

Interaction Between Leaf and Seed Production in White Clover (*Trifolium repens* L.)¹

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ABSTRACT

Two unrelated experiments, one using cv. G18 the other cv. Huia white clover, demonstrated that during the flowering cum seed set phase there is a continual partitioning of resources between vegetative and flowering processes. There is a sequential and often compensatory adjustment in floret and ovule formation, ovule fertilization, seeds per floret, and seed size according to the period of nutritional stress on individual stolons.

The first experiment showed that differences in leaf density and size found on unirrigated and irrigated plots were also modified by minor variations in within-plot moisture holding capacities. These moisture variations generated a 3.3 fold difference in leaf density, a direct linear relationship between leaf and inflorescence density and seed yield. Inflorescence density, seed numbers and seed yield were greater from irrigated crops for a given leaf size. Regardless of irrigation, maximizing ovule numbers taken through to mature seed almost totally accounted for seed yield. The sequential sampling of the second experiment showed that seed yield per inflorescence varied only in relation to the moisture stress during the life of the floret. Moisture stress did not affect crop flowering but reduced yield per inflorescence. Regardless of time of flowering the number of seeds per floret decreased with the order of floret opening within individual inflorescences.

Additional index words: irrigation; leaf size; componentry; nutrient partitioning

INTRODUCTION

White clover (*Trifolium repens* L.) is a major forage legume in many temperate regions of the world. Because of its importance there have been many investigations of its characteristics. Most studies have been from two points of view (i) growth rates and other characteristics of leaf growth for forage production, and (ii) flowering and its components for seed production. However, frequently the management differences needed to produce a high yielding reproductive rather than a vegetative, crop go unrecognized. Maximizing herbage production requires an understanding of leaf area index (LAI) and associated photosynthetic activity, whereby frequency and intensity of leaf removal equates with maintaining highest possible growth rates (Brougham 1958,

1962). By contrast, commercial seed production is a one-harvest-only operation. Consequently emphasis must be directed at maximizing leaf numbers (inflorescence numbers) at the same total LAI value (Clifford 1980, 1985a). As such the nutritional requirements to produce leaf numbers rather than leaf bulk could differ. Therefore, this paper explores the possible relationships between the leaf and seed production, firstly by a review of the literature and secondly by reference to two field trials.

INTERACTION BETWEEN LEAVES AND INFLORESCENCES

Morphology. Axillary buds form in leaf axils (Erith 1924). These may develop into either an inflorescence or a secondary stolon, but never both at the same site (Thomas 1961, 1980). The change in axillary bud initiation to either secondary stolon or inflorescence formation is controlled by the interaction of short day lengths and low temperature (Thomas 1980, 1981a). In New Zealand field conditions, axillary buds formed in September and October will generally produce inflorescences between October and January; buds produced at other times usually form secondary stolons (Thomas 1980, 1981a). In field stands primary stolons with intact apical meristems (e.g. not lost by grazing) will have grown 4-5 nodes and subtending leaves before a secondary stolon becomes obvious. Continued growth of both the primary and secondary stolons suggests a partitioning of nutrients between the two, with approximately a regular number of nodes and leaves developing before further secondary stolon appearance. However, whereas a growing secondary or tertiary stolon develops to nutritional self-sufficiency, an inflorescence must be totally supported by the stolon to which it is appended through all its developmental phases.

Inflorescence development occurs in an ordered sequence of floret formation, ovary, ovule and pollen grain formation, inflorescence opening, fertilization, ovule maturation, and seed maturation (Thomas 1961, 1980, 1981b). In field stands development is greatest for the inflorescence closest to the stolon base, commonly with no inflorescence at the next youngest node, a much delayed inflorescence development at the next successive node, and usually a maximum of 2-3 inflorescences per stolon (Clifford 1985b).

Crop nutrition. The crop's nutritional requirement over the reproductive phase must be understood to ensure highest possible seed yields. Nutrition, in the broader sense, means the photosynthetic input from leaves, any translocation from other plant parts, and adequate moisture and minerals. Therefore, the extent to which the crop environment can be

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modified, consistent with obtaining the best compromise between vegetative and dependent reproductive growth, will ultimately determine seed yield.

The environment. Site radiant energy levels and, for the most part, soil fertility are inflexible. Therefore, the only way to manipulate any deleterious affects of soil fertility on growth, will be to limit soil moisture availability for plant uptake.

In general, constraining soil moisture reduces leaf size. As a result more inflorescences with lower floret numbers are formed to give higher seed yields (Clifford, 1985a). Care must be taken to ensure that the wilting point is not reached, and thereby severely limiting photosynthetic activity (Hagen et al., 1957). Prolonged moisture stress can limit later leaf development (Clifford, 1985a, 1986; Johnson & Raguse, 1985).

All these results are of mean seasonal effects, of the inflorescence formation — ovule provisioning sequence, which occurs many times over the three-month reproductive phase. Further, they add nothing to the reasons why only about half the ovules formed develop through to mature seed (Clifford, 1979, 1985b; Thomas, 1981b).

In most seasons, soil moisture availability either fluctuates or dwindles over the flowering-seed set period. As such, there may be only a limited time when unsupplemented moisture supply facilitates the conditions to maximize seed yield. Therefore the effects of competition between vegetative and reproductive requirements will vary within seasons. It is even possible that competition may occur within individual inflorescences under certain conditions.

The possibility of these interactions between vegetative growth and the relatively fixed sequence of inflorescence development stages, combined with their repetition level over the three-month period, offer a new way of looking at crop characteristics for determining maximum yield.

An explanation of results using this approach was explored in the following two experiments. In the first, the mean seasonal effects of soil moisture variations on nutrient availability as measured by leaf size and/or numbers, and as subsequently reflected in seed yield and some of its components are discussed. In the second, within-season environmental effects on inflorescence formation and subsequent provisioning potential, in relation to the crop flowering pattern, are examined.

MATERIALS AND METHODS

Experiment 1

At Lincoln, New Zealand (latitude 43°S 38'S) on a Wakanui silt loam (Udic Ustochrept) in early March 1981 cv. Grasslands 18 white clover (large-leaved cultivar) was precision seeded at 30-cm row spacings at a sowing rate of 3 kg ha⁻¹ (Clifford, 1986). The crop was closed to flower in mid-November 1981. By mid-December soil moisture was approaching wilting point, so half the 16 plots were irrigated weekly (December 16, 1981 to January 30, 1982 inclusive) at a rate of 50% plant available soil moisture in the top 20 cm of soil. Prior to each re-application of water, soils were back to almost wilting point. Wilting point was 23 mm and field capacity at 69 mm moisture content.

On 9 February (unirrigated) and 24 February 1982 (irrigated), 15 quadrats of 0.5 x 0.3 m were chosen on each area to cover the widest range in leaf sizes. The difference in date refer to their suitability for harvest. Individual trifoliolate leaf areas for 40 leaves per quadrat were measured. The resultant mean leaf size per quadrat was converted to its inverse (1/leaf size) or the leaf numbers required to cover an area of 1 m².

Total inflorescences per quadrat were counted, collected, then hand-threshed and cleaned for seed yield and 1000-seed weight determination. Soil moisture at harvest was recorded for two cores, 2.5 mm diameter x 20 cm depth for all sites on irrigated crops, but only eight sites on non-irrigated crops.

A correlation matrix was used on both unirrigated and irrigated data to test the strength of relationships of measured variables initially with soil moisture and subsequently amongst themselves. Regression analysis was then applied to the data to test for differences in slope and intercept of plant components relative to irrigation treatments.

Experiment 2

This experiment was conducted at Lincoln College Mixed Cropping Unit, latitude 43°38'S, on a Templeton silt loam (Udic Ustochrept), with a non-irrigated cv. Grasslands Huia white clover crop spring undersown on a cereal crop in 1978 and closed to flower in mid-November 1979. Inflorescences which had just started flowering (1-5 florets open) were tagged weekly from 5 December to 16 January inclusive. For each of the seven dates there were four replicates of 10 inflorescences from sites of approximately 1 m². For the same dates and inflorescence development stage, inflorescences available for pollination were counted on six 0.25 m² quadrat per plot. Five weeks after each tagging, inflorescences were collected for assessment in the laboratory. For each tagging date florets on each seedhead were sequentially removed first to last in flowering order. The florets were then aggregated into four lots (quarters) according to time of flowering on each inflorescence. Floret numbers and seeds per quarter were recorded but yield and 1000-seed weight per quarter were for the cleaned bulk samples for each quarter from each tagging date.

RESULTS AND DISCUSSION

Firstly, it must be stated that the results for experiment 1 deal specifically with the measured reproductive response gradients imposed by variations in soil moisture holding capacity along some discrete bands that were attributable to previous land use history. Therefore, in the context presented they bear no relationship to the mean crop yields for the large uniform area of the experiment from which they were derived (826 vs. 572 kg ha⁻¹ respectively for irrigated and unirrigated November-closed crops (Clifford, 1986)). Rather the overall data are proffered as an explanation of white clover's reproductive reaction to both variation and fluctuation in plant-available soil moisture.

Experiment 1

A leaf number range of the order of 3.3 times gave about a two-fold effect on seed yield and its components (Table 1) (Clifford 1985a). Apart from unit seed weight all components decreased with decrease in leaf numbers m⁻². Whereas unirri-

Table 1. Effect of leaf number range on seed yield and its components in G18 white clover

Measurement	Leaf number extremes ¹			
	Unirrigated		Irrigated	
	Highest 2240	Lowest 720	Highest 1890	Lowest 560
Seed yield (kg ha ⁻¹)	1020	520	1080	600
Inflorescences (m ²)	1030	570	1180	660
Seed numbers (ha ⁻⁶)	1.57	0.84	1.86	0.89
1000-seed weight (g)	0.65	0.62	0.58	0.68

¹Leaf numbers to cover 1 m²

gated unit seed weights remained static, for irrigated crops reduction in leaf numbers m⁻² gave an increase in 1000-seed weight.

For both unirrigated and irrigated crops leaf size was positively correlated with soil moisture availability (Table 2) (Clifford, 1985a), however, the response patterns differed. Firstly, measurements in the irrigated treatment were taken 15 days after unirrigated measurements. Secondly, two days prior to taking irrigated soil moisture samples 15 mm of rain fell. Relationships of soil moisture with either leaf size or leaf number were for the most part deemed to be similar, particularly as subsequent relationships were dominantly with leaf numbers.

For both irrigated and unirrigated crops, increase in inflorescence numbers was positively correlated with increase in leaf numbers (Table 2). However, for any given leaf number, irrigated compared with unirrigated crops produced an additional 180 inflorescences m⁻² (r² = 70). This difference between irrigated and unirrigated crops, rather than being an

irrigation-imposed change in the reproductive nature of stolons, is an artifact of the experimental technique used. Leaf numbers m⁻², equivalent to LAI = 1, were calculated from leaf size and, therefore, bear no relationship to the actual LAI value (3+) over that period. Had total leaf numbers per unit area been gathered, then the additional growth concept for the same leaf size would have been obvious. Thus, irrigation allowed better utilization of the available photosynthetic space through more growth.

A similar positive relationship for both irrigated and unirrigated crops existed between leaf numbers and seed numbers per unit area produced (Table 2). Again, irrigation was advantaged for the same leaf numbers by the development of an additional 0.14 x 10² seeds m⁻² over unirrigated plots, and for the same reasons (r² = 57).

Of note was the positive relationship, for both unirrigated and irrigated crops, between inflorescence numbers and seed numbers per unit area formed (Table 2). For both unirrigated and irrigated treatments this relationship took the form of a common linear response (r² = 75). This result suggests that the irrigation responses were solely the result of additional stolon growth, which was similar in nature to that expressed on unirrigated treatments.

For both unirrigated and irrigated crops, total seed yield was most positively correlated with seed numbers formed m⁻² and to a lesser extent, in order of importance, inflorescences m⁻² and leaf numbers m⁻² (Table 2). However, only for unirrigated crops did increase in soil moisture coupled with increased leaf size seriously reduce seed yield (Table 2). Combined analysis of both unirrigated and irrigated data showed that the relationships of total yield with seeds m⁻² (r² = 96, Fig. 1a) and inflorescences m⁻² (r² = 70, Fig. 1b) took the form of a common positive linear response. For both unirrigated and irrigated crops the slope of the response for increase

Table 2. Correlation coefficients for the inter-relationships developed from soil moisture effects on the reproductive phase in unirrigated and irrigated white clover seed crops.

	Soil moisture (%)	Leaf size (cm ²)	Leaf numbers (m ⁻²)	Inflorescence numbers (m ⁻²)	Seed numbers (m ⁻²)	Seed numbers/inflorescence	1000-seed weight (g)	Yield/inflorescence ⁻¹ (mg)
Unirrigated								
Leaf sizes (cm ²)	0.983							
Leaves m ⁻²	-0.975	0.956						
Inflorescences m ⁻²	-0.869	-0.877	0.895					
Seeds m ⁻²	-0.875	-0.904	0.895	0.895				
Seeds/inflorescence	0.252	0.148	-0.206	-0.435	-0.004			
1000-seed weight (g)	0.464	0.148	-0.033	-0.133	-0.072	0.168		
Yield/inflorescence (mg)	0.325	0.180	-0.206	-0.443	-0.030	0.968	0.409	
Total yield (kg ha ⁻¹)	-0.853	-0.870	0.885	0.865	0.985	0.045	0.089	0.055
Irrigated								
Leaf sizes (cm ²)	0.870							
Leaves m ⁻²	-0.779	-0.937						
Inflorescences m ⁻²	-0.603	-0.665	0.760					
Seeds m ⁻²	-0.432	-0.620	0.664	0.847				
Seeds/inflorescence	0.243	-0.049	-0.040	-0.154	0.382			
1000-seed weight (g)	0.837	0.746	-0.629	-0.679	-0.648	-0.033		
Yield/inflorescence (mg)	0.555	0.242	-0.289	-0.431	0.070	0.913	0.366	
Total yield (kg ha ⁻¹)	-0.276	-0.532	0.607	0.790	0.977	0.443	-0.478	0.192

P 0.05 > 0.483; P 0.01 > 0.606; P 0.001 > 0.725; n = 15

in seed yield with increase in leaf numbers was similar ($r^2 = 57$, Fig. 1c). Irrigated compared with unirrigated gave an additional 119 kg ha⁻¹ greater yield from stands containing the same leaf numbers, through more growth.

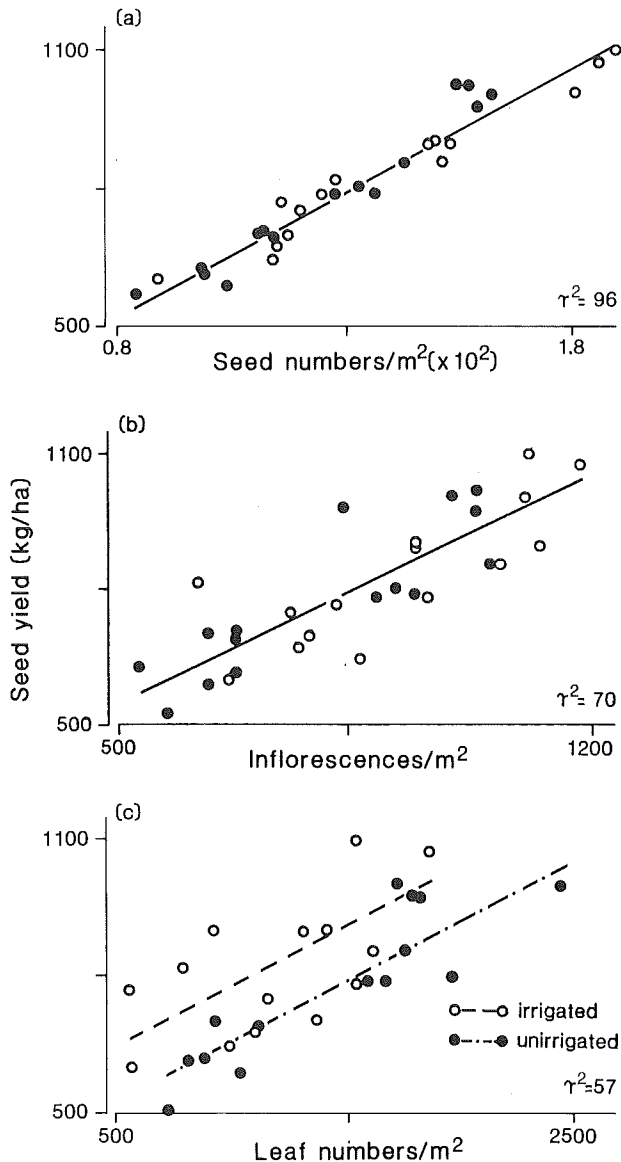


Fig. 1. Interactions between (a) seed numbers, (b) inflorescence numbers, (c) leaf numbers, and seed yield in 'G18' white clover.

So far, the results emphasize (i) the obligatory nature of the leaf, inflorescence formation through to mature seed sequence and (ii) the ability to increase sequence replication through irrigation (Clifford, 1986). At no stage did ovule provisioning (1000-seed weight) assume a dominant role in maximizing seed yields (Table 2). Therefore, ovule provisioning is secondary to maximizing seed numbers taken through to maturity (Clifford, 1986). Nevertheless, Table 2 shows some important variants to the overall result. For irrigated crops only, soil moisture had a dominant positive effect on 1000-seed weight

because of increased leaf size (Table 2). As a corollary, increase in leaf, inflorescence and seed numbers all had a negative effect. For unirrigated crops, there was inference that enhanced soil moistures were associated with increased 1000-seed weights, but here unassociated with any increase in leaf size. Therefore per-leaf photosynthetic efficiency may have been increased. Of the major components of total yield, only for irrigated 1000-seed weights did the addition of a second component enhance the relationship gained (irrigated 1000-seed weight = $0.354 + 0.026$ soil moisture^{***} - 0.037 seed numbers ha⁻¹* (pooled $r^2 = 70$)). Irrigation enhanced seed weight, the effect being modified by any increase in seed numbers for provisioning. This result gives a clear indication that there are insufficient assimilates available to satisfy the demands of a high level of provisioning within a potentially high yielding crop. Therefore, should any seed quality factor associated with increase in unit seed weight, prove to be of agronomic importance, its attainment may be at the expense of a large drop in seed yield. This feature is evidenced in the irrigation extremes of Table 1. A 17% increase in 1000-seed weight almost halved the resultant seed yield.

For both unirrigated and irrigated crops the total lack of any relationships with seeds per inflorescence indicate that the level of fertilization achieved was, at least, adequate to utilize all available assimilates (Table 2). For both unirrigated and irrigated crops seeds per inflorescence was the only correlation with yield per inflorescence, accounting for more than 90% of the total variance (Table 2). Thus, maximizing ovule numbers for provisioning through to maturity dominates within inflorescences, as well as on a per unit area basis. This control over provisioning by fertilized ovule numbers suggests that pollination was not a limitation to seed yield. Rather, the extent of competition for nutrients with other plant functions either restricted the amount of fertilization taking place, and/or promoted subsequent fertilized ovule abortion, to a stage where maximum numbers were able to be sustained to a base provisioning level.

Experiment 2

The basic data for this experiment, using a different cultivar (Huia) in a different season, not only aids the understanding of environmental effects on the reproductive phase within individual inflorescences over the flowering duration of the crop, but also adds to the knowledge on resource partitioning both within and between reproductive and vegetative growth.

Rainfall over November and December 1979 (56 mm and 34 mm, respectively) was evenly distributed, but only about half the 'normal' for that period. This lower precipitation coupled with very high evaporation from December 23-25 inclusive (42 mm) imposed a week of severe moisture stress. This stress period was overcome by a 104 mm rainfall on 2 January 1980.

Data on yield/inflorescence and its components are given in Table 3. Only the extremes for yield/inflorescence were significantly different. Even this difference would not have occurred in the absence of the severe moisture stress period that affected inflorescences that began flowering on 26 December (tagging 4; Fig. 2).

Moisture stress effects were more dominant in some of the components of yield/inflorescence, particularly in relation to

time (i) to complete flowering on individual inflorescences (7 ± 1 days) and (ii) for provisioning (28 days, Hyde et al, 1959). Floret numbers/inflorescence appeared to be unaffected by short-term moisture stress at this time, their differentiation having occurred much earlier (Thomas 1981b) (Table 3). However numbers of seeds per floret were affected, tagging date 4 being more affected than 5 (Table 3). Therefore moisture stress either limited fertilization or promoted some early abortion in inflorescences flowering over that period. By contrast, because ovule provisioning (1000-seed weight) was more widespread (Table 3), the later stages of tagging 3 were affected more than tagging 2. Tagging 4 showed a widespread limitation of nutrients for provisioning, while for 5 only the early stage would have been affected. Of note was that only tagging 3 showed a major departure from the similar relationship between nutrients available for provisioning in relation to seed numbers set (1000-seed weight : seeds per inflorescence ratio; Table 3). This result suggests that once fertilized ovules reach a certain development stage they are retained at the expense of normal provisioning, rather than some being aborted to maintain the provisioning level of the remainder. The constancy of the ratio for the other tagging dates suggests that initial level of ovule fertilization gained is related to future provisioning potential.

Because flowering on individual inflorescence occurs over seven days, competition for nutrients amongst ovaries at different developmental stages would also be expected, at least within the moisture stress phase. However, regardless of time of flowering, as flowering progressed on individual inflorescences, seed numbers per floret for each subsequent flowering quarter of the inflorescence significantly declined: $3.99 \times 3.77 \times 3.51 \times 3.00$ seeds/floret for the first to last quarter respectively (Fig. 2A). Thus, nutrient available for servicing ovules declines in relation to distance along the stalk (pedicel). Therefore, apart from the occasional sharp environmental change (Fig. 2A, taggings 1 and 3, 3rd to 4th quarter), the dwindling of assimilate along the pedicel also appears to be relatively constant. Thus, it seems that ovule fertilization, or rather the ensuring of this phase, is the critical factor in determining seed yield/inflorescence.

Once fertilized ovule numbers per inflorescence have been determined their subsequent provisioning (seed weight) will reflect the level of photosynthetic response of the contributing leaves as determined by the prevailing environmental conditions.

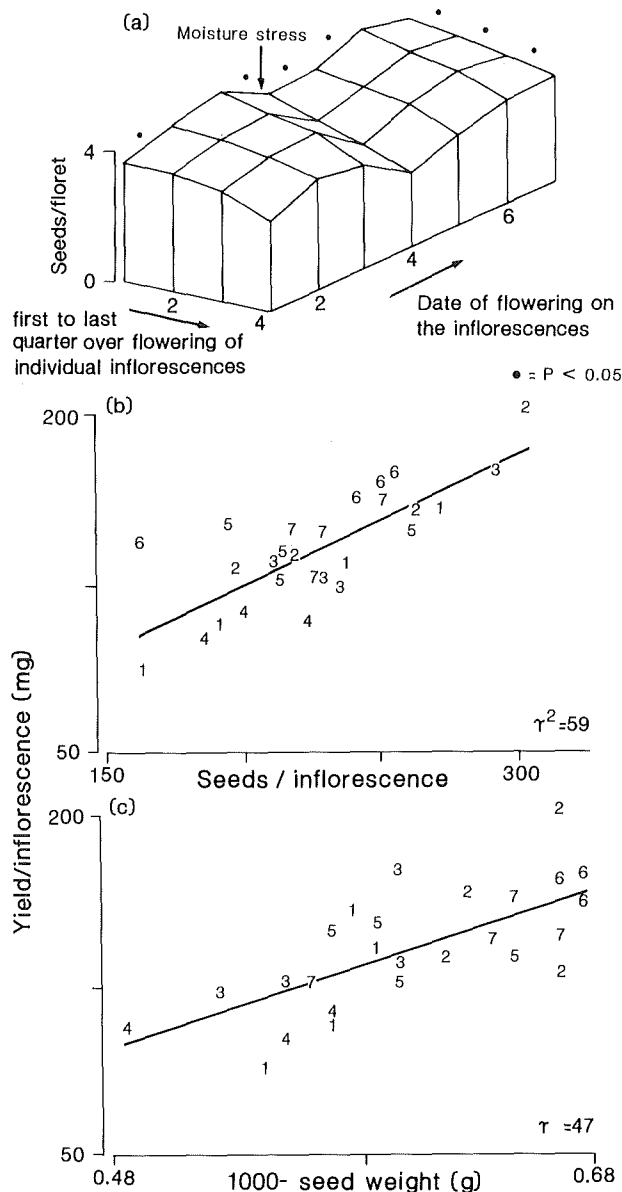


Fig. 2. Variations in seeds per floret within the inflorescence and components of yield per inflorescence with time of flowering within the season for Huia white clover. Sampling date - 1 = 5 Dec. '83; 2 = 12 Dec.; 3 = 19 Dec.; 4 = 26 Dec.; 5 = 2 Jan. '84; 6 = 9 Jan.; 7 = 16 Jan.

Table 3. Effect of flowering time on yield per inflorescence and its components for Huia white clover, (Exp. 2, 1978-79 season)

	Start of flowering on inflorescence ¹							± SEM	LSD 5%
	December				January				
	1	2	3	4	5	6	7		
Yield/inflorescence (mg)	123	159	138	104	141	163	146		56.5
Florets/inflorescence	63.3	64.4	61.1	65.8	64.5	64.0	62.0	2.78	
Seeds/floret	3.39	3.79	3.91	3.03	3.40	3.80	3.65		0.270
Seeds/inflorescence	215	244	242	200	219	243	230	17.8	
1000-seed weight (g)	0.57	0.65	0.57	0.52	0.60	0.67	0.63		0.063
1000-seed weight x 10 ³ : seeds/inflorescence	2.7	2.7	2.4	2.6	2.7	2.8	2.7		

¹ 1, 2, 3, 4 = Dec. 5, 12, 19, 26; 5, 6, 7 = Jan. 2, 9, 16.

The relationship between yield per inflorescence and its components was:

$$\begin{aligned} \text{yield/inflorescence (mg)} &= 86.8 - 0.89 \text{ florets/inflorescence}^{***} \\ &+ 0.55 \text{ seeds/inflorescence}^{***} + 263 \text{ 1000-seed weight}^{***} \\ (r^2 &= 90). \end{aligned}$$

Regardless of time of flowering, yield per inflorescence was proportional to seed numbers per inflorescence ($r^2 = 59$, Fig. 2B), and similarly to 1000-seed weight ($r^2 = 47$, Fig. 2B). Of note for both relationships is the spread of tagging dates (1-7) which indicates that these relationships existed throughout flowering. However, no relationship could be found between yield/inflorescence and floret numbers per inflorescence. This lack of a relationship suggests that, under certain conditions, growth (floral expression) imposes additional competition for nutrients, at the expense of fertilization and/or subsequent provisioning levels.

In this season, the period of moisture stress appeared to have no obvious effect on the 'typical' crop flowering pattern gained (Clifford, 1980) (Fig. 3). Therefore, the deleterious effects of moisture stress exhibited on seeds per floret (Table 3, taggings 4 and 5), and 1000-seed weight (taggings 3-5 inclusive), were at the expense of maintaining the overall flowering pattern. Based on these associations, it must be concluded that, the mere fact of a crop is flowering well, does not necessarily indicate the lack of an additional moisture requirement to maximize yield per inflorescence. In this case, two-thirds of the total flowering of (965 m^{-2}) was affected to a varying degree. If 160 mg per inflorescence (Table 3, taggings 2 and 6) is considered to be the achievable yield of the non-limited situation, the calculated seed loss incurred through lack of moisture was about 200 kg ha^{-1} .

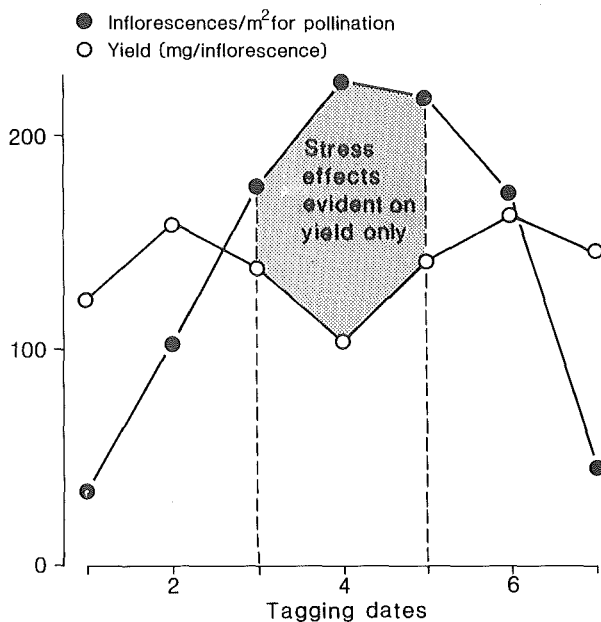


Fig. 3. Inflorescences available for pollination and soil moisture stress effects on yield per inflorescence at each tagging date (means of 4 replications). Sampling date - 1 = 5 Dec. '83; 2 = 12 Dec.; 3 = 19 Dec.; 4 = 26 Dec.; 5 = 2 Jan. '84; 6 = 9 Jan.; 7 = 16 Jan.

Overall the results for experiment 2 highlight the fact that a diminishing of food resource for partitioning between vegetative and reproductive processes need not always happen as flowering progresses (Thomas, 1981b). Further, that for any particular inflorescence, the nutrient resource available will always be less than that needed to fulfill its reproductive potential.

The strength of this type of appraisal of seed production data is in the fact that it adequately explains the results gained by other researchers. For instance, Foulds (1978) when assessing the response of *Trifolium repens* to soil moisture supply found that high and low soil moisture treatments respectively produced 33 and 4 inflorescences per plant, 80 and 64 florets/inflorescence, 2.2 and 2.4 seeds per floret to give 177 and 152 seeds per inflorescence. Initially low moisture curtailed plant growth and thereby leaf size and inflorescence numbers per plant and the numbers of florets per inflorescence able to be formed (Clifford, 1985a). However, the lower floret numbers per inflorescence on low moisture treatments enabled more fertilized ovules per floret to be taken through to maturity, thereby partially offsetting the disparity in seed numbers per inflorescence. Unfortunately this study presented no seed weight or yield data. A further example is the studies of Binek (1983) using the cultivar 'Podkowa'. In this case reduction of head number per plant to 40 and 20 respectively, increased, compared with the control, numbers of seeds/head by 58 and 69% and weight of seeds per head by 71 and 78%. However, numbers of florets per head and 1000-seed weight were only slightly affected (an increase by 6-8%). Pod numbers and weight of seeds per head were influenced by weather conditions rather than variability in 1000-seed weight. Firstly, removal of inflorescences would allow more assimilate for partitioning within the remaining vegetative-reproductive units. Secondly, because the supporting leaves and associated inflorescences were predominantly already formed, no major differences owing to enhanced nutrition in numbers of florets per head would be expected. Consequently, major compensation came by taking more fertilized ovules per inflorescence through to maturity, rather than large increases in unit seed weight. Even though plant compensation for head removal invoked large changes in yield per inflorescence, these were not reflected in differences between treatments in yield/plant. Therefore, it must be concluded that head removal *per se* had no additional effect on either total assimilate production or its subsequent partitioning between the plants vegetative and reproductive requirements. By contrast, Experiment 1 (Table 1) shows that best yields were gained at highest inflorescence densities. Clifford (1979, 1980, 1985b) found that while highest inflorescence densities were synonymous with greatest floret numbers per unit area, this was not so for either floret or seed numbers per inflorescence. Therefore, maximizing seed yield ha^{-1} would seem to be consistent with ensuring the best compromise between florets per inflorescence and total floret numbers per unit area whereby the highest seed numbers possible are formed.

CONCLUSIONS

It is acknowledged that for seed production of any particular cultivar the per-stolon relationships between leaf size and/or numbers with aspects of inflorescence formation and

subsequent provisioning have as yet to be adequately defined. Further, these aspects may fluctuate both within and amongst cultivars in relation to (a) variation in plant types which constitute any particular cultivar, and (b) light competition effects as promoted by any imposed alteration to the reproductive: vegetative stolon ratios which may change the ability of the reproductive stolon leaves to dominate the upper canopy layer, thereby ensuring maximum photosynthetic response. Even so, the relationships gained for the association of soil moisture and/or irrigation with, from leaf numbers and/or size through the reproductive components to seed yield per unit area, have indicated the probable pathways for nutritional resource partitioning within the reproductive phase in the white clover plant. These findings, coupled with the relationships for what happens within the individual inflorescence enabled the following conclusions to be drawn.

1. Where moisture stress occurs at a time of active flowering, floral expression will be maintained at the expense of fertilized ovule numbers and their subsequent provisioning.
2. Except where atypical environmental fluctuations occur there seems to be a constant relationship between the numbers of fertilized ovules taken through to maturity and their provisioning level.
3. Any constraint after fertilization occurs favor ovule retention at the expense of provisioning.
4. The use of moisture constraint to limit leaf size will also be associated with reductions in floret numbers per inflorescence and probably ovules per ovary.
5. The generally more beneficial environmental conditions for leaf formation, associated with the laying down of floret and ovule numbers per inflorescence, compared to the frequently less conducive conditions for nutrient production at the ovule fertilization-provisioning stage, combined with *a priori* servicing of vegetative growth, indicates that only a proportion of the ovules formed will ever be taken through to maturity.

Overall it is contended that the white clover stolon uses a most efficient sequential growth system, as pre-determined by apical dominance, to not only optimize utilization of food resources available for reproduction, but also in a way that some seed will be formed even under the most stressful climatic conditions. Therefore, to obtain the highest possible seed yields for any cultivar growing in a harmonious seed production environment the following requirements seem pertinent.

- (i) Ensuring an adequate stolon density of high reproductive to vegetative ratio by the time of closing the crop to flower.
- (ii) Regulating moisture application and thereby leaf numbers and their photosynthetic efficiency to provide the best compromise possible between floret numbers per unit area formed and the provisioning of fertilized ovules contained therein.

ACKNOWLEDGEMENTS

The G.F. Tate, supervisor Lincoln College Mixed Cropping Unit for crop use. Mrs. M.A. Hanson and Mr. D.R. Stevens, Grasslands Division for technical assistance, Miss E.

Stevenson and Mr. A.R. Wallace, Applied Maths Division, Lincoln for assistance with analyses. Dr. D. Scott, Grasslands Division for helpful discussion on the presentation of these results. Dr. R.W. Brougham, past Director of Grasslands Division, for freedom to develop this aspect of fundamental research.

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