Seasonal growth and development of Caucasian and white clovers under irrigated and dryland conditions

A.D. BLACK, D.J. MOOT and R.J. LUCAS
Soil, Plant and Ecological Sciences Division, P.O. Box 84, Lincoln University, Canterbury
blacka1@lincoln.ac.nz

Abstract

Dry matter (DM) production of sown monocultures of Caucasian and white clovers was compared under irrigated and dryland (non-irrigated) conditions in their third year. Caucasian clover produced 11.9 t DM/ha when irrigated and 9.4 t DM/ha under dryland conditions, and both treatments exceeded white clover by ~2.5 t DM/ha. This increase in yield reflected ~23 kg DM/ha/day higher production rates in spring and summer. During this period, production rates of irrigated treatments increased by 11 kg DM/ha/day/ºC for Caucasian compared with 8 kg DM/ha/day/ºC for white clover as mean daily air temperature increased from 8-16 ºC. In late summer/autumn, production rates of Caucasian clover decreased more than white clover when air temperature dropped from 16-9 ºC.

Growth (photosynthesis) and development (leaf appearance) characteristics of each species were also examined. Leaf photosynthesis was ~6 µmol $CO_2/m^2/s$ higher for Caucasian than for white clover irrespective of measured air temperatures (7-28 ºC) and soil moisture from 1.00-0.39 of water holding capacity (WHC, 512 mm to 1.5 m depth). Both clovers had similar ranges of optimum temperature (21-25 ºC) and soil moisture (1.00-0.86 of WHC) for photosynthesis. These results could explain the observed higher production rates for Caucasian clover in spring and summer, under both irrigated and dryland conditions. Lower production rates of Caucasian clover in autumn may be attributed to a similar phyllochron (126 ºCd), but higher base temperature (5 ºC) than for white clover (1 ºC), and hence a slower recovery to canopy closure post grazing. This study shows that Caucasian clover has potential to increase spring and summer legume production, in combination or as the sole legume species in both irrigated and dryland grass/clover pastures in lowland temperate environments of New Zealand.

Key words: irrigation, photosynthesis, phyllochron, seasonal production, *Trifolium ambiguum* M. Bieb, *T. repens*

Introduction

Caucasian clover (*Trifolium ambiguum* M. Bieb) is a persistent legume species that perenniates underground with rhizomes and forms a deep taproot system (Forde *et al.* 1989; Strachan *et al.* 1994; Taylor & Smith 1998). Under irrigation, Caucasian clover/ryegrass (*Lolium perenne*) pastures have been shown to produce greater total legume content than white clover (*Trifolium repens*)/ryegrass pastures from spring - autumn, but the greatest advantage was in summer (Black *et al.* 2000). Caucasian clover has also produced more legume than white clover in mixed pastures under dryland conditions (Watson *et al.* 1998; Black & Lucas 2000). However, the reasons for relative differences in seasonal DM production that contribute to differences in botanical composition between Caucasian and white clovers are unclear.

A comparison of seasonal DM production under irrigated and dryland conditions can be used to examine the suitability of Caucasian and white clovers in lowland permanent pastures. This approach integrates the effects of seasonal changes in temperature and moisture under dryland conditions, and the irrigation treatments allow the temperature responses to be examined. In Canterbury, seasonal DM production of Caucasian and white clovers has been compared under high (Olsen P 22 µg/ml, sulphate-S 14 µg/g) and low (Olsen P 10 µg/ml, sulphate-S 9 µg/g) fertility conditions in irrigated ryegrass pastures (Black *et al.* 2000). Similarly, in coastal Bay of Plenty, Watson *et al.* (1998) measured seasonal DM production of the two clovers in ryegrass pastures under drought conditions. In both cases, the suitability of Caucasian clover for the local conditions was highlighted, but application of results beyond the site and season of investigation is limited. An examination of the physiological basis for differences in DM production provides greater insight and offers confidence that general recommendations can be made about the suitability of Caucasian clover for wider inclusion in New Zealand pastures.

Thus, the initial objective of this research was to compare the DM production of Caucasian and white clovers when temperature and moisture differed, but fertility was non-limiting. The second objective was to relate any differences in seasonal DM production to growth (leaf photosynthesis rate) and development (leaf appearance rate) characteristics of each species. To do this, monocultures of the two clovers were established under irrigated and dryland conditions. Species comparisons of DM production were concentrated in year 3 after sowing, when both clovers had developed complete canopies. Results for years 2 and 3 were used for detailed measurement of plant growth and development characteristics.

Materials and methods

Site and design

The experiment was located at Lincoln University (43º 39'S, 172º 28'E, 11 m a.s.l.), Canterbury on a Wakanui silt loam soil (Cox 1978) with a mean (± s.e.) water holding capacity (WHC) of 512 ± 16.0 mm to 1.50 m depth. The experimental area was fertilised with sulphur superphosphate (8% P, 19% S) at 250 kg/ha based on soil test results in July 1999 (Table 1). Further tests in May 2001 indicated that soil fertility was adequate for maximum clover growth.

A split-plot design was used with three replicates of fully irrigated or dryland (non-irrigated) treatments as main plots. Subplots were monocultures of 'Grasslands Demand' white clover (2 kg/ha) and hexaploid 'Endura' Caucasian clover (8 kg/ha) sown on 9 November 1999. Subplots were 4.2 x 6.0 m drilled into a cultivated seedbed with an Øyjoord cone seeder. Seed was inoculated with the *Rhizobium trifolii* strain CC275e for white clover and ICC148 for Caucasian clover.

Irrigation

In year 1, all plots were irrigated to prevent a deficit of 25 mm to 0.50 m soil depth to ensure both clovers established. In years 2 and 3, water was applied to the irrigated treatment at 8-10 mm/hr, using a T-tape irrigation system. Water was applied post grazing to prevent a deficit of 100 mm to 1.50 m depth using a soil water budget:

$$A = \Sigma E_P - (R + I) \qquad \text{Equation 1}$$

where the amount of water required (A) is equal to the difference between estimated potential evapotranspiration (E_P, mm/day) and rainfall (R) plus irrigation (I) in the previous period. Rainfall and E_P were recorded at Broadfields, 3 km north of the experimental site (Table 2; Figure 1a).

Management

The experimental area was grazed with young sheep for 4-14 days, at 28-37 day intervals. Regrowth periods were extended to 45-70 days during the cool May-September period. Weed control included '2,4-DB' at 2.4 kg a.i./ha in December 1999 and hand weeding of mainly wireweed (*Polygonum aviculare*). 'Gallant' at 250 g a.i./ha was sprayed in September each year to control annual poa (*Poa annua*) and barley grass (*Hordeum* spp.).

Pasture measurements

Dry matter production in year 3 was measured at 7-15 day intervals using a capacitance probe (Mozaic

Table 1 Soil test (0-150 mm) results in July 1999 and May 2001 for the experimental area at Lincoln University, Canterbury.

	pH (H_2O)	Olsen P (μg/ml)	SO_4-S (μg/g)	Ca^{++} (Same units for K, Mg and Na)	K^+ (meq/100 g)	Mg^{++}	Na^+
July 1999	6.2	27	5	7.2	1.0	1.0	0.14
May 2001	6.2	25	8	8.2	1.1	1.1	0.24

Table 2 Rainfall and Penman's potential evapotranspiration (E_P), and the amount and timing of irrigation water applied to the irrigated treatment, from 1 July to 30 June in 2000/01 and 2001/02 at Lincoln University, Canterbury.

Year	Rainfall (mm)	E_P (mm)	Irrigation (mm)	Timing of irrigation
2000/01	485	1 048	507	21 Nov.-20 Apr.
2001/02	699	953	251	19 Nov.-24 Mar.

Systems Ltd., NZ). Measurements began immediately post grazing and finished on the day of the next grazing. For the final measurement, the probe was calibrated using a paired sample of probe reading and herbage mass from a 0.2 m^2 quadrat cut to 30 mm above ground level. Subsamples were taken to determine botanical composition before dry weight was measured.

Net photosynthesis rate was measured at midday ± 1 hr on cloudless, sunny days in years 2 and 3. Measurements were made on a random sample of three of the youngest fully expanded intact leaves in each treatment, using a LI-COR LI-6400 photosynthesis system (Lincoln, Nebraska, USA) at a maximum photosynthetic photon flux density of 1 700 ±100 $\mu mol/m^2/s$. The response to air temperature (at the time of photosynthesis measurements) was examined under irrigation. The response to soil moisture (on the day of photosynthesis measurements) was examined under dryland conditions, when air temperature was within the optimum range of 20-25 ºC for growth of temperate perennial clover species (Mitchell 1956).

Leaf appearance was measured at 5-7 day intervals in year 2. Emerged leaves were counted on five shoot apices in each subplot. New shoots were tagged post grazing. Leaf appearance was regressed as a function of thermal time (Tt), expressed in degree-days (ºCd), to calculate the phyllochron (ºCd/leaf). Thermal time was calculated using the equation:

$$Tt = \Sigma[(Tmax + Tmin)/2] - T_b \qquad \text{Equation 2}$$

where Tmax and Tmin are maximum and minimum daily air temperatures, and T_b is the base temperature below which no development takes place. Initially, a T_b of 1 ºC was used for both clovers (Black *et al.* 2002).

Environmental conditions

Air temperature was recorded from a single probe placed in a Stevenson screen adjacent to the experimental area. Temperatures were recorded every 5 minutes and integrated every hour with a DT100 data logger to determine daily mean, maximum and minimum temperatures (Figure 1a).

Volumetric soil moisture content (SMC, mm^3/mm^3) was measured at 7-14 day intervals in years 2 and 3. Measurements were made to 0.2 m depth using time domain reflectometry (Trace system, Soil Moisture Equipment, California, USA), and from 0.25 to 2.25 m depth using a neutron probe (Troxler Electronic Industries Inc., Research Triangle Park, North Carolina, USA).

Soil moisture content on the day of photosynthesis measurements was calculated using a soil water balance:

$$SMC = SMC_i + (R + I) - \text{daily } E_A \qquad \text{Equation 3}$$

where SMC_i is the initial SMC and E_A is the actual evapotranspiration for each 7–14 day period. Daily E_A was calculated as E_A divided by the sum of E_P for the same period, and then multiplied by daily E_P:

$$\text{Daily } E_A = (E_A/\Sigma E_P)*E_P \qquad \text{Equation 4}$$

Soil moisture content was expressed as a ratio of SMC:WHC to 1.5 m depth (Figure 1b). This approach allows the extrapolation of results to a range of soil types (McKenzie *et al.* 1999). The maximum SMC was 512 mm (WHC) on 12 September 2000. The minimum SMC was 200 mm (0.39 of WHC) for white clover and 230 mm (0.45 of WHC) for Caucasian clover under dryland conditions on 25 April 2001. At this time, the maximum water extraction depth was defined as the point where SMC no longer differed from the previous measurement. Both clovers had extracted water to 1.45 m depth (Figure 2a).

Dryland treatments received 166 mm of irrigation water from 22 August-20 September 2001 because rainfall had not recharged soil moisture completely during winter (Figure 1b). Moisture stress under dryland conditions was lower in year 3 than in year 2. For both clovers, the minimum SMC was 328 mm (0.64 of WHC) on 22 March 2002, and extraction depth was 1.20 m (Figure 2b).

Statistical analysis

Treatment differences were identified and the standard error (s.e.) and standard error of means (s.e.m.) calculated using analysis of variance by the GENSTAT 6th Edition statistical package. The response of leaf photosynthesis rate to temperature and soil moisture was described using a two-piece 'broken stick' model (Draper & Smith 1998).

Results

Annual clover yield

Annual clover yield was 2.5 t DM/ha greater ($P<0.05$) for Caucasian (11.9 t DM/ha) than for white (9.4 t DM/ha) clover under irrigation (Table 3). For both clovers, production was lower ($P<0.01$) under dryland conditions, but the yield advantage ($P<0.05$) for Caucasian was similar at 9.4 t DM/ha compared

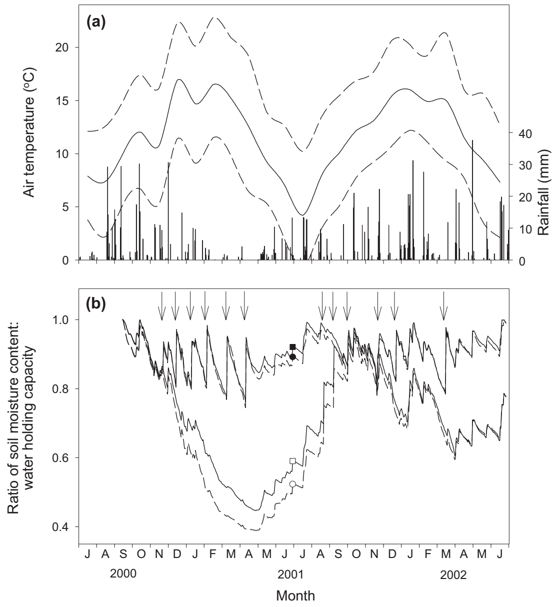

Figure 1 (a) Daily air temperature mean (——), maximum and minimum (- - -), and daily rainfall (bars) from 1 July 2000 to 30 June 2002 at Lincoln University, Canterbury. (b) Daily ratio of soil moisture content:water holding capacity (512 mm to 1.50 m depth) for Caucasian (■ ——) and white (●- - -) clovers under irrigated (closed symbols) and dryland (open symbols) conditions. Arrows indicate irrigation events.

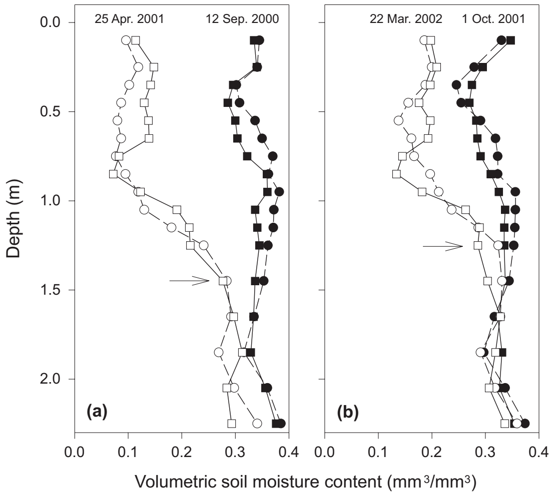

Figure 2 Maximum (closed symbols) and minimum (open symbols) volumetric soil moisture contents for Caucasian (■——) and white (●- - -) clovers under dryland conditions in (a) 2000/01 and (b) 2001/02. Arrows indicate the maximum water extraction depth.

Table 3 Dry matter (DM) production and mean botanical composition for Caucasian (CC) and white (WC) clovers under irrigated and dryland conditions in 2001/02 at Lincoln University, Canterbury.

Irrigation	Species	Clover DM (t/ha)	Clover (%)	Weeds (%)	Dead (%)
Irrigated	CC	11.9_a	89	8	3
	WC	9.4_b	91	7	2
Dryland	CC	9.4_b	83	14	3
	WC	7.0_c	84	13	3
	s.e.m.	0.44	3.1	3.0	0.7

Note: Within columns, values with the same or no letter subscript are not significantly different (α=0.05) according to Fisher's protected least significant difference test.

with 7.0 t DM/ha for white clover. Weed content was ~8% when irrigated, and ~14% under dryland conditions.

Clover herbage mass

Both clovers began production at the same time in spring (Period 1), and yielded ~0.5 t DM/ha by 20 September, under irrigation (Figure 3a). Production then increased for Caucasian clover, with yields between 2.5 and 3.2 t DM/ha from 4 October-10 March (Periods 2-5), before they declined to 0.6 t DM/ha on 23 April (Period 6) and 0.1 t DM/ha on 25 June (Period 7). Yields for Caucasian clover were ~0.8 t DM/ha greater (P<0.05) than for white clover from October-March, but 0.4 t DM/ha lower (P<0.05) in April.

Under dryland conditions, both species produced 0.4 t DM/ha in Period 1 (Figure 3b). However, Caucasian clover yielded between 2.1 and 2.5 t DM/ha from 4 October-10 March (Periods 2-5), which was ~0.7 t DM/ha greater (P<0.01) than for white clover. Both clovers yielded ~0.3 t DM/ha in April.

Clover production rate

Under irrigation, production rates increased rapidly for Caucasian clover between July and mid-October and then increased at a slower rate to a mid-January peak of 98 kg DM/ha/day (Figure 4). This rate then declined to 16 kg DM/ha/day in March-April and 1 kg DM/ha/day in May-June. These rates were ~23 kg DM/ha/day higher (P<0.01) than for white clover from mid-October to late February, but 10 kg

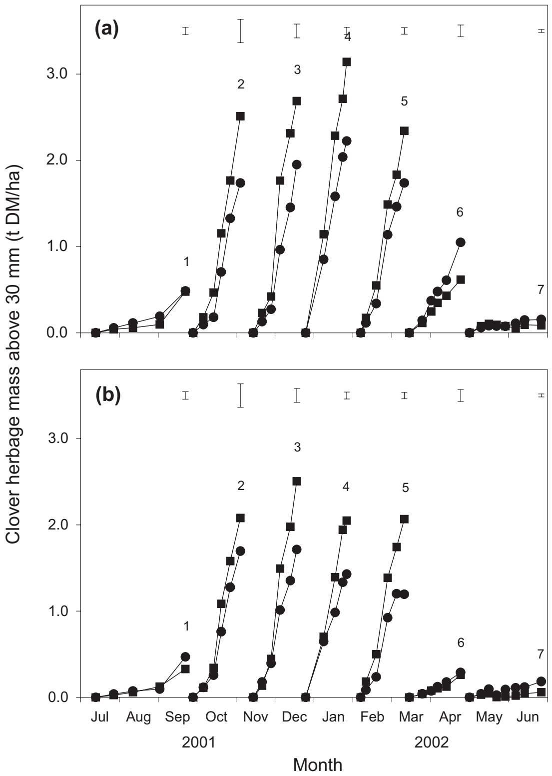

Figure 3 Herbage mass (above 30 mm) of Caucasian (■) and white (●) clovers under (a) irrigated and (b) dryland conditions in 2001/02 at Lincoln University, Canterbury. Bars represent the standard error of the mean for final yields. Numbers refer to rotation within a season.

DM/ha/day lower (P<0.01) in March-April.

For both clovers, production rates were lower (P<0.05) under dryland than irrigated conditions from mid-January to March-April, but Caucasian clover was still ~23 kg DM/ha/day higher (P<0.01) than white clover in Periods 4-5 (Figure 4). Both clovers averaged 7 kg DM/ha/day in March-April without irrigation.

Relationships between clover production rate and mean daily air temperature in the same regrowth period were examined under irrigation (Figure 5). Production rates were linearly related (R^2= 0.97, s.e.=6.3) to air temperature from 8-16 ºC between July and December (Periods 1-4). This enabled the increase in spring/early summer production rate to be estimated as 11 kg DM/ha/day/ºC for Caucasian compared with 8 kg DM/ha/day/ºC for white clover.

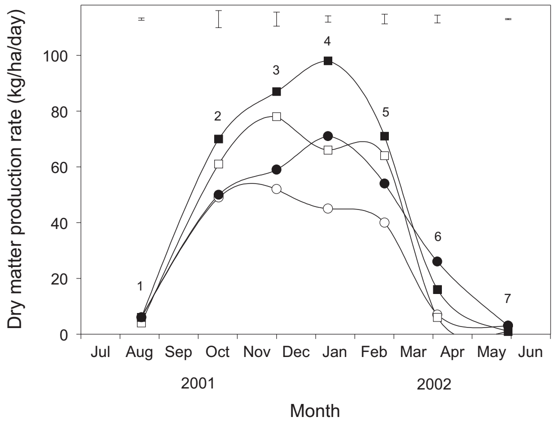

Figure 4 Dry matter production rate of Caucasian (■) and white (●) clovers under irrigated (closed symbols) and dryland (open symbols) conditions in 2001/02. Bars represent the standard error of the mean. Numbers refer to rotation within a season.

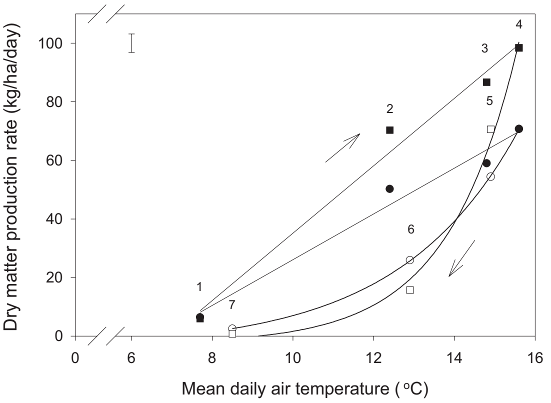

Figure 5 Response of dry matter production rate of Caucasian (■) and white (●) clovers to mean daily air temperature under irrigation in spring (closed symbols) and autumn (open symbols) in 2001/02. Arrows indicate the direction of temperature change. The bar represents the maximum standard error for regressions. Numbers refer to rotation within a season.

However, between December and June (Periods 4-7), exponential functions (R^2=0.98, s.e.= 6.1) were fitted to production rates, which declined as air temperature dropped from 16-9 ºC (Figure 5). Notable was that the production rate of Caucasian clover was affected more than white clover during this period. For example, Caucasian clover produced 16 kg DM/ha/day at 13 ºC (Period 6) compared with 26 kg DM/ha/day for white clover. In both cases, the autumn production rate was less than half that achieved for the same temperature in spring.

Leaf photosynthesis rate

Based on the fitted 'broken stick' model (R^2 = 0.94; s.e. = 1.8), the minimum leaf photosynthesis rate for Caucasian clover was 13 μmol $CO_2/m^2/s$ at the lowest measured air temperature of 7 ºC (Figure 6a). This rate then increased by an average of 1.5 μmol $CO_2/m^2/s/$ºC to a maximum of 37 μmol $CO_2/m^2/s$ at 23.7 ºC before it declined by 2.3 μmol $CO_2/m^2/s/$ºC to be 27 μmol $CO_2/m^2/s$ at the highest measured air temperature of 28 ºC. These rates were ~6 μmol $CO_2/m^2/s$ higher ($P<0.05$) than for white clover at all temperatures.

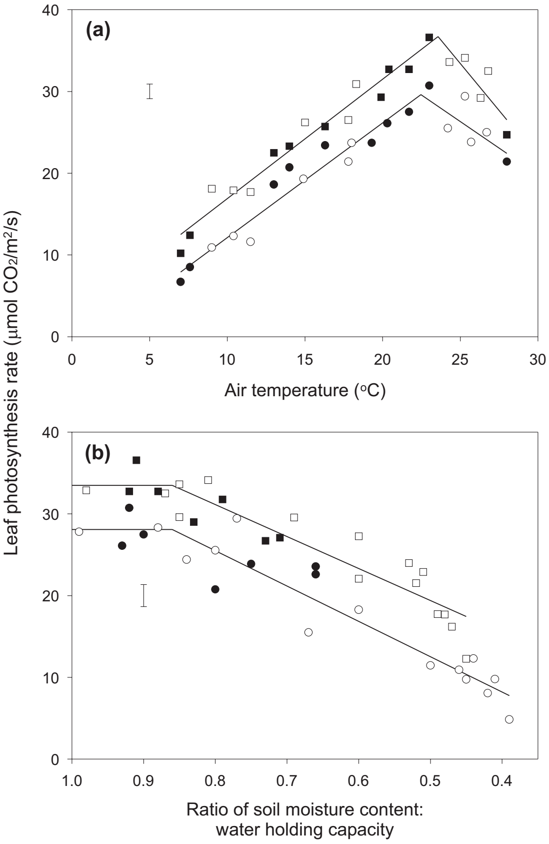

Figure 6 Response of net leaf photosynthesis rate of Caucasian (■) and white (●) clovers to (a) air temperature and (b) soil moisture - expressed as a ratio of soil moisture content:water holding capacity (512 mm to 1.50 m depth). Data are separated for periods 1 Jul.-31 Dec. (closed symbols) and 1 Jan.-30 Jun. (open symbols). Bars represent the standard error for the 'broken stick' model.

Leaf photosynthesis rates were also ~6 μmol $CO_2/m^2/s$ higher ($P<0.05$) for Caucasian than white clover as the ratio of SMC:WHC decreased from 1.00–0.45 (Figure 6b). For Caucasian clover, the maximum leaf photosynthesis rate was ~33 μmol $CO_2/m^2/s$ from 1.00–0.86 of WHC, using the 'broken stick' model (R^2 = 0.84, s.e. = 2.7). The rate then declined by 3.9 μmol $CO_2/m^2/s$ per 0.10 unit change in SMC:WHC to a minimum of 17 μmol $CO_2/m^2/s$ at 0.45 of WHC. White clover followed the same pattern, and leaf photosynthesis rates declined by 4.3 μmol $CO_2/m^2/s$ per 0.10 unit change in SMC:WHC to be 8 μmol $CO_2/m^2/s$ at 0.39 of WHC.

Leaf appearance rate

Leaf appearance rate was constant in Tt (T_b = 1 ºC) for white clover in year 2 (Figure 7). This enabled the phyllochron (± s.e.) to be calculated as 126 ± 19.9 ºCd. For Caucasian clover, the phyllochron was 157 ± 25.9 ºCd from August–May (Periods 2-8), but this increased to 314 ± 33.5 ºCd in July (Period 1) and 359 ± 42.7 ºCd in June (Period 9). These results indicated that T_b = 1 ºC was incorrect for Caucasian clover. Thus, several T_b values were tested to minimise the coefficient of variation for the mean phyllochron, and a T_b of 5 ºC was found to be most suitable. Using this higher T_b gave a similar phyllochron (126±30.1 ºCd) to white clover.

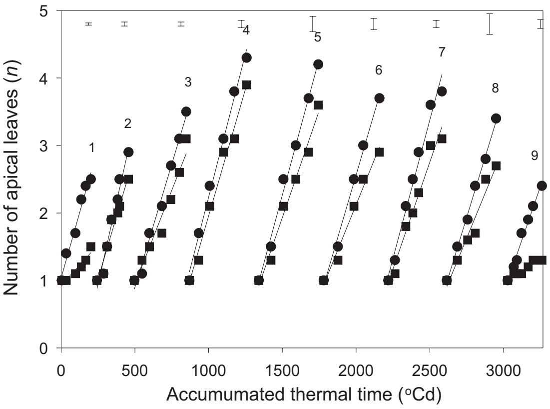

Figure 7 Leaf appearance rate for apical leaves of Caucasian (■) and white (●) clovers as a function of accumulated thermal time under irrigation in 2000/01. Bars represent the standard error of the mean for final number of leaves. Numbers refer to rotation within a season.

Discussion

The establishment of monocultures of white and Caucasian clovers is uncommon in pastoral farming for a variety of practical reasons. However, this research has shown significant differences in growth and development between the two species that can provide some explanation for their relative performance in grass/clover pastures.

In their third year, the sown monocultures of Caucasian clover produced 11.9 t DM/ha when irrigated and 9.4 t DM/ha under dryland conditions, and both treatments exceeded white clover by ~2.5 t DM/ha (Table 3). This production advantage was achieved through ~23 kg DM/ha/day higher production rates than white clover in spring and summer, under both irrigated and dryland conditions, but particularly when irrigated (Figure 4). The seasonal patterns of DM production (Figures 3 and 4) offer insight into the timing and extent of temperature and moisture limitations (Figure 1) operating on the two clovers.

The magnitude of the response in clover production rate to temperature is of particular interest in spring/early summer, when demand for high quality pasture is increasing. In this study, Caucasian clover responded more (11 kg DM/ha/day/ºC) than white clover (8 kg DM/ha/day/ºC) to increases in mean daily air temperature from 8-16 ºC in spring/early summer, when soil moisture was non-limiting (Figure 5). These relationships are consistent with results from ryegrass/white clover pastures in spring (Baars & Waller 1979; Radcliffe & Baars 1987). Further analyses (Black unpublished data) have also shown that Caucasian clover responds more (5 kg DM/ha/day/ºC) than white (2 kg DM/ha/day/ºC) to increases in mean daily air temperature in mixture with ryegrass in spring/early summer.

It seems likely that the greater production for Caucasian clover in spring and summer was conferred by its higher leaf photosynthesis rate (Figure 6a) across the range of air temperatures experienced during this time. Furthermore, this study has shown that the optimum temperature range for photosynthesis of Caucasian and white clovers is the same. Specifically, the optimum temperature range to give ≥90% of the maximum leaf photosynthesis rate was approximately 21-25 ºC, which is consistent with Mitchell (1956) for growth of white clover. Thus, for any given canopy leaf area index, the canopy photosynthesis rate of Caucasian clover can be expected to exceed that of white clover and give more assimilate per unit leaf area. Confirmation of this would provide an explanation for the production advantage of Caucasian clover observed in ryegrass/clover pastures under irrigation (Black *et al.* 2000).

The same mechanism also offers insight into the greater production for Caucasian than for white clover previously reported from mixed pastures under dryland conditions (Watson *et al.* 1998; Black & Lucas 2000). For both clovers, the optimum soil moisture range to give ≥90% of the maximum leaf photosynthesis rate was the same at 1.00-0.86 of WHC (Figure 6b). The onset of moisture stress resulted in a similar decrease in leaf photosynthesis rate, but the leaf photosynthesis rate for Caucasian clover was higher than for white clover irrespective of soil moisture. The consequence of this difference was highlighted in early March (Period 5), when Caucasian clover produced 0.8 t DM/ha more than white clover under dryland conditions (Figure 3b). This occurred when soil moisture was 0.68 of WHC (Figure 1b), which equates to a potential soil moisture deficit of 164 mm.

It remains to be seen if the taproot of Caucasian clover is able to extract water from greater depths than white clover and therefore provide an additional advantage from access to more water in summer. Indeed, the current lack of any differences in extraction depth (Figure 2) suggests that white clover still had an active taproot in its third year. However, it has long been recognised that white clover loses its taproot within 1-2.5 years (Westbrooks & Tesar 1955; Brock *et al.* 2000). Any potential advantage from greater rooting depth for Caucasian clover would not be expected until after the white clover taproot has senesced.

The hysteresis in the relationships between production rate and mean daily air temperature (Figure 5) meant that autumn production of Caucasian clover was affected more in Period 6 than that of white clover (Figure 3a). This is consistent with other results, which have shown a more rapid reduction in clover production for Caucasian than for white clover in ryegrass pastures in autumn (Black *et al.* 2000). In this study, the effect of temperature on leaf photosynthesis rates for both clovers appeared to be the same irrespective of the time of year when measurements were taken (Figure 6a). The slower leaf appearance rate for Caucasian clover in autumn (Figure 7) may have caused the lower production rate during this period.

The phyllochron was the same for both species (126 ºCd), but the higher T_b requirement for Caucasian (5 ºC) than for white clover (1 ºC) means Caucasian clover takes longer to accumulate the Tt necessary to produce a new leaf. For example, assuming a mean air temperature of 10 ºC, white clover is predicted to have produced a new leaf after 14 days, compared with 25 days for Caucasian clover. This is because Caucasian clover would only accumulate 5 ºCd (heat units) each day, due to its T_b of 5 ºC, compared with 9 ºCd for white clover. The impact of a higher T_b will be greatest at the beginning and end of the growing season, when temperatures are most limiting. Thus, Caucasian clover can be expected to take longer to recover than white clover post grazing in autumn when temperatures are declining.

The higher T_b requirement for Caucasian clover also provides a physiological explanation for its perceived winter dormancy. Indeed, a 'winter dormant' species can be simply quantified as one that has a high T_b for development. This is consistent for other pasture species such as chicory (*Cichorium intybus*), which is dormant for 2-3 months in winter and requires a T_b of 4.5 ºC (Moot *et al.* 2000). Species such as white clover, with a T_b of ~1 ºC, display more cool season activity and potentially have a longer growing season than those with a higher T_b.

Further research is necessary to determine if the higher T_b was the dominant factor responsible for the lower production of Caucasian clover in autumn, or if a change in the partitioning of carbohydrates and protein, contributed. Peterson *et al.* (1994) observed an increase in total nonstructural carbohydrate concentrations in crowns, rhizomes and roots of Caucasian clover in autumn. This indicates assimilate partitioning similar to that occurring in other perennial legumes such as lucerne (*Medicago sativa*), which also has a large taproot (Moot *et al.* 2003). It is also possible that the remobilisation of stored assimilates in spring (Peterson *et al.* 1994) contributed to the production advantage of Caucasian clover during this period. This suggests that a longer frequency of defoliation in autumn than in spring and summer may be required to assist Caucasian clover production and persistence.

Conclusions

This study has provided quantifiable explanations for differences in seasonal DM production observed between Caucasian and white clovers. The results confirm that Caucasian clover has potential to increase legume production in environments where high quality pastures are required in spring and summer. Caucasian clover may not be suited to environments where high cool season production is demanded, but it is suited to cool environments where persistence is important. Specific conclusions were:

1. Caucasian clover produced ~2.5 t DM/ha more annual yield than white clover under both irrigated and dryland conditions. This was due to ~23 kg DM/ha/day higher production rates than white clover in spring and summer, when mean daily air temperature was increasing from 8-16 ºC.
2. The production advantage of Caucasian clover in spring and summer occurred when its leaf photosynthesis rate was ~6 µmol $CO_2/m^2/s$ higher than white clover irrespective of temperature or soil moisture. Both clovers had similar ranges of optimum temperature (21–25 ºC) and soil moisture (1.00-0.86 of water holding capacity) for photosynthesis.
3. Caucasian clover had a phyllochron of 126 ± 30.1 ºCd, which was the same as white clover, but the T_b requirement was higher for Caucasian (5 ºC) than for white (1 ºC).

ACKNOWLEDGEMENTS

Alistair Black acknowledges the C. Alma Baker, Struthers and Pukehou Poutu Trusts for financial assistance during his PhD studies at Lincoln University.

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