Seed development of arrowleaf, balansa, gland and Persian clover

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Abstract
The development process from floral bud formation to seed maturity of four top flowering annual clovers was quantified from a field experiment across 10 sowing dates at Lincoln University, Canterbury, New Zealand. For each species, a numeric reproductive scale was created as a field guide to document morphological changes as the bud progresses through reproductive development. The duration from bud visible to open flower was 341 °C days for 'Cefalu' arrowleaf, 215 °C days for 'Bolta' balansa, 196 °C days for 'Prima' gland and 186 °C days for 'Mihi' Persian clover. The inflorescence then required a further 274-689 °C days, 185 °C days , 256 ˚C days and 425 °C days for each respective species to reach physiological maturity. This was indicated when 50% of seeds had turned red/brown for 'Cefalu' arrowleaf, 100% pods turned yellow for 'Bolta' balansa, 100% of seeds were yellow and hard for 'Prima' gland, and pods turned brown with the first sign of colour change in seeds for 'Mihi' Persian clover. These results can be used to facilitate on farm decision making in relation to grazing management or seed set for subsequent regeneration.

Keywords: floral development chart, harvest maturity, peak flowering, pollination, seed filling, thermal time, *Trifolium vesiculosum, T. michelianum, T. glanduliferum, T. resupinatum*

Introduction
In annual crops, flower initiation is critical because it marks the starting point for reproductive development towards crop maturity and completion of their life cycle. The process of legume flowering begins when the shoot at the main stem changes from producing new young leaves to producing a flower bud. These flower buds will form an inflorescence and these will develop into seed pods. However, in a population of plants, pollination and seed maturity do not occur within a uniform time period. To determine a suitable time for seed harvest or re-introduce livestock for grazing, farmers need to know the majority of seeds are physiologically mature. This is because harvesting before physiological maturity may result in immature seeds with reduced seed quality and germination (Samarah 2006). Late harvest risks seed yield losses due to seed shattering (Siddique & Wright 2003). Thus, a biological indicator of physiological maturity is required to indicate harvest time. Maximum seed dry weight is a commonly used parameter to define seed physiological maturity, with the assumption that seed filling has ended at this phase (Hyde 1950). Evaluation of physiological maturity based on maximum seed dry weight has been conducted on various legume crops such as peas (*Pisum sativum*) (Deunff & Rachidian 1988), and white lupin (*Lupinus albus*) (Clapham & Barnes 1990), and will be used in this study to determine seed maturity in annual clovers. Under field conditions, seed morphological appearance at maturity can be tracked by using a visual reproductive development scale. Development scales are numbered in the order of ontogenetical stages of appearance, as inflorescence progresses from bud visible to seed maturity. Each ontogenetical stage is identified with a field observable picture and brief description. For cereals, the Zadoks code (Zadoks *et al*. 1974) documents developmental stages from germination to seed ripening. Similarly, a development scale for several legume cash crops has been developed (e.g. pea (Knott 1987) and recently Monks (2009) generated a reproductive development scale for balansa clover (*Trifolium michelianum*). This describes the progress of individual inflorescence from bud visible to seed shatter, and this scale will be used to track reproductive development of balansa clover and to generate a similar scale for arrowleaf (*T. vesiculosum*), gland (*T. glanduliferum*) and Persian (*T. resupinatum*) clovers. Thus, this study aims to quantify the duration of seed development (from bud visible to physiological maturity) based on the generated reproductive development scale of these four species of annual clovers.

Materials and methods
Four replicates of 'Cefalu' arrowleaf, 'Bolta' balansa, 'Prima' gland and 'Mihi' Persian clover were sown at Lincoln University, Canterbury, New Zealand (43°38′S, 172°28′E, 11 m a.s.l.) on 10 dates at monthly intervals (Table 1). The experimental design was a split-plot factorial in randomised complete blocks with sowing date as main plots and species as sub-plots (3×2 m). Information on the site location and crop management were described previously by Nori *et al.*(2014). In this location, monthly rainfall ranged from 153 mm in

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May 2010 to 9 mm in November 2009 (Figure 1). The mean daily air temperature ranged from 5.6°C (July 2010) to 16.8°C in December 2010. Unscarified seeds of annual clovers were sown as monoculture at 6 kg/ha ('Cefalu' arrowleaf), 4 kg/ha ('Bolta' balansa and 'Prima' gland) and 5 kg/ha ('Mihi' Persian) based on the final germination tests and seed weight data. The aim was to produce a monoculture of each species (at ca. 400 seedlings/m^2) that could be used to monitor plant development. Air temperature was recorded from a sensor placed at 1.2 m above the ground. Plots were not grazed throughout the crops' life span.

In each subplot, 10 plants were marked for detailed reproductive measurements. Date of flowering was

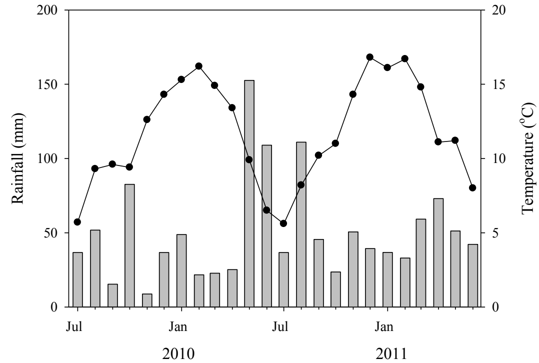

Figure 1 Monthly rainfall (bars) and mean daily air temperature (●) from 1 July 2009 to 30 June 2011. Data were obtained from Broadfields meteorological station (2 km north of the site), Canterbury, New Zealand.

Table 1 The sowing dates and date of flowering for four species of annual clovers sown at Lincoln University, Canterbury, New Zealand.

Sowing date	Date of flowering (first bud visible in 50% of marked plants)			
	'Cefalu' arrowleaf	'Bolta' balansa	'Prima' gland	'Mihi' Persian
26/2/2010	21/9/10	14/9/10	16/7/10	16/11/10
30/3/2010	16/10/10	1/10/10	9/9/10	20/11/10
4/5/2010	23/10/10	8/10/10	22/9/10	20/11/10
3/6/2010	24/10/10	15/10/10	28/9/10	22/11/10
7/7/2010	8/11/10	22/10/10	12/10/10	23/11/10
14/8/2010	19/11/10	8/11/10	29/10/10	3/12/10
25/9/2010	16/12/10	6/12/10	20/11/10	16/12/10
9/11/2010	20/1/11	31/12/10	25/12/10	5/2/11
20/12/2010	5/3/11	10/2/11	7/2/11	-
19/1/2011	29/4/11	31/3/11	9/3/11	-

Each date of flowering is means of four replicates.

Table 2 Numeric scale outlining the ontogenetical progress of an arrowleaf clover inflorescence.

1	The inflorescence bud is visible in the axil of a leaf
2	The peduncle is visible, the calyx is green (G or GY) and no corolla are visible
3	A single corolla is visible
4	>80% of florets within the inflorescence have a visible corolla
5	Full flower – 100% of corolla have the standard unfolded from the wings
6	<50% of the inflorescence turned brown as an indication of pollination[1]
7	>50% of the inflorescence are brown. Pods are formed within the inflorescence starting from the basal inflorescence
8	50% of pods are formed in the inflorescence
9	>90% of the inflorescence is brown. > 50% of pods are formed
10	Seeds in the bottom pod turned yellow
11	Seeds in the bottom pod turned red/brown. 50% of seeds turned yellow.
12	50% of seeds turned red/brown
13	100% of seeds turned red/brown (5 YR 5/10, 2.5 YR 3/8, 10 R 3/2)

Note: Values within parentheses correspond to Munsell (1977) colour charts for plant tissues.
[1]Petals that are brown/wilted with age are not counted. For a revised scale, refer to Nori (2013).

determined when 50% of the marked plants had their first inflorescence bud visible in the axil of a leaf. A reproductive development scale was generated with a numeric score that represented the ontogenetical changes in the inflorescence from bud visible to harvest maturity in arrowleaf, balansa, gland and Persian clovers. For balansa clover, the reproductive development scale was generated previously by Monks (2009) (Table 3) and was used to track seed development of balansa clover in this study. Meanwhile, the scales created for arrowleaf, gland and Persian clover inflorescences (Tables 2, 4 and 5) were based on Monks (2009) with modification to account for the different reproductive structures for each species.

One hundred inflorescences per subplot were tagged at the first sign of pollination (stage 6). Following inflorescence marking, five inflorescences were harvested at 4 day intervals. These were dissected and observed in detail using numeric scores from the reproductive development scale before dry weight measurement. Harvesting and recording stopped when 100% of seeds had turned red/brown (stage 13 for arrowleaf clover) and the seed pods had shattered (stage 16 for balansa, stage 13 for gland and stage

Table 3 Numeric scale outlining the ontogenetical progress of a balansa clover inflorescence.(From Monks 2009).

1	The inflorescence bud is visible in the axil of a leaf
2	The peduncle is visible, the calyx is green (G or GY) and no corolla are visible
3	A single corolla is visible
4	>80% of florets within the inflorescence have a visible corolla
5	Full flower – 100% of corolla have the standard unfolded from the wings
6	All florets within inflorescence show browning as an indication of pollination[1]
7	Abscission layer formed and florets have drooped downwards
8	Pods are visible within inflorescence
9	>50% of outer pedicles show red (R) colouring
10	50% of pods are red
11	100% of pods are red
12	50% of pods are yellow (2.5Y (8/8 to 10) or 5Y (8/8 to 10)
13	100% of pods are yellow
14	First sign of seeds darkening (7.5YR (6/8) to 5 YR (2/3))
15	100% of seeds are dark (7.5 YR (6/8) to 5 YR (2/3))
16	Seed shatter upon burst pods

Note: Values within parentheses correspond to Munsell (1977) colour charts for plant tissues.
[1]Petals that are brown/wilted with age are not counted.For a revised scale, refer to Nori (2013).

Table 4 Numeric scale outlining the ontogenetical progress of a gland clover inflorescence.

1	The inflorescence bud is visible in the axil of a leaf
2	The peduncle is visible, the calyx is green (G or GY) and no corolla are visible
3	A single corolla is visible
4	>80% of florets within the inflorescence have a visible corolla
5	Full flower – 100% of corolla have the standard unfolded from the wings
6	Florets on the base inflorescence turned purple as an indication of pollination[1]
7	Florets on the top inflorescence turned purple. Abscission layer formed starting from the base inflorescence
8	Pods are visible within the inflorescence
9	Pods enlarge, green (G or GY) in colour
10	Formation of one or more complete seed. Seeds are green in colour (5 GY (5/10 to 6/8))
11	Pods are green yellow (2.5 GY (8/4 to 8/6)). First sign of seed yellowing (5 Y 8/4 to 2.5 GY 8/10)
12	Seeds are hard and 100% of seeds are yellow (2.5 Y 8/6 to 5 Y 8/8)
13	Seeds shatter upon rubbing

Note: Values within parentheses correspond to Munsell (1977) colour charts for plant tissues.
[1]Petals that are purple/wilted with age are not counted. For a revised scale, refer to Nori (2013).

12 for Persian clover). The time from first floral bud visible to seed maturity was quantified using thermal time calculated using the equations in Jones & Kiniry (1986). The dry weight of inflorescence was plotted against thermal time from pollination to determine physiological maturity of the seed. The maximum dry weight of the inflorescence marked seed physiological maturity (Hyde 1950). It was assumed that the increase in total inflorescence weight was reasonably related to the seed filling and that any decrease in dry weight (pod dessication, etc.) began at the time of seed maturity (Davies & Williams 1986).

Results

Flowering occurred in all plots except for 'Mihi' Persian clover sown on 20 December 2010 and 19 January 2011. The plants sown on these dates died in August 2011, with no signs of reproductive development. The thermal

Table 5 Numeric scale outlining the ontogenetical progress of a Persian clover inflorescence.

1	The inflorescence bud is visible in the axil of a leaf
2	The peduncle is visible, the calyx is green (G or GY) and no corolla are visible
3	A single corolla is visible
4	>80% of florets within the inflorescence have a visible corolla
5	Full flower – 100% of corolla have the standard unfolded from the wings
6	Florets turned brown as an indicator of pollination starting from the basal inflorescence[1]
7	All florets within the inflorescence turned brown
8	Inflorescence swell, pods start to form within the inflorescence
9	Pods enlarge, green in colour
10	Pods turned yellow. Seeds are green in colour
11	Pods turned brown. First sign of seeds change colour
12	Pods burst

Note: Values within parentheses correspond to Munsell (1977) colour charts for plant tissues.
[1]Petals that are brown/wilted with age are not counted. For a revised scale, refer to Nori (2013).

Table 6 Thermal time accumulation (°C days) from bud visible to open flower in 'Cefalu' arrowleaf, 'Bolta' balansa, 'Prima' gland and 'Mihi' Persian clovers sown on 10 different dates in Lincoln University, Canterbury, New Zealand.

Sowing date	Species			
	'Cefalu' arrowleaf	'Bolta' balansa	'Prima' gland	'Mihi' Persian
26/2/2010	341	237	214	210
30/3/2010	369	215	219	204
4/5/2010	366	230	216	208
3/6/2010	354	227	198	180
7/7/2010	326	237	218	172
14/8/2010	304	197	184	163
25/9/2010	303	190	181	167
9/11/2010	327	206	167	182
20/12/2010	378	192	175	-
19/1/2011	-	222	185	-
Mean	341	215	196	186
S.E.M.	7.4	4.5	5.2	6.4
P-value	0.148	0.059	0.175	0.430

Thermal time quantified based on air temperature (T_b = 0°C). S.E.M., standard error of the mean.

Table 7 Inflorescence maximum dry weight (g) of 'Cefalu' arrowleaf, 'Bolta' balansa, 'Prima' gland and 'Mihi' Persian clovers sown on 10 different dates in Lincoln University, Canterbury, New Zealand.

Sowing date	Species			
	'Cefalu' balansa	'Bolta' arrowleaf	'Prima' gland	'Mihi' Persian
26/2/2010	0.73	0.28	0.10	0.11
30/3/2010	0.83	0.26	0.12	0.12
4/5/2010	0.94	0.27	0.12	0.11
3/6/2010	0.71	0.21	0.13	0.11
7/7/2010	0.70	0.20	0.12	0.10
14/8/2010	0.67	0.18	0.10	0.08
25/9/2010	0.74	0.19	0.10	0.08
9/11/2010	0.64	0.14	0.11	0.07
20/12/2010	-	0.13	0.10	-
19/1/2011	-	-	-	-
Mean	0.74	0.21	0.11	0.10
S.E.M.	0.029	0.009	0.003	0.004
P-value	0.168	<.001	0.017	0.008
L.S.D. (5%)	-	0.036	0.019	0.030

S.E.M. standard error of the mean.L.S.D., Least significant differences

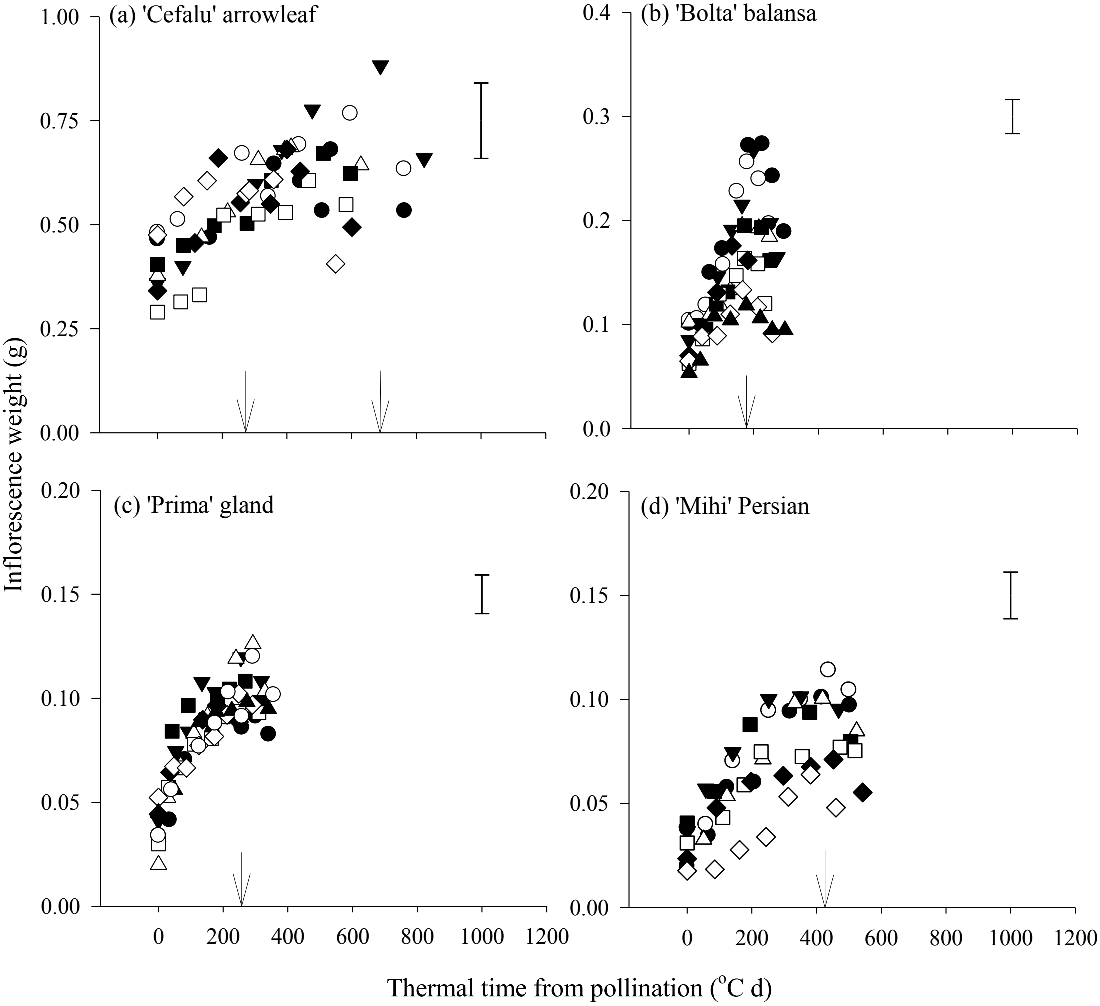

Figure 2 The inflorescence weight of (a) 'Cefalu' arrowleaf (b) 'Bolta' balansa (c) 'Prima' gland and (d) 'Mihi' Persian clovers against thermal time from pollination (stage 6) for crops sown on different dates at Lincoln University, Canterbury, New Zealand. 26 Feb 10 (●), 30 Mar 10 (○), 4 May 10 (▼), 3 Jun 10 (△), 7 Jul 10 (■), 14 Aug 10 (□), 25 Sep 10 (◆), 9 Nov 10 (◇), 20 Dec 10 (▲). Arrows indicate physiological maturity. Error bars represent the maximum standard error of the mean. Note: Thermal time analysis used air temperature (T_b = 0°C for arrowleaf and Persian, T_b = 5.2°C for balansa and T_b = 4.3°C for gland clover (Nori *et al.* 2014)). For statistical results across 10 sowing dates, refer to Nori *et al.* (2014).

time accumulation from bud visible to open flower averaged 341 °C days for 'Cefalu' arrowleaf, 215 °C days for 'Bolta' balansa, 196 °C days for 'Prima' gland and 186 °C days for 'Mihi' Persian clovers across all sowing dates (Table 6). 'Cefalu' arrowleaf clover sown on 19 January 2011 had visible buds on 29 April 2011 but these did not develop any further.

In all species, inflorescences for plants sown on 19 January 2011 rotted due to continuous autumn rainfall and lack of pollination in May 2011 and failed to reach physiological maturity (Table 7). The maximum weight of inflorescence in all species differed ($P<0.05$) with sowing date, except for 'Cefalu' arrowleaf clover.

The maximum weight of inflorescence in 'Cefalu' arrowleaf clover averaged 0.74 g across all sowing dates. For 'Bolta' balansa clover, the weight of inflorescence declined with successive sowing dates from 0.28 g for February sown plants that flowered in early spring to 0.13 g for December sown plants that flowered in mid-summer. The maximum weight of inflorescence in 'Prima' gland clover ranged from 0.10 to 0.13 g. For 'Mihi' Persian clover, the maximum weight of inflorescence averaged 0.11 g for those that flowered in late spring (sown between February and June) but decreased with seasonal changes down to 0.07 g in late summer (November sown). The inflorescence reached its maximum weight (physiological maturity) after 274–689 °C days for 'Cefalu' arrowleaf, 185 °C days for 'Bolta'

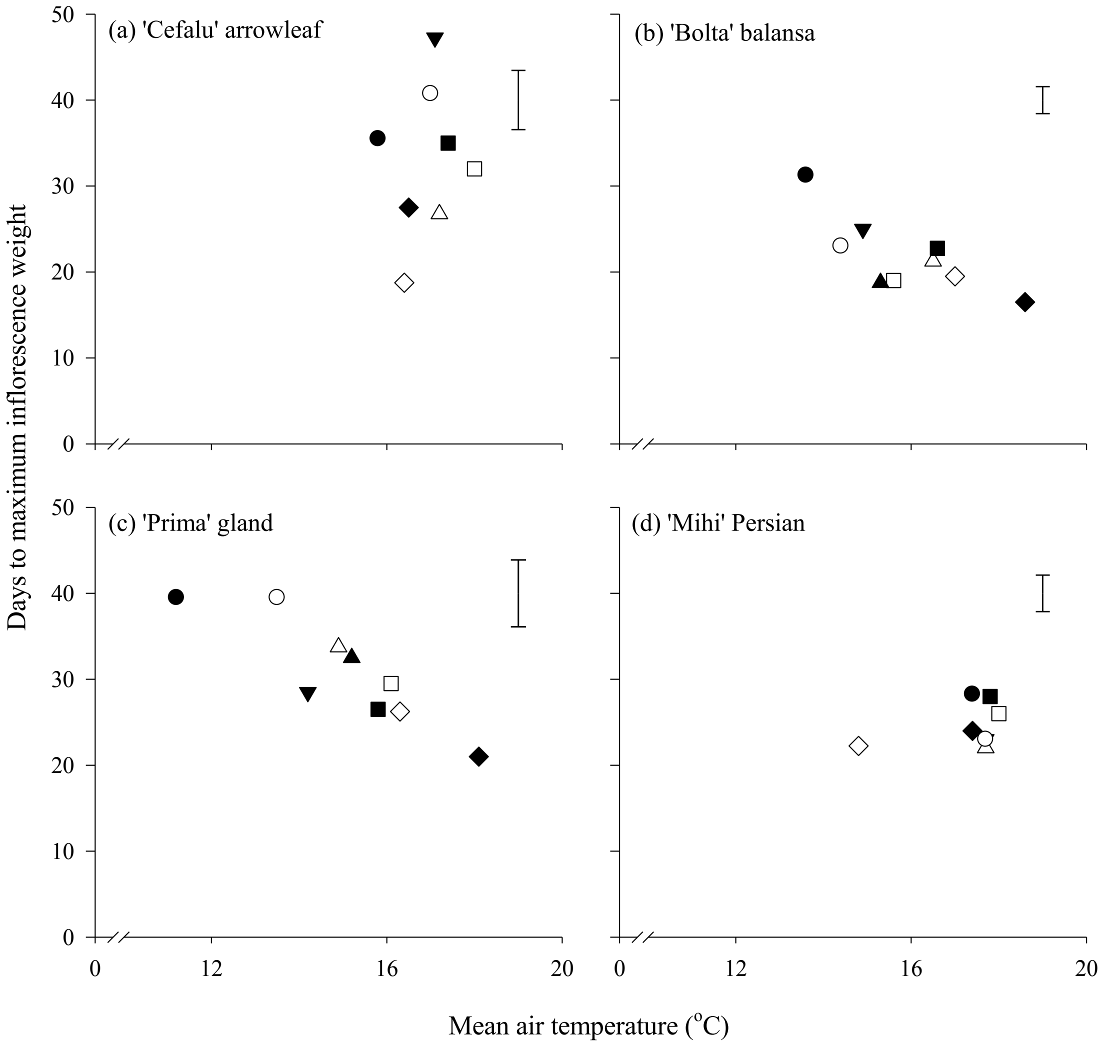

Figure 3 Days to maximum inflorescence weight for (a) 'Cefalu' arrowleaf, (b) 'Bolta' balansa, (c) 'Prima' gland and (d) 'Mihi' Persian clover against mean daily temperature from pollination (stage 6) to maximum inflorescence weightsown on 10 different dates at Lincoln University, Canterbury, New Zealand on 26 Feb 10 (●), 30 Mar 10 (○), 4 May 10 (▼), 3 Jun 10 (△), 7 Jul 10 (■), 14 Aug 10 (□), 25 Sep 10 (◆), 9 Nov 10 (◇), 20 Dec 10 (▲). Error bars represent the maximum standard error of the mean.

balansa, 256 °C days for 'Prima' gland and 425 °C days for 'Mihi' Persian clover (Figure 2). The differences in thermal time requirements for physiological maturity across 10 sowing dates for these four species were reported previously by Nori *et al.* (2014). This event occurred when 50% of seeds turned red/brown (stage 12) in 'Cefalu' arrowleaf, 100% of pods were yellow (stage 13) in 'Bolta' balansa, seeds were hard and 100% of seeds were yellow (stage 12) in 'Prima' gland and pods turned brown and the first sign of seeds changing colour (stage 11) in 'Mihi' Persian clover in accordance with the visual reproductive development scale (Tables 2–5).

Discussion

The time to first flower in these four annual clovers was affected by the photoperiod at the time of crop emergence (Nori *et al.* 2014). In most sowing dates (February–November), these species only flowered when day length was increasing in spring and summer (Table 1). As these are cross-pollinated species, flowering at these seasons gives favourable conditions (warm temperatures and low moisture) for pollinating insects, thus promotes seed development process. Therefore, it is not recommended to sow annual clovers in summer, particularly between December and January. This is because these plants will flower in autumn, but the inflorescence will not develop into seed but decay instead due to wet and cold conditions (Table 7). In all species, inflorescence weight was the heaviest when seed filling occurred during mid-spring to early summer and was associated with autumn sown plants. For spring sown plants that experienced seed filling during summer, the warmer ambient temperature which coincided with summer moisture deficits accelerated plant senescence. This shortened the duration of seed filling (Figure 3) in days which would reduce total light interception and therefore photosynthate supply, and as a consequence produce the lower inflorescence weights. The maximum weight of inflorescence marks the end of seed filling. The seeds are physiologically mature at this point and ready to be harvested, grazed to open the sward and to spread faeces, or allowed to drop in a pasture situation. The visual reproductive development scale was created as tools to help farmers to recognise the sign of seed maturity to ensure some regeneration of seed in the following seasons. It is suggested that when half of the seeds have turned red/brown in arrowleaf (stage 12, Table 2), pods become yellow in balansa (stage 13, Table 3), gland clover seeds are yellow and hard (stage 12, Table 4), and the first sign of seed colour change in Persian clover (stage 11, Table 5) is an appropriate time for harvest/grazing. Quantifying duration of seed development in thermal time provides a uniform measurement which can be applied over a broad range of climatic conditions. For example, 'Mihi' Persian clover required 425 °C days from full flower (peak flowering) to physiological maturity (maximum inflorescence weight). Translated into calendar days, this means 'Mihi' Persian clover seeds would take 28 days to mature if the average daily temperature was a constant 15°C. Based on long term mean temperature data, a theoretical chronological time to seed harvest following peak flowering can be estimated for a range of sites in New Zealand (Table 8). Following physiological maturity, grazing can resume to remove top growth and open up the sward. The bare ground will assist seed softening (Quinlivan 1965), thus increase the chances of seedling regeneration (Craig & Ballard 2000; Monks *et al.* 2008) in the next season. Small seeded annual clovers consumed by grazing livestock are expected to pass through the animal gut unharmed and return to the soil via faeces (Edward *et al.* 1998; Russi *et al.* 1992). This method of seed dispersal would

Table 8 Predicted chronological time (days) to seed harvest following peak flowering in 'Cefalu' arrowleaf, 'Bolta' balansa, 'Prima' gland and 'Mihi' Persian clovers at four locations in New Zealand (days calculated from NIWA meteorological data, using a T_b =0°C for arrowleaf and Persian, T_b = 5.2°C for balansa and T_b = 4.3°C for gland clover).

Species	Location	Date of peak flowering				
		1 Oct	1 Nov	1 Dec	1 Jan	1 Feb
'Cefalu'arrowleaf	Napier	48	32	25	21	14
	Blenheim	56	36	27	22	16
	Lincoln	-*	39	30	24	17
	Lake Tekapo	-*	46	34	26	19
'Bolta'balansa	Napier	13	11	10	9	10
	Blenheim	15	13	11	10	11
	Lincoln	16	14	12	11	12
	Lake Tekapo	21	17	14	12	13
'Prima' gland	Napier	18	16	14	13	13
	Blenheim	21	18	16	14	15
	Lincoln	23	20	17	15	16
	Lake Tekapo	29	23	19	17	17
'Mihi' Persian	Napier	-	-	23	22	22
	Blenheim	-	-	26	24	24
	Lincoln	-	-	28	26	27
	Lake Tekapo	-	-	32	28	29

Note: *It is unlikely that 'Cefalu' arrowleaf clover grown in Lincoln and Lake Tekapo will flower as early as September because temperatures in these locations are much colder. 'Mihi' Persian clover requires a specific photoperiod between 15.4 and 16.6 hours to flower (Nori *et al.* 2014). This means that 'Mihi' Persian clover will not flower until mid-November.

appear the most effective for arrowleaf, gland and Persian clovers, to ensure their seeds are shed on the ground, because their seeds do not shatter upon burst pods (Nori 2013). Knowing the duration and the end-point of seed development for each clover species will enable farmers to decide the time of seed harvesting, the time grazing can be resumed, and the time for preparation of seeds for pasture regeneration in the following season.

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