Cardinal temperatures and vernalisation requirements for a selection of vegetables for seed production

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Abstract

The cardinal temperatures and vernalisation requirements for a selection of vegetables for seed production were studied. Experiment one assessed the rate of germination (1/days) for 10 vegetable species over a range of 5-40°C, in order to calculate the cardinal temperatures for germination (base, optimum and maximum). Experiment two examined the vernalisation response of imbibed cabbage, carrot and red beet seeds, plus perennial ryegrass as a control over durations of 0-12 weeks at 4°C. Red beet and ryegrass had positive vernalisation responses with anthesis occurring in plants from the 4-12 week durations in red beet, and all durations in ryegrass. No vernalisation treatment induced flowering in cabbage and carrots. The number of days to anthesis and the final number of main stem leaves did not differ (P=0.143 and P=0.323 respectively) among vernalisation durations in red beet, but did in ryegrass (P<0.001 and P<0.01 respectively). Red beet may have reached vernalisation saturation at ≤4 weeks, resulting in a minimum number of leaves produced for all durations. There is potential for the sowing date of red beet to be changed to spring for successfully vernalised seeds, which would reduce the expenses of weed, pest and disease control and give opportunity of other land uses over the winter period.

***Additional keywords*:** biennial, cabbage (*Brassica oleracea*), carrot (*Daucus carota*), germination, perennial ryegrass (*Lolium perenne*), photoperiod, red beet (*Beta vulgaris*)

Introduction

The seed industry is an important part of New Zealand's economy and land based industries. Annual seed exports from New Zealand in 2010 and 2011 were valued at approximately $136 million per year, excluding cereal seeds (Hampton *et al.*, 2012). Of the $136 million, carrots (*Daucus carota* L.) contribute an average of $11.35 million per year. Carrot plants for seed production have a biennial lifecycle, meaning they take 13-14 months from sowing to harvesting of a seed crop (South Pacific Seeds, 2014). Carrot seed crops require long term land commitment due to their biennial life cycle and high capital input crop due to disease susceptibility and low competiveness against weeds. Cabbage (*Brassica oleracea* L.) contributes on average $4.6 million per year (Hampton *et al.* 2012), and is also a biennial seed crop with similar growing seasons and pest and disease issues to carrot. A decrease in the growing period required for biennial seed

crops, such as carrot, will reduce disease pressure such as *Sclerotinia sclerotiorum*, *Rhizoctonia solani* and *Alternaria radicina* as well as decrease the effect of difficult weeds which germinate in winter and early spring such as wireweed (*Polygonum aviculare* L.), field pansy (*Viola arvebsis* Murray), black nightshade (*Solanum nigrum* L.) and cleavers (*Galium aparine* L.). The reduction in pest pressure may minimise production expenses for vegetable seed crops. Many biennial vegetable species require a vernalisation period before they become reproductive and flower (Alessandro and Galmarini, 2007). The range of effective temperatures, the duration required and receptive stages vary for different species and cultivars, and for many vegetable seed species have not been precisely determined (Chouard, 1960; Atherton *et al*., 1990; Alessandro and Galmarini, 2007). Red beet (*Beta vulgaris* L.) has the ability to receive vernalisation as an imbibed seed (Chouard, 1960), which may suggest that other species could also have this ability. Vernalisation of the imbibed seed embryo could give the potential to establish seed crops post-winter, resulting in a shortened seed production cycle and decreased time for exposure to pests and disease.

An understanding of the cardinal temperatures is required for aligning the timing of sowing, germination and emergence with favourable environmental conditions for seedling growth and development (Monks *et al*., 2009). This study aims to expand the knowledge on seed vernalisation and the cardinal temperatures for important vegetable seed crops.

Materials and Methods

Experiment 1: Determination of cardinal temperatures

The rate of germination was compared for ten vegetable species including Asian radish (*Raphanus sativus* L.), cabbage, carrot, Chinese cabbage (*Brassica rapa* L.), mustard (*Brassica juncea* L.), onion (*Allium cepa* L.), pak choi (*Brassica rapa* L.), parsnip (*Pastinaca sativa* L.), red beet and red radish (*Raphanus sativus* L.) (Table 1). Perennial ryegrass (*Lolium perenne* L.) was included in the comparison as cardinal temperatures have been well defined. Three replicates of 50 seeds per species were placed on moist filter paper, in Petri dishes, in unlit incubators. The incubators were set at a range of constant temperatures from 5.0 to 40.0°C (± 0.5°C) at 5°C increments. Petri dishes were organised randomly in the incubators. Filter paper was kept moist when necessary with reverse osmosis (RO) water to ensure moisture was non-limiting for germination.

All species were sourced from South Pacific Seeds Ltd except for parsnip which was purchased from a Mitre10™ gardening centre in Christchurch. The perennial ryegrass cultivar was ‘Grasslands Samson’ and contained the AR37 endophyte. The ryegrass seed was also coated with Gaucho® insecticide.

Table 1: The vegetable species used in this experiment.

Species	Variety
Carrot *Daucus carota*	Hybrid Carrot No 31
Red beet *Beta vulgaris*	Hybrid Red beet KR-333
Cabbage *Brassica oleracea*	Hybrid Cabbage No 164
Mustard *Brassica juncea*	Hybrid Chinese Mustard CMF-18
Chinese cabbage *Brassica rapa*	Hybrid Chinese Cabbage CCF-31
Pak choi *Brassica rapa*	Hybrid Pak Choi No 4
Red radish *Raphanus sativus*	Hybrid Radish No 108 3.75-4.0
Asian radish *Raphanus sativus*	Hybrid RR Radish N34514
Onion *Allium cepa*	OP Onion Baron >2.4
Parsnip *Pastinaca sativa*	not available

Germination was scored daily, except for the first three days at temperatures >25°C which were scored twice daily. Germinated seedlings were removed from the dish for ease of counting each day. Germination was counted as a seed with a radicle of ≥1 mm in length. This measure was by eye, as measuring with any device was not practical. Germination was counted until at least 50% of the seeds had germinated. In cases where 50% germination was not reached, the experiment ceased when no further seeds had germinated for five consecutive days. Non germinated seeds were not tested for viability after removal from the petri dish.

The rate of germination was calculated for each temperature treatment for all species. Firstly the number of days to 50% germination was determined. Secondly, the inverse of the number of days to 50% germination (1/days) was calculated as the germination rate. To determine cardinal temperatures for each species, multiple (a minimum of two) linear regression lines were fitted to mean data points of the germination rate (50% germination) for each temperature. The base temperature for germination was calculated where the regression for the lower temperature treatments crossed the x-axis. The optimum temperature was determined where the regressions intersected at the highest rate of germination. The maximum temperature was calculated where the regression for the higher temperatures crossed the x-axis.

Thermal time (°C days) was calculated for germination for each species. This was done for each temperature treatment minus the calculated base temperature related to the species and accumulated for the number of days to 50% germination.

Experiment 2: Determination of vernalisation requirement

Cabbage, carrot, red beet and perennial ryegrass were used for the vernalisation experiment. Imbibed seeds were exposed to a range of cold period durations. The seeds used were from the same source as experiment one. These vegetable species were chosen as they have similar biennial lifecycles when grown as a seed crop, and ryegrass is a well-documented comparison successfully vernalised as an imbibed seed (Cooper, 1960; Heide, 1994).

Experiment 2 took place in an incubator in the Field Service Centre at Lincoln University. The duration treatments used were 0, 2, 4, 6, 8, 10 and 12 weeks. The

temperature used for vernalisation of all species was a constant 4°C (± 0.5°C) with no light. The experiment began with the longest vernalisation duration period. This consisted of 15 seeds of each species being placed in separate petri dishes on wetted filter paper. This was replicated six times, giving a total of 24 dishes per duration treatment. Petri dishes were kept moist with RO water when necessary which was at room temperature when added.

The longest duration (12 weeks) started on the 22 March 2013, followed by the declining durations being added into the incubator every two weeks, so that after 12 weeks all treatments had been in the incubator for the required length of time. The zero week vernalisation treatment was germinated at room temperature. Three weeks into the vernalisation period, while still at 4°C, some of the species, particularly cabbage, germinated and began to develop leaves. These seedlings were planted into trays moved to another incubator still at 4°C, but with 24 hour lighting. The trays contained the same potting mix which was to be used in the glasshouse component of the study. Light readings were taken with a Skye Spectro Sense at the top, bottom and middle of the incubator, and the average light reading in the incubator was 2.8 $\mu M/m^2$.

On completion of the vernalisation periods (13 June 2013), all seeds and seedlings in trays were planted into pots and transferred to a glasshouse. Four seeds/seedlings were planted into a 2.5 l pot filled with a 3-4 month bark and pumice composite potting mix. The pots were arranged in a complete randomised block design in the glasshouse with the replicates blocked. Plants were watered as required.

Air temperature in the glasshouse was measured every two hours. The average temperature for each month the experiment ran was between 18.1 and 19.9°C with the minimum temperature for the period 17°C. The photoperiod was 20 hours to saturate any photoperiod requirements consisting of natural and artificial lighting during daylight hours, and artificial lighting during night hours.

The number of days from when the vernalisation period finished (13 June) to anthesis (flowering) was recorded. At flowering, the plant was harvested by cutting off at the base, and the final main stem leaf number was counted. In perennial ryegrass this count was taken from the main stem in the primary tiller. Counts were taken for each plant in each pot. Plants were numbered from 1 to 4 determined by the order in which each plant flowered. The final leaf counts were made on 12 October 2013. At the end of the sampling period, carrot and cabbage from the longest vernalisation treatments were dissected under microscope to determine if any floral development of the apical meristem had occurred.

Data was analysed for individual species using Genstat Version 15 (VSN International Ltd, UK) by a one-way ANOVA. The significant differences between means were separated using the least significant difference (LSD) test at a 5% level. Regression analysis was conducted on both the number of days to anthesis and the main stem leaf number for red beet and ryegrass.

Results

Base temperature experiment

The base temperatures of the species involved ranged from -0.2 to 6.1°C (Table 2) with examples given in Figure 1 of the species used in Experiment 2. The optimum

temperatures ranged from 15.4 to 35.9°C, but most of the species were around 28 to 30°C. The maximum temperatures for germination ranged from 37.4 to 45.5°C, but for most species around 40 to 42°C.

Parsnip had the lowest cardinal temperatures, particularly the optimum temperature at 15.4°C, which was almost half that of all the other species, except for onion. Parsnip and onion were the only species which had maximum temperatures of less than 40°C. Mustard had the highest base temperature at 6.1°C, but had similar optimum and maximum temperatures to other species. Red beet had the highest optimum temperature at 35.9°C and the second highest maximum temperature (44.4°C) after pak choi at 45.5°C.

Thermal time to 50% germination varied between species with Chinese cabbage and red radish requiring the least thermal time while parsnip required the greatest amount of thermal time (Table 2).

Table 2: The base, optimum, maximum temperature and thermal time requirement (°C) for germination determined by linear regression for the selected vegetable species and perennial ryegrass. Thermal time requirement for germination calculated using species base temperature.

Species	Base temperature (°C)	Optimum temperature (°C)	Maximum temperature (°C)	Thermal time germination (°C days)
Asian radish	3.3	29.7	41.3	19.2
Cabbage	1.4	30.7	41.9	26.4
Carrot	0.1	30.9	40.7	97.2
Chinese cabbage	4.6	35.2	42.9	17.1
Mustard	6.1	31.1	40.7	20.0
Onion	1.2	21.5	39.6	74.7
Pak choi	3.1	29.4	45.5	16.8
Parsnip	-0.2	15.4	37.4	167.4
Red beet	4.2	35.9	44.4	60.4
Red radish	1.5	28.7	41.6	17.1
Ryegrass	1.1	29.3	40.4	86.0

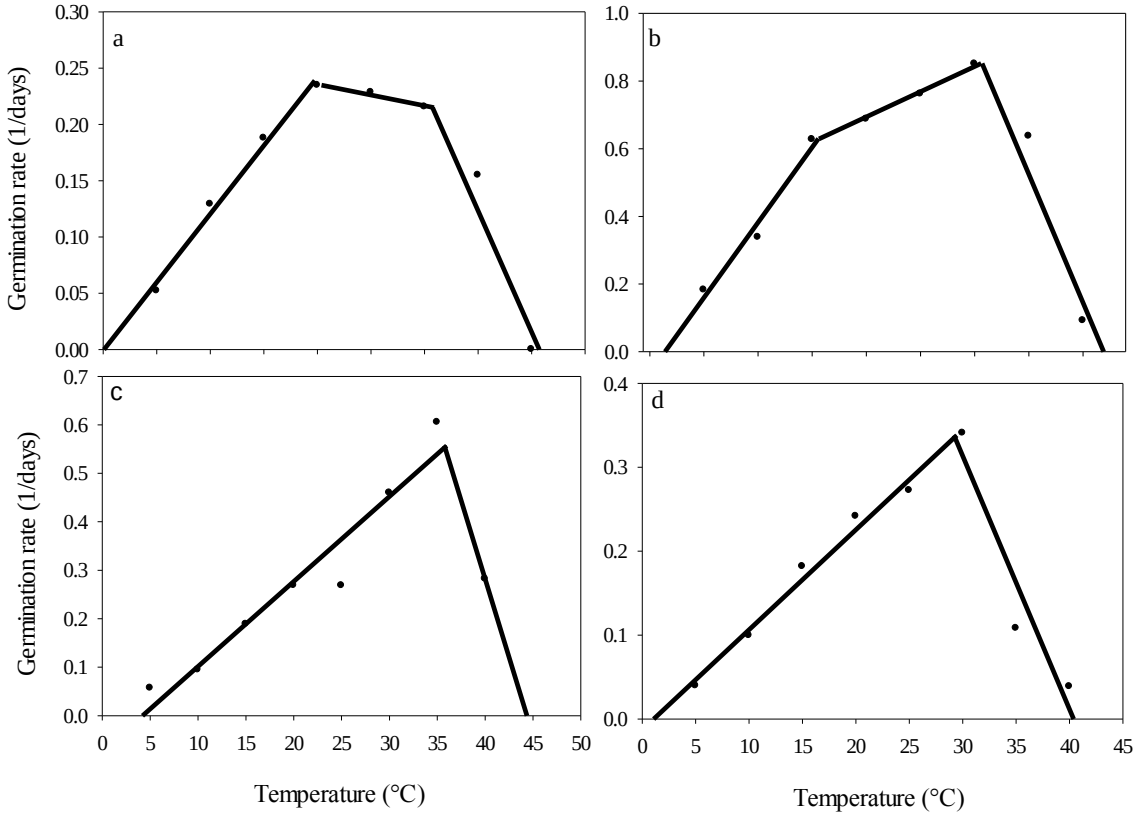

Figure 1: Germination rate of carrot (a), cabbage (b), red beet (c) and perennial ryegrass (d) at eight different temperatures.

Vernalisation experiment

Perennial ryegrass and red beet plants showed a positive response to the vernalisation treatment as imbibed seeds, where flowering occurred in plant exposed to vernalisation durations of ≥4 weeks. Three carrot plants flowered in total for the entire experiment, but were from different vernalisation durations (one each from 6 week, 8 week and 10 week treatments). There was no visual evidence of reproductive development on the apices among vernalisation durations for carrot or cabbage plants at the end of the experiment.

The number of plants which flowered on average per pot (out of four) generally increased as the vernalisation duration increased and plateaued for perennial ryegrass and red beet at six and eight weeks respectively (Figure 2, $P<0.001$). The number of plants per pot that flowered between species was different ($P<0.001$), with ryegrass having a higher number of plants at every vernalisation treatment compared with red beet. At zero and two week vernalisation treatments, no flowering occurred in any plants from any replicate of red beet. At the four week vernalisation treatment red beet plants began to show limited flowering, with one plant per pot on average flowering. This was similar at the six week treatment, but thereafter for the eight, 10 and 12 week vernalisation treatments, flowering occurred in two to three plants per pot on average. Anthesis in the ryegrass occurred in one plant on average in the zero and two week vernalisation treatments, then increased to

two plants in the four week treatment and three to four plants in the six, eight and ten week treatments. At the twelve week treatment all four ryegrass plants flowered in every pot.

The duration of the vernalisation period did not affect (P=0.143) the number of days to flowering in red beet and averaged 93 days (Figure 3a). The main stem leaf number of the red beet plants was not different between the 12 and four week vernalisation treatments and averaged 30 leaves (P=0.323) (Figure 3b).

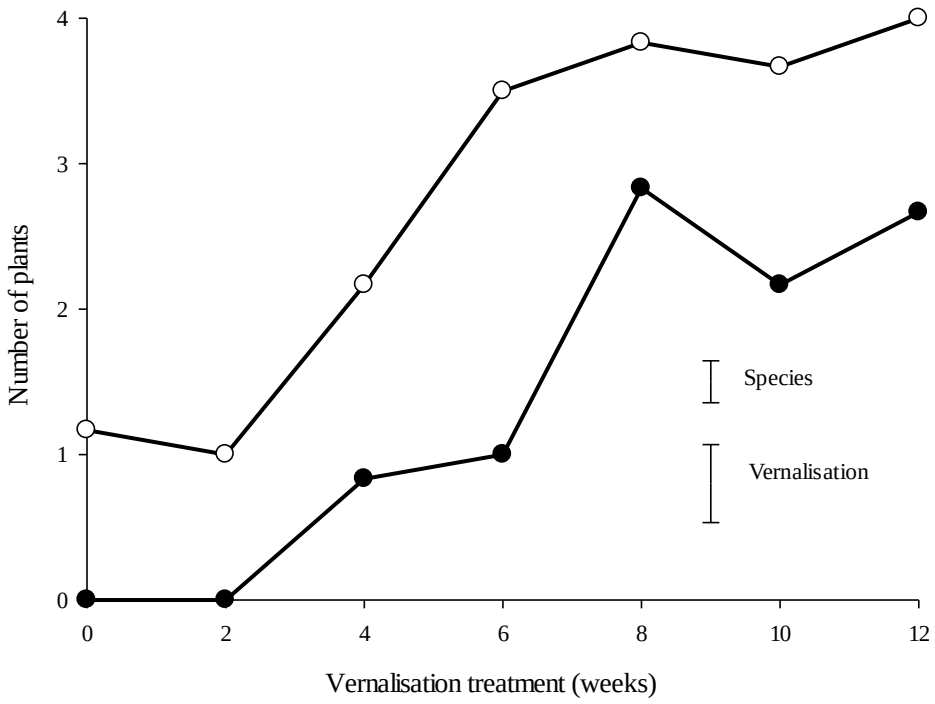

Figure 2: The number of plants that flowered per pot (out of a possible 4) over vernalisation durations of 0-12 weeks, for perennial ryegrass (○) and red beet (●). The effect of vernalisation (LSD 0.537, p <0.001) and species (LSD 0.287, P <0.001) was significant with no interaction.

The duration of the vernalisation period affected (P<0.001) the number of days from when treatment ended to when anthesis occurred for perennial ryegrass (Figure 4a). Plants exposed to 12 weeks vernalisation flowered in fewer days (68 days). The number of days to anthesis increased continually as vernalisation duration decreased. Following two weeks of vernalisation ryegrass plants took 108 days to flower, which was 39 days longer than the 12 week treatment. The greatest change in the number of days to anthesis occurred following two and four weeks of vernalisation (17 days difference). The duration of vernalisation had a significant

effect on the average number of main stem leaves/nodes present at anthesis in perennial ryegrass (P=0.004) (Figure 4b). There was little reduction in the main stem leaf number between eight and twelve weeks vernalisation (<0.5 leaves), but there was a decrease of 1.5 leaves between two and six weeks vernalisation.

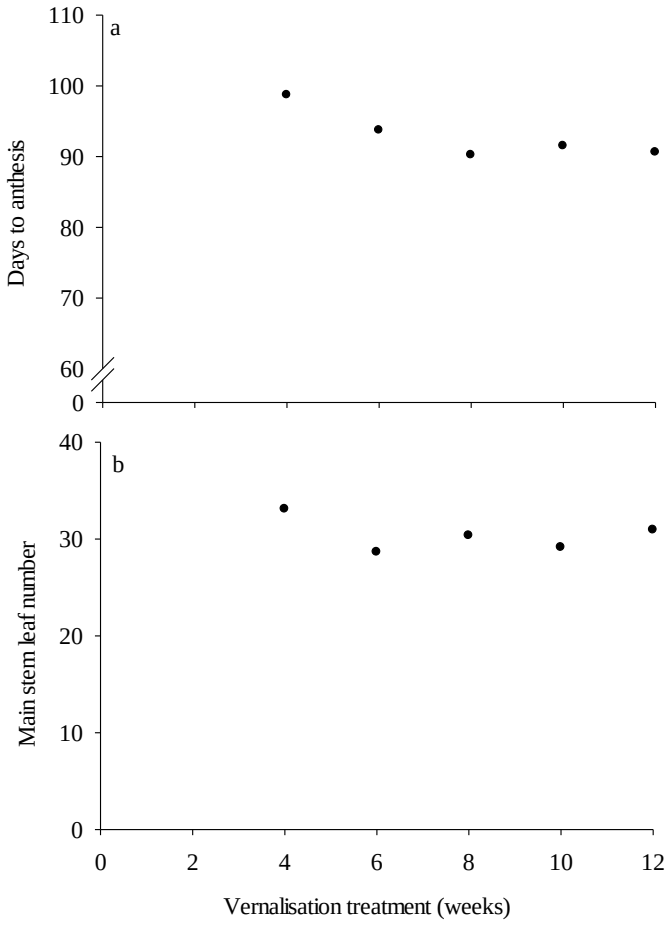

Figure 3: a) The number of days on average from the end of the vernalisation period until anthesis and b) the main stem leaf number in red beet over a vernalisation range of 0-12 weeks.

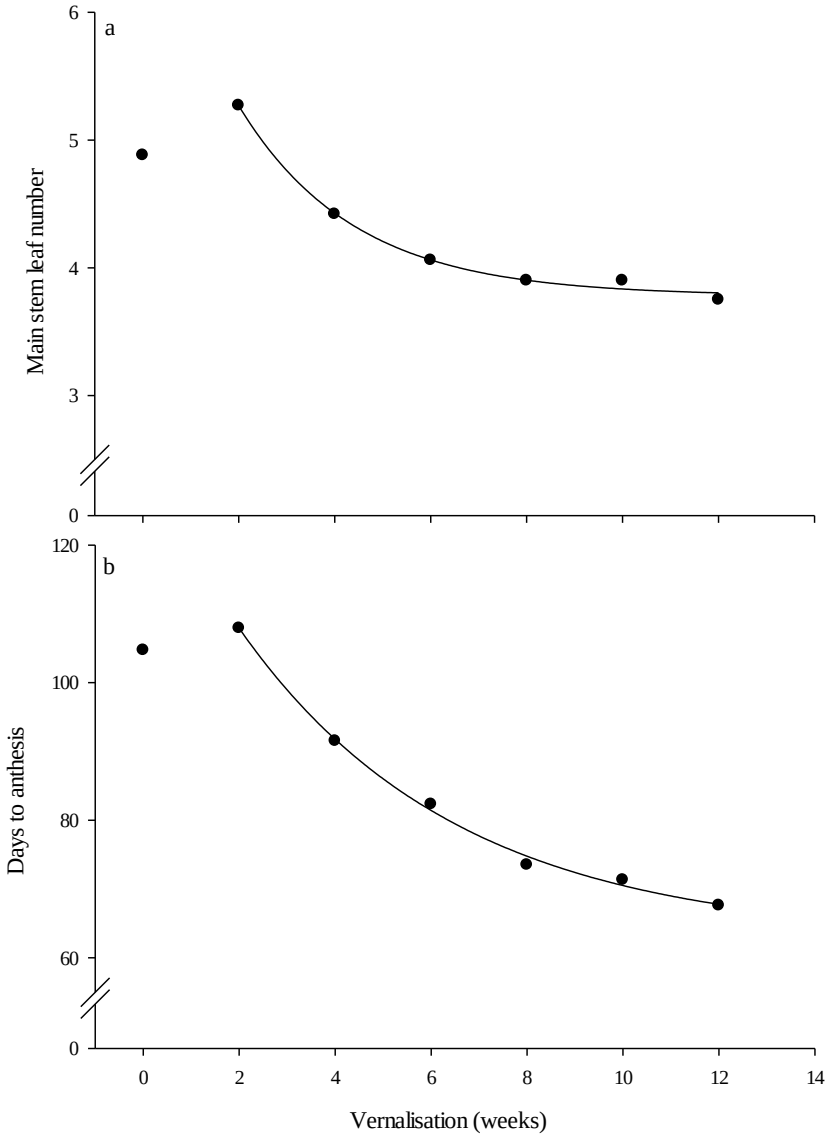

Figure 4: a) The number of days on average from the end of the vernalisation period until anthesis ($y=62.86+70.12e^{(-0.22x)}$, $R^2=0.99$) and b) the main stem leaf number ($y=3.78+3.42e^{(-0.42x)}$, $R^2=0.99$) in perennial ryegrass over a vernalisation range of 0-12 weeks. Regressions do not include 0 week vernalisation treatments.

Discussion

Cardinal temperature experiment

For most species tested, germination rate increased as a linear function of temperature up to the optimum temperature. Germination rate was reduced at low and high temperatures, similar to results shown by (Moot *et al*., 2000a) and consistent with a sigmoid response (Angus *et al*., 1980). All species exhibited a linear reduction in germination rate at supra-optimal temperatures for germination which allowed estimation of T_{max}. The most favourable temperatures germination were 20, 25 and 30°C, with these being the only temperatures where all species reached ≥50% germination. Bierhuizen and Wagenvoort (1974) stated that carrot and onion were generally slower than other vegetables species to germinate but they did not include red beet. Both species took between 3-5 days for 50% germination between 15-25°C while most other vegetable species reached ≥50% germination in 0.5-2.5 days at their optimum temperatures. Bierhuizen and Wagenvoort (1974), reported similar germination time frames for carrot and onion for the temperature range used in this experiment. Parsnip was the slowest vegetable to germinate at every temperature treatment in this experiment, with no germination occurring at any temperature in less than 5 days.

The calculated base temperature for all species tested ranged -0.2 to 6.1°C. This range is consistent with those published for many temperate, annual crops (Angus *et al*., 1980) and similar to the forage species reported by Moot *et al.* (2000b). The base temperature reported for ryegrass is similar to the 1.9 to 2.4°C reported by (Moot *et al*., 2000a) with variation possible in the definition of when germination has occurred. The base temperature calculated for carrot was 0.1°C, which is consistent with Suojala (2000) where they concluded the base temperature for germination of carrot was close to 0°C. Base temperature may be calculated to be below 0°C, which is difficult to explain biologically (Yang *et al*., 1995). The only species which was calculated in this experiment to have a base temperature below zero was parsnip, at -0.2°C.

Vernalisation experiment

No flowering occurred in any cabbage plants from any vernalisation duration while only three plants flowered in the carrot treatment. This could be assumed to be due to the imbibed seeds being insensitive to vernalisation, a juvenile stage was not able to be overcome. Wiebe (1990) stated cabbage was only sensitive to vernalisation when a plant had 4-15 leaves initiated and that carrot required at least 8 leaves initiated to be receptive to vernalisation. It is notable that the three carrot plants did flower were all from vernalisation durations of ≥6 weeks, perhaps suggesting some vernalisation effect. Kelly and George (1998) stated that although most vegetables for seed production are biennial, there is occasionally a tendency for a small number of plants to act as an annual and bolt (stem elongate) prematurely. This may explain reason for three carrot plants flowering. It may also be due to genetic variation in the carrot seed used. Chouard (1960) stated that some carrot cultivars in the past have been known to be able to be vernalised as imbibed seeds. The information presented by Chouard (1960) is very limited and contrasts to almost all other literature. This suggests there may be potential for plant breeders to develop this trait although it

may conflict with other desirable traits for vegetable production.

Flowering occurred in both red beet and perennial ryegrass. The number of days to anthesis was not reduced by vernalisation duration in red beet. It is important to note that no flowering occurred for 0-2 week vernalisation period. In comparison the number of days to anthesis was significantly affected by vernalisation duration in perennial ryegrass. Wiebe (1990) stated that when red beet is vernalised at its optimum temperature, of 5 to 9°C, it should only need to be exposed to the low temperature for three weeks to initiate flowering. In this study, two weeks of exposure at 4°C was not enough for red beet seed to be vernalised and thus flowering did not occur. It should be noted that the four week vernalisation period for red beet only enabled one out four plants within the pot to flower. It was not until eight weeks vernalisation that more than two plants per pot flowered. Leopold and Kriedmann (1975) demonstrated that perennial ryegrass plants showed a strong vernalisation response. Plants exposed to two weeks vernalisation took 160 days to flower compared with plants exposed for 13 weeks taking less than 30 days to flower. The results of this experiment showed some flowering in the zero week treatment, and flowering occurred after about 105 days in the two week vernalisation treatment although only one plant on average flowered in each pot. The differences may be due to the vernalisation requirement (often associated with germplasm origin) and glasshouse conditions. Differences can be expected between perennial ryegrass cultivars and it is often unknown if they have an obligative or facultative vernalisation requirement. The average glasshouse temperature (18.1°C) at the start of the experiment in June was similar to the maximum temperature where vernalisation can still be accumulated for some species.

The number of days to anthesis is affected by final main stem leaf number. The main stem leaf number did not change over vernalisation duration treatments in red beet plants, which is why there was also no differences in the number of days to anthesis. This suggests red beet has an obligate response to vernalisation. In comparison, the main stem leaf number increased as vernalisation duration decreased in perennial ryegrass, suggesting a facultative vernalisation response. In perennial ryegrass it is likely that primordium production continued while in the incubator. This causes a confounding effect between vernalisation effectiveness lowering the final leaf number, and response of vegetative growth to temperature (Robertson *et al*., 1996). Continued development of leaves was possible in the ryegrass in this study because the vernalisation temperature used was 4°C, and the base temperature for germination and development in perennial ryegrass was less than this, at 1.1°C. Whereas red beet had a calculated base temperature of 4.2°C, which was similar to the vernalisation temperature used, therefore no leaf development occurred during the vernalisation treatment. Development throughout vernalisation treatments has been reported occasionally in the literature (e.g., Robertson, 1996), but in young plants as opposed to imbibed seeds. Craigon *et al.* (1995) considered the possibility of development in young wheat plants during vernalisation treatment, and suggested that plants would advance towards reproductive development at an increasing rate as vernalisation accumulated towards saturation, a facultative response.

Perennial ryegrass still requires exposure to long photoperiod for flowering to be initiated. For red beet it may be possible that this can also occur in imbibed seeds, with the maximum number of primordia already developed on the apex by the end of the vernalisation period, an obligate response (the seed is fully vernalised). Another possible reason for there being no differences in the main stem leaf number could be the minimum number of leaves possible were formed in all vernalisation treatments. That a minimum number of leaves can be produced has been well documented for some species, but there are no reports in the literature for red beet.

Application to the vegetable seed industry

Arable farmers who grow biennial vegetable seed crops such as cabbage, carrot and red beet are often faced with crop rotation, weed, pest and disease issues related to the length of time the crop is in the ground, including over-winter. The positive vernalisation response of imbibed red beet seeds suggests that there is potential for the sowing date to be after winter, as opposed to late summer/early autumn. This could shorten the lifecycle from greater than 12 months, to 7-8 months. The effect that this would have on seed yield is unknown but agronomic management related to sowing density would likely need to be changed. Vernalisation as imbibed seeds does not appear to be a solution for cabbage or carrot seed crops. The ability of red beet seeds to be successfully vernalised means that this process could take place in a controlled environment, and the seeds could be transplanted into the field in optimum growing conditions during spring. The removal of the winter period from the red beet lifecycle would potentially decrease the overall costs of diseases such as downy mildew and weeds including cleavers and field pansy, as this period is where many issues arise. The number of species which could be included in the crop rotation may also be improved by changing the sowing date of red beet seed crops to spring, as well as allowing for the opportunity for other land uses over the winter period.

Conclusions

Cardinal temperatures were determined for a range of vegetable species. The base temperature, optimum temperature and maximum temperature for germination in carrot were 0.1, 30.9 and 40.7°C respectively. Red beet cardinal temperatures were 4.2, 35.9 and 44.4°C. Cabbage and carrot were not successfully vernalised as imbibed seeds, which was most likely due to insensitivity to vernalisation as an imbibed seed or juvenile plant. Red beet showed a positive vernalisation response as an imbibed seed, resulting in anthesis after 4-12 weeks exposure to 4°C and 20 hours light. As expected, ryegrass also responded positively to vernalisation, with anthesis occurring in all vernalisation treatments, confirming that the vernalisation conditions used were suitable for ryegrass at least. The number of days from the end of the vernalisation period to anthesis differed significantly in ryegrass, with a general decrease in days as vernalisation duration increased. Red beet did not have significant differences in the number of days to anthesis between the 4-12 week vernalisation durations. There is potential for the sowing date of red beet seed crops to be moved to spring, resulting in decreased weed, pest and disease expenses, and the possibility of opportunity cost of a short term winter crop.

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