number of inflorescences was probably due to a greater development of lateral
24 branches that are, therefore, regulated differently than the main stem by temperature and
25 photoperiod

1 Plants sown from May onwards (SD III, IV, and V) required a higher thermal time to complete
2 all flowering and ripening sub-phases, except for the ripening of 1st green achenes (phase 70-85)
3 that was constant across sowing dates. The cardinal intervals that best uniformed the length of this
4 sub-phase were higher than those of other sub-phases, 10-25°C and 5-30°C, suggesting that fruit
5 ripening needs higher temperatures than vegetative growth, flowering and fruit growth. This
6 explains the findings of Funatsuki et al. (2000), that low temperatures during seed ripening
7 prolonged the time of maturation in buckwheat cultivars with both determinate (Kitawase D) and
8 indeterminate (Kitawaseoba) growth habit, and were a primary cause of reduced grain yield in late
9 summer sowings.

10 The longer duration of the flowering and fruit growth phases could not be attributed to
11 differences in the number of main stem metamers or in the number of inflorescences produced,
12 since both parameters differed greatly between SD III and the later sowings. Thus, other parameters
13 such as the number of flowers produced by each inflorescence and factors affecting seed setting
14 should be taken into account (Taylor & Obendorf 2001). Michiyama et al. (2003) reported that day
15 length was a primary cause of differences in flower and grain production, and that grain yield was
16 reduced by long days, especially in the autumn ecotype. In the present research, however, variations
17 in grain yield corresponded neither to trends observed in the length of vegetative and reproductive
18 phases and sub-phases, nor in plant height and in the number of inflorescences. Nevertheless, the
19 highest yield was obtained in SD V in correspondence with long vegetative and reproductive phases
20 and with the highest number of inflorescences. Our findings contrast with the hypothesis of Quinet
21 et al. (2004) that for grain yield it would be advantageous to grow buckwheat in short days, and
22 suggest that yield is more stable in short days, but best performances are obtained with long days.

23 The response of buckwheat to long days has been investigated by testing constant day lengths in
24 Japanese summer and autumn ecotypes and in the European variety La Harpe (Michiyama et al.
25 2003 and 2005; Quinet et al. 2004), whereas, to the best of our knowledge, increasing or declining
26 day lengths have never been taken into account. One reason for this could be that buckwheat is

1 generally cultivated as a short-day summer-autumn crop throughout the world (Campbell 1997,
2 Slawinska & Obendorf, 2001, Michiyama et al. 2007) and, therefore, plants grow mostly in
3 declining day lengths. We found, however, that differences in the thermal time of phases were also
4 associated with trends in day length, and plants prolonged growth phases when they experienced, at
5 least for a period, declining day length. When this occurred, either during the reproductive phase
6 only (SD III) or in both the vegetative and the reproductive phases (SD IV, IVa and V), the entire
7 growth cycle was longer than in plants that grew entirely in increasing day length (SD I, II and IIa).
8 In particular, we found that the number of inflorescences per plant and also grain yield were highest
9 when plants were entirely grown in declining day length (SD V).

10 Irrespectively of the photoperiodic signal, however, the mechanism controlling plant growth and,
11 consequently, the duration of phases, is still unclear. Cawoy et al. (2009) hypothesized that the
12 availability of resources internal to the inflorescence regulates the percentage of fertile flowers,
13 while Taylor and Obendorf (2001) found that the frequency of flower fertilization declined with
14 plant age, but was not related to the amount of developing fruits in the inflorescence. We did not
15 perform a quantitative analysis, however we suggest that the first formed inflorescence (+INF)
16 plays a key role in determining the length of the entire growth period. Indeed, we observed that the
17 complete ripening, or abortion, of fruits in this inflorescence (stage 86) was closely followed by
18 plant senescence and that, consistently with findings of Michiyama et al. (2003), a long growth
19 cycle was associated with a high number of flowers in that inflorescence. Further investigations are
20 needed to elucidate this point.

21 To sum up, we found that sowing time changed the growth habit of buckwheat plants and the
22 amount of GDD required to complete the development phases. Accordingly, two types of growth
23 cycle length were highlighted. In plants sown in March and April (SD I, II and IIa), the vegetative
24 and the reproductive phases were both short, and the thermal time of the entire cycle was 900-
25 950°Cd with a cardinal interval 5-25°C. In contrast, in plants sown in May and June either the
26 reproductive phase (SD III) or both (SD IV, VIa and V) were long, and the cycle lasted 1270-

1 1300°Cd. These last values are consistent with those reported for buckwheat sown in May in the
2 north of USA (Edwardson 1995) and can, therefore, be used to estimate the optimal time for fruit
3 harvest when buckwheat is grown in long days.

4 Changes in growth habit and the different duration of flowering in response to sowing date
5 affected the relation between flowering and ripening stages. This could impair the use of easily
6 recognizable growth stages for the identification of optimal harvest times, in particular for the
7 maximum accumulation of biomass in stem and leaves, which is generally associated with the peak
8 of flowering (Cawoy et al. 2009). However, we observed that, with a short cycle, full flowering
9 (stage 65) corresponded to the appearance of 1st green fruits in +INF (stage 70), while, with a long
10 cycle, it corresponded to the appearance of 1st green fruits in TINF (stage 71), because of the later
11 flowering on the lateral branches. Since green leaves and flowers retain the highest rutin
12 concentration within the plant (Baumgartel et al. 2010; Gupta et al. 2011; Ahmed et al. 2014), the
13 stages 70 and 71 can be used to identify the best harvest time for both forage and rutin yield, when
14 plants are grown in short or long days, respectively.

15 Especially in long cycle plants, the optimal time for fruit harvest is difficult to identify, because
16 of sequential ripening and the overlap with seed shattering (Edwardson 1995; Funatsuki et al.
17 2000). From our observations, the best time for fruit harvest seem to be when no more green
18 achenes are present in the TINF cluster (stage 87). At this stage, all the main stem inflorescences
19 are ripe, while there may still be green achenes on the lower branches. In line with findings of
20 Taylor and Obendorf (2001), however, these never developed into fruits and, thus, they do not
21 contribute to seed yield. Our calculations suggest that, taking a cardinal temperature interval of 10-
22 25°C, fruit harvest can be planned approximately 160°Cd after the appearance of the first brown
23 achenes in +INF (stage 85), when plants reach full flowering (stage 65) with a day length shorter
24 than 15 h, i.e. before 1st June in the present study, but approximately 370°Cd after stage 85 when
25 they flower later.

1 In conclusion, despite the rather high heterogeneity of plants and the influence of sowing date on
2 growth parameters, the phasic development of buckwheat can be described through an ordered
3 sequence of growth stages that are mainly based on easily recognizable changes occurring in the
4 first and the terminal clusters of inflorescences formed on the main stem. Sowing date did not affect
5 the occurrence of stages, but changed the plant growth habit and the correspondence between
6 flowering and ripening stages. In the present study, plants of the European variety Lileja, exposed to
7 day length longer than 15 h at initial growth stages, showed increased size and more profuse
8 flowering, and required a longer thermal time to complete all phases. However, large size and long
9 flowering corresponded to high grain yield only in plants sown in mid June, so we hypothesize that
10 other factors, such as declining photoperiod, may influence seed-setting. Though quantitative
11 analyses are necessary to confirm our statements, we suggest a correspondence of ripening growth
12 stages with the optimal time for forage and fruit harvest. The stage for forage harvest, generally
13 coinciding with full flowering, changes with the length of the growth cycle and, therefore, with
14 sowing date. In specific, it corresponds to the appearance of green achenes in the oldest
15 inflorescence (stage 70) in short growth cycles, and with their appearance in the terminal cluster of
16 inflorescences (stage 71) in long ones. The best time for grain harvest, indeed, corresponds to the
17 complete ripening of achenes on the main stem inflorescences (stage 87) with all sowing dates and
18 cycle length.

19 **References**

- 20 Adhikari KN, Campbell CG. 1998. In vitro germination and viability of buckwheat (*Fagopyrum*
21 *esculentum* Moench) pollen. *Euphytica* 102: 87-92.
- 22 Ahmed A, Khalid N, Ahmad A, Abbasi NA, Latif MSZ, Randhawa MA. 2014. Phytochemicals and
23 biofunctional properties of buckwheat: a review. *J. Agr. Sci. (Camb.)* 152: 349-369.
- 24 Amelchanka SL, Kreuzer M, Leiber F. 2010. Utility of buckwheat (*Fagopyrum esculentum*
25 Moench) as feed: Effects of forage and grain on in vitro ruminal fermentation and
26 performance of dairy cows. *Anim. Feed Sci. Technol.* 155: 111-121.

- 1 Baumgertel A, Loebers A, Kreis W. 2010. Buckwheat as a source for the herbal drug *Fagopyri*
2 *herba*: rutin content and activity of flavonoid-degrading enzymes during plant development.
3 Eur. J. Plant Sci. Biotechnol. 4: (Special Issue I) 82-86.
- 4 Brunori An, Brunori Al, Baviello G, Marconi E, Colonna M, Ricci M, Mandarino P. 2006. Yield
5 assessment of twenty buckwheat (*Fagopyrum esculentum* Moench and *Fagopyrum tataricum*
6 Gaertn.) varieties grown in Central (Molise) and Southern Italy (Basilicata and Calabria).
7 *Fagopyrum* 23: 83-90.
- 8 Campbell CG. 1997. Buckwheat. *Fagopyrum esculentum* Moench. Promoting the conservation and
9 use of underutilized and neglected crops. 19. Rome (I): International Plant Genetic Resources
10 Institute.
- 11 Cawoy V, Ledent JF, Kinet JM, Jacquemart AL. 2009. Floral biology of common buckwheat
12 (*Fagopyrum esculentum* Moench). Eur. J. Plant Sci. Biotechnol. 3: (Special Issue I) 1-9.
- 13 Cha SW, Cha YH, Rho CW, Kim TS, Kwon KC. 1989. Variation of yield related characters on
14 different planting times in local buckwheat *Fagopyrum esculentum* Moench. Upland Ind.
15 Crops 31: 43-49.
- 16 Edwardson SE. 1995. Using growing degree days to estimate optimum windrowing time in
17 buckwheat. In Matano T, Ujihara A, editors. Current Advances in Buckwheat Research,
18 Proceedings 6th International Symposium on buckwheat; 1995 24-29 Aug; Shinshu (China).
19 Shinshu Univ. Press; p. 509-514
- 20 Funatsuki H, Maruyama-Funatsuki W, Fujino K, Agatsuma M. 2000. Ripening habit of buckwheat.
21 Crop Sci. 40: 1103-1108.
- 22 Goeritz M, Kawiani R, Loges R, Schwarz K, Kämper M, Ehmsen T, Taube F. 2009. Ertragsleistung
23 und Rutingehalte verschiedener Buchweizensorten unter ökologischen Anbaubedingungen
24 [Grain yield and rutin content of different buckwheat varieties in organic farming]. In: Mayer
25 J, Alföldi T, Leiber F, Dubois D, Fried P, Heckendorn F, Hillmann E, Klocke P, Lüscher A,
26 Riedel S, Stolze M, Strasser F, van der Heijden M, Willer H, editors. Werte - Wege -

- 1 Wirkungen: Biolandbau im Spannungsfeld zwischen Ernährungssicherung, Markt und
2 Klimawandel, vol. 1 Boden, Pflanzenbau, Agrartechnik, Umwelt- und Naturschutz,
3 Biolandbau international, Wissensmanagement. Proceedings 10th Wissenschaftstagung
4 Ökologischer Landbau; 2009 11-13 Feb; Zürich (CH). Berlin (D): Verlag Dr. Köster; p. 215-
5 218.
- 6 Gupta N, Sharma SK, Rana JC, Chauhan RS. 2011. Expression of flavonoid biosynthesis genes vis-
7 à-vis rutin content variation in different growth stages of *Fagopyrum* species. J. Plant Physiol.
8 168: 2117-2123.
- 9 Halbrecq B, Romedenne P, Ledent JF. 2005. Evolution of flowering, ripening and seed set in
10 buckwheat (*Fagopyrum esculentum* Moench): quantitative analysis. Eur. J. Agron. 23: 209-
11 224.
- 12 Hess M, Barralis G, Bleiholder H, Buhrs L, Eggers Th, Hack H, Stauss R. 1997. Use of the
13 extended BBCH scale – general for the descriptions of the growth stages of mono- and
14 dicotyledonous weed species. Weed Res. 37: 433-441.
- 15 Kajfež-Bogataj L. 1988. A simple model for allocation of assimilates at different stages of
16 buckwheat plant development. *Fagopyrum* 8: 23-26.
- 17 Kälber T, Kreuzer M, Leiber F. 2012. Silages containing buckwheat and chicory: quality,
18 digestibility and nitrogen utilisation by lactating cows. Arch. Anim. Nutr. 66: 50-65.
- 19 Köppen W. 1936. Das geographische System der Klimate. [The geographic system of climates]. In
20 Köppen W., Geiger R., editors. Handbuch der Klimatologie, [Handbook of climatology], vol
21 1 Part C. Berlin: Gebrüder Borntraeger; p. 1-44.
- 22 Marshall HG, Pomeranz Y. 1982. Buckwheat: Description, breeding, production and, utilization. In
23 Pomeranz Y, editor. Advances in Cereal Science and Technology, vol. 5. St. Paul (Minnesota,
24 USA): American Association of Cereal Chemists Incorporated; p. 157-210.
- 25 McMaster GS, Wilhelm WW. 1997. Growing degree-days: one equation, two interpretations. Agric.
26 For. Meteorol. 87: 291–300.

- 1 Meier U. 2001. BBCH Monograph. Growth stages of mono- and dicotyledonous plants. 2nd
2 edition. Federal Biological Research Centre for Agriculture and Forestry. Berlin (D):
3 Blackwell.
- 4 Michiyama H, Arikuni M, Hirano T, Hayashi H. 2003. Influence of day length before and after the
5 start of anthesis on the growth, flowering and seed-setting in common buckwheat
6 (*Fagopyrum esculentum* Moench). Plant Prod. Sci. 6: 235-242.
- 7 Michiyama H, Tsuchimoto K, Tani KI, Hirano T, Hayashi H, Campbell CG. 2003. Influence of day
8 length on stem growth, flowering, morphology of flower clusters, and seed-set in buckwheat
9 (*Fagopyrum esculentum* Moench). Plant Prod. Sci. 8: 44-50.
- 10 Michiyama H, Yoshimura K, Hirano T, Hayashi H. 2007. Influence of air temperature on varietal
11 differences between summer and autumn ecotype in buckwheat. Pages 242-246 in Proc. 10th
12 International Symposium on buckwheat. Yanhling, Shaanxi, China.
- 13 Quinet M, Cawoy V, Lefèvre I, van Miegroet F, Jacquemart AL, Kinet JM. 2004. Inflorescence
14 structure and control of flowering time and duration by light in buckwheat (*Fagopyrum*
15 *esculentum* Moench). J. Exp. Bot. 55: 1509-1517.
- 16 Slawinska J, Obendorf RL. 2001. Buckwheat seed set in planta and durlimiting seed set in
17 buckwheat.ing in vitro inflorescence culture: evaluation of temperature and water deficit
18 stress. Seed Sci. Res. 11: 223-233.
- 19 Steel RGD, Torrie JH, Dickey DA. 1997. Principles and Procedure of Statistics: A Biometrical
20 Approach. New York (NY, USA): McGraw-Hill.
- 21 Tahir I, Farouk S. 1988. Review article on buckwheat. *Fagopyrum* 8: 33-53.
- 22 Taylor DP, Obendorf RL. 2001. Quantitative assessment of some factors limiting seed set in
23 buckwheat. Crop Sci. 41: 1792-1799.

- 1 Appendix 1. A visual scale for buckwheat growth stages. Codes and descriptions follow the extended
2
3
4 2 BBCH scale (Hess et al. 1997).
5
6 3
7
8 4
9
10 5
11
12 6
13
14 7
15
16 8
17
18 9
19
20 10
21
22 11
23
24 12
25
26 13
27
28 14
29
30 15
31
32 16
33
34 17
35
36 18
37
38 19
39
40 20
41
42 21
43
44 22
45
46 23
47
48 24
49
50 25
51
52
53
54
55
56
57
58
59
60

1 Table 1. A scale for buckwheat growth stages. Codes and descriptions follow the extended BBCH
 2 scale¹. In brackets the 3-digit code for leaf development. Since flowering and fruiting phases overlap for
 3 a long period, distinct codes were reported in two parallel columns. A visual scale is reported in the
 4 appendix.

Code	Growth stage	Description
00	Dry seed	Sowing date or start of experiment
09	Emergence	Cotyledons break through soil surface
10	Cotyledon	Cotyledons completely unfolded
(100)		
11	1 st leaf	First true leaf at node 1 (N1) unfolded
(101)		
12	2 nd leaf	Two true leaves unfolded at N1 and N2
(102)		
13	3 rd leaf	Three true leaves unfolded at N1, N2 and N3
(103)		
14	4 th leaf	Four true leaves unfolded at N1, N2, N3 and N4
(104)		
1.	... leaf	Stages continuous till ...
21	Branching	1 st side shoot visible
50	Blossoming	1 st inflorescence bud visible through an unfolding leaf at the main stem apex (+INF)
60	1 st Flowers open	1-2 flowers open at the base of the first formed inflorescence (+INF)

1			
2	62	Beginning of flowering	1-2 flowers open in the terminal
3			
4			inflorescence (TINF)
5			
6			
7	65	Full flowering	Open flowers in most inflorescences
8			
9			
10	70	1 st Green fruits	1-2 well developed green achenes visible at
11			the base of +INF
12			
13			
14	71	Fruits begin to develop	1-2 well developed green achenes in TINF
15			
16			
17	80	Beginning of fruit ripening	Angles of oldest achenes in TINF turn
18			
19			brownish-red
20			
21			
22	66	Advanced flowering	No more flowers open in +INF
23			
24			
25	67	Late main stem flowering	No more than 1-2 flowers open at the same
26			
27			time in TINF. Flowers open in branches
28			
29			
30	85	1 st Brown fruits	1-2 brown achenes visible at the base of
31			+INF
32			
33			
34			
35	68	End of main stem flowering	No more flowers open in TINF.
36			
37			Still a few flowers open in branches
38			
39			
40	69	End of branch flowering	No more flowers open in the whole plant
41			
42			
43	86	Advanced fruit ripening	All achenes brown in +INF
44			
45			
46	87	Late fruit ripening	All achenes in TINF and in other main stem
47			inflorescences are dark brown
48			
49			
50			
51	88	End of fruit ripening	All achenes dark brown or aborted
52			
53			
54	90	Beginning of plant senescence	Leaf margins turn yellow and start to wither
55			
56	97	Plant dead	The stem turns brown, dries up and becomes
57			
58			
59			
60			

fragile

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1. Hess et al. 1997.

For Peer Review Only

1 Table 2. Timing of principal growth stages of buckwheat plants sown at 20-day intervals throughout
 2 spring 2014. Reported dates were averaged over five replicate pots.

Code	Growth stage	Timing of growth stage				
00	Dry seed (Sowing)	24 Mar.	14 Apr.	5 May	26 May	17 June
10	Cotyledon	4 Apr.	24 Apr.	12 May	5 June	28 June
13	3 rd leaf	22 Apr.	10 May	26 May	17 June	8 July
50	Blossoming	22 Apr.	10 May	27 May	19 June	10 July
60	1 st Flowers open	30 Apr.	17 May	3 June	24 June	17 July
62	Beginning of flowering	5 May	19 May	5 June	26 June	22 July
65	Full flowering	9 May	23 May	17 June	10 July	1 Aug.
66	Advanced flowering	19 May	3 June	13 July	4 Aug.	11 Aug.
67	Late main stem flowering	22 May	5 June	15 July	4 Aug.	17 Aug.
68	End of main stem flowering	30 May	10 June	17 July	6 Aug.	1 Sep.
69	End of branch flowering	3 June	13 June	28 July	10 Aug.	5 Sep.
70	1 st Green fruits	7 May	23 May	11 June	2 July	24 July
71	Fruits begin to develop	12 May	26 May	17 June	10 July	1 Aug.
85	1 st Brown fruits	26 May	8 June	23 June	15 July	4 Aug.
86	Advanced fruit ripening	6 June	18 June	24 July	10 Aug.	5 Sep.
87	Late fruit ripening	13 June	25 June	1 Aug.	15 Aug.	8 Sep.
88	End of fruit ripening	19 June	3 July	4 Aug.	20 Aug.	10 Sep.
90	Beginning of plant senescence	27 May	9 June	22 July	1 Aug.	10 Aug.

3

1 Table 3. Duration of the entire growth cycle and of the vegetative (0-60) and reproductive
 2 (60-88) phases in days and thermal times (GDD), as affected by sowing date (SD) in 2014.
 3 Thermal time is reported for the Tb and Tut intervals 0-20°C and 5-25°C.

		Length of growth phases				
Code interval	Phase	SD I	SD II	SD III	SD IV	SD V
0-88	Cycle					
	Days	87 ^{ab}	80 ^b	91 ^a	86 ^{ab}	85 ^{ab}
	GDD (0-25°C)	1334 ^b	1347 ^b	1726 ^a	1716 ^a	1724 ^a
	GDD (5-25°C)	905 ^b	951 ^b	1271 ^a	1286 ^a	1299 ^a
0-60	Vegetative					
	Days	37 ^a	33 ^b	29 ^c	29 ^c	30 ^{bc}
	GDD (0-25°C)	482 ^b	468 ^b	476 ^b	542 ^a	602 ^a
	GDD (5-25°C)	304 ^c	307 ^c	331 ^c	397 ^b	452 ^a
60-88	Reproductive					
	Days	50 ^{bc}	47 ^c	62 ^a	57 ^{ab}	55 ^b
	GDD (0-25°C)	851 ^b	879 ^b	1250 ^a	1174 ^a	1122 ^a
	GDD (5-25°C)	601 ^b	644 ^b	940 ^a	889 ^a	847 ^a

4 Means in a row followed by the same letter are not significantly different ($p < 0.05$).

5
6
7

1 Table 4. Duration of reproductive sub-phases in days and thermal times (GDD), as affected by
 2 sowing date (SD) in 2014. Thermal time is reported for the Tb and Tut intervals that performed
 3 best at reducing differences among sowing dates.

Length of reproductive sub-phases						
Code interval	Reproductive sub-phase	SD I	SD II	SD III	SD IV	SD V
60-68	Main stem flowering					
	GDD (5-25°C)	328 ^b	302 ^b	651 ^a	672 ^a	715 ^a
	GDD (5-30°C)	332 ^b	321 ^b	715 ^a	732 ^a	787 ^a
68-69	Late flowering					
	GDD (5-25°C)	48 ^b	47 ^b	179 ^a	64 ^b	55 ^b
	GDD (5-30°C)	50 ^c	54 ^{bc}	198 ^a	74 ^b	61 ^b
60-70	1 st fruits growth					
	GDD (0-25°C)	100 ^b	103 ^b	150 ^a	164 ^a	148 ^a
	GDD (5-30°C)	65 ^b	75 ^b	126 ^a	133 ^a	126 ^a
70-85	1 st fruits ripening					
	GDD (10-25°C)	131 ^a	124 ^{ab}	114 ^b	131 ^a	121 ^{ab}
	GDD (5-30°C)	218 ^a	211 ^{ab}	190 ^b	212 ^{ab}	190 ^b
85-87	Main stem fruits ripening					
	GDD (10-25°C)	152 ^c	166 ^c	413 ^a	344 ^b	351 ^b
	GDD (5-30°C)	262 ^c	277 ^c	662 ^a	551 ^b	582 ^b

4 Means in a row followed by the same letter are not significantly different ($p < 0.05$).

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

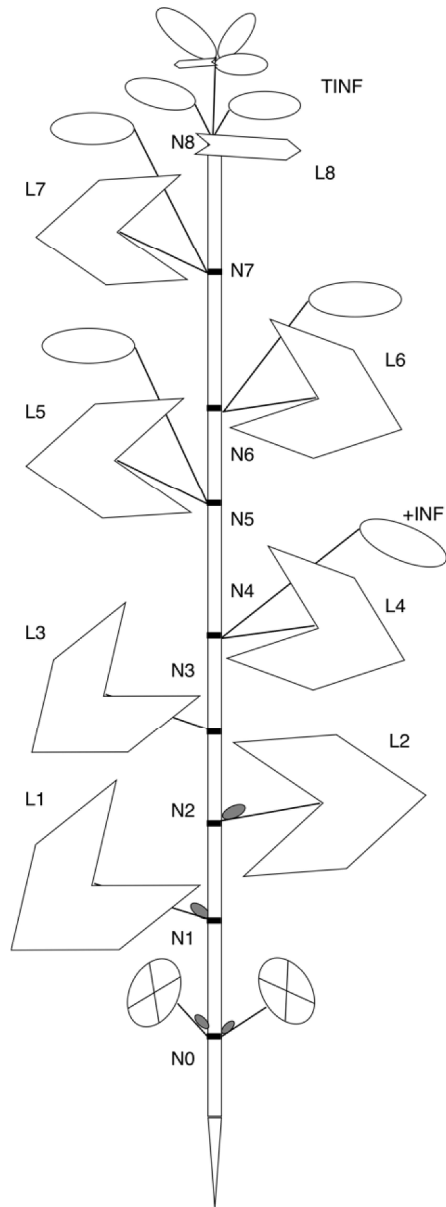
Legends to figures

Figure 1. Schematic drawing of plant architecture. Numbers indicate sequential metamer development. N, node; L, leaf; +INF, first inflorescence; TINF, terminal inflorescence cluster. Crossed ovals represent cotyledons; grey ovals, axillary buds; blank ovals, inflorescences.

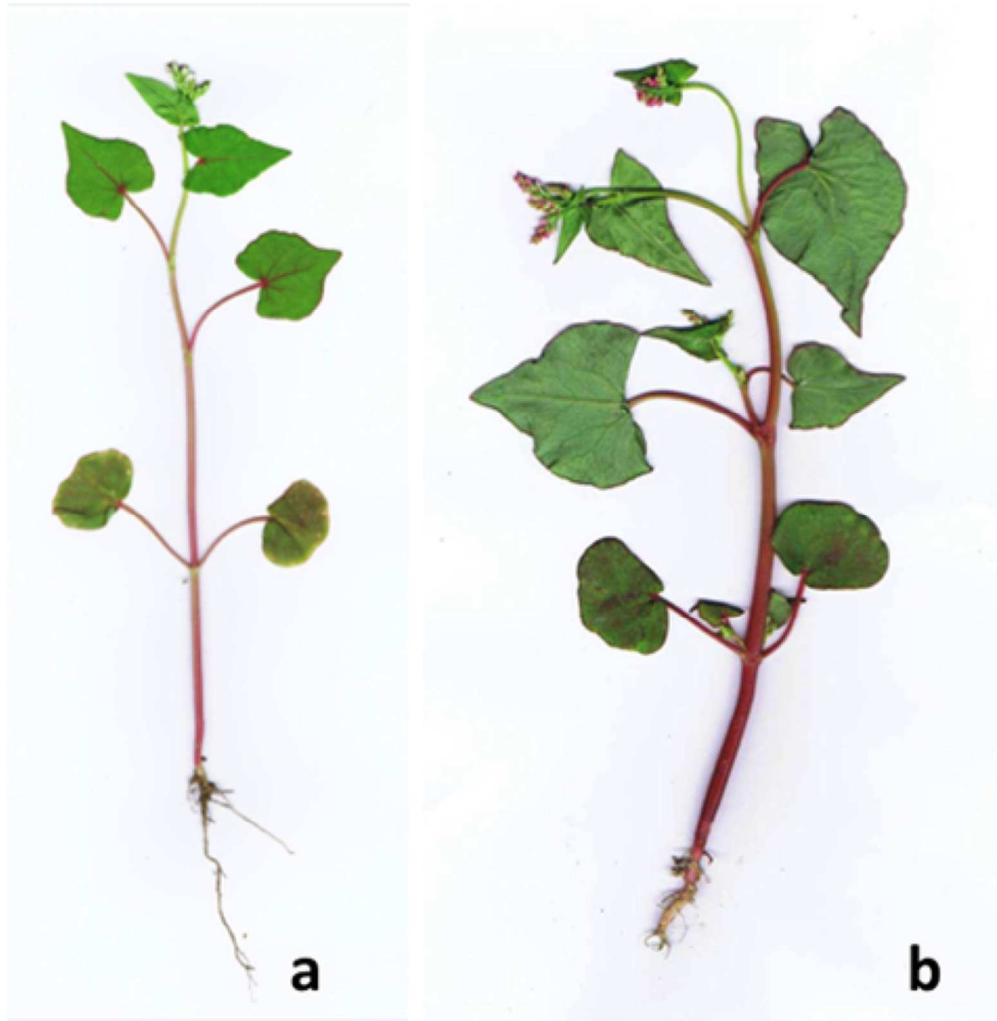
Figure 2. Different branching of buckwheat plants at the stages 3rd leaf (stage 13) and blossoming (stage 50). a, no branches (SD I); b, four branch primordia (SD IV).

Figure 3. Inflorescence TINF (a) showing mature fruits and flowers (SD III). Inflorescence +INF (b) showing all stages of flowering and fruit ripening (SD V).

Figure 4. Main stem height, number of inflorescences and grain yield of buckwheat plants, as affected by sowing date. Data are means of five replicates and vertical bars denote LSD.



Schematic drawing of plant architecture. Numbers indicate sequential metamer development. N, node; L, leaf; +INF, first inflorescence; TINF, terminal inflorescence cluster. Crossed ovals represent cotyledons; grey ovals, axillary buds; blank ovals, inflorescences.
219x594mm (300 x 300 DPI)



Different branching of buckwheat plants at the stages 3rd leaf (stage 13) and blossoming (stage 50). a, no branches (SD I); b, four branch primordia (SD IV).
82x84mm (300 x 300 DPI)



Inflorescence TINF (a) showing mature fruits and flowers (SD III). Inflorescence +INF (b) showing all stages of flowering and fruit ripening (SD V).
131x212mm (300 x 300 DPI)

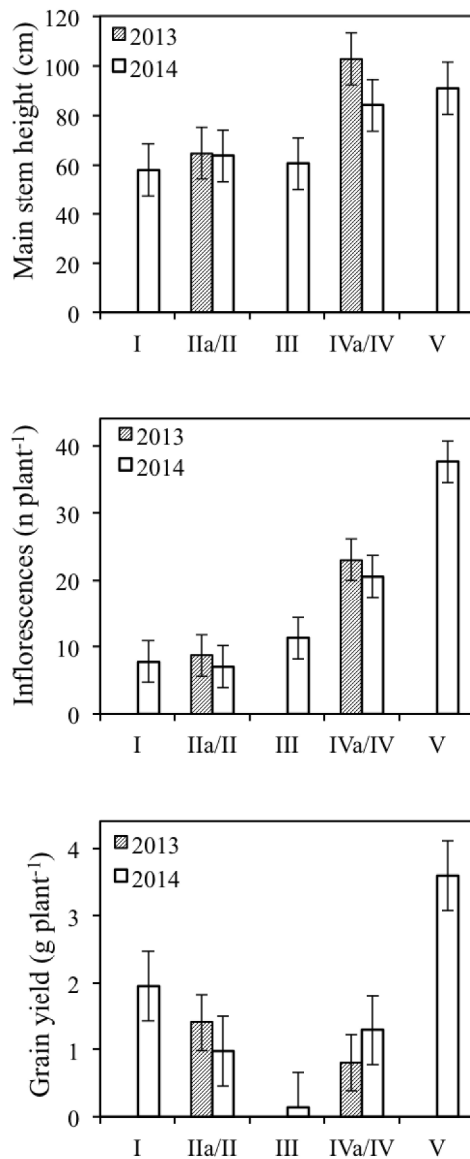


Figure 4. Main stem height, number of inflorescences and grain yield of buckwheat plants, as affected by sowing date. Data are means of five replicates and vertical bars denote LSD.

210x522mm (300 x 300 DPI)

Appendix 1. A visual scale for buckwheat growth stages. Codes and descriptions follow the extended BBCH scale (Hess et al. 1997).



10 Cotyledon
Cotyledons completely unfolded



11 (101) 1st leaf
First true leaf at node 1 (N1) unfolded



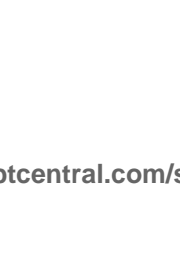
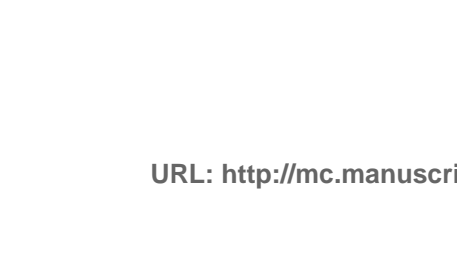
12 (102) 2nd leaf
Two true leaves unfolded at N1 and N2



13 (103) 3rd leaf
Three true leaves unfolded at N1, N2 and N3



21 Branching
1st side shoot visible



14 (104) 4th leaf
Four true leaves unfolded at N1, N2, N3 and N4

50 Blossoming
1st inflorescence bud visible through an unfolding leaf at the main stem apex (+INF)



60 1st Flowers open
1-2 flowers open at the base of the first formed
inflorescence (+INF)



62 Beginning of flowering
1-2 flowers open in the terminal inflorescence (TINF)



65 Full flowering
Open flowers in most inflorescences



67 Late main stem flowering
No more than 1-2 flowers open at the same time in
TINF. Flowers open in branches



70 1st Green fruits
1-2 well developed green achenes visible at the base
of +INF



71 Fruits begin to develop
1-2 well developed green achenes in TINF



80 Beginning of fruit ripening
Angles of oldest achenes in TINF turn brownish-red



85 1st Brown fruits
1-2 brown achenes visible at the base of +INF



86 Advanced fruit ripening
All achenes brown in +INF



87 Late fruit ripening
All achenes in TINF and in other main stem
inflorescences are dark brown

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60



88 End of fruit ripening
All achenes dark brown or aborted

For Peer Review Only