Producing High Seed Yields from High Forage Producing White Clover Cultivars

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ABSTRACT

Consistently high seed yields from white clover are intimately associated with an understanding of the reproductive dependency on vegetative growth in this apical dominant species. Inflorescences form in leaf axils, and therefore leaf numbers per unit area supporting inflorescences are a prime determinant of seed yield. In general, the larger the mean leaf size the greater the negative effect on seed yield. Management practices are discussed, which should (i) produce a satisfactory stolon density of high reproductive to vegetative ratio, and ensure adequate space for floral expression; (ii) minimize the effects of high soil fertility on growth and leaf size through constraining soil moisture available for plant nutrient uptake, while maintaining sufficient photosynthetic efficiency for both maximum inflorescence expression and nectar secretion. Explanations of moisture stress effects on flowering and the variation in these effects on the components of yield per inflorescence are presented.

Additional index words: **seed production, vegetative growth, reproductive growth, genetic factors, environment, leaf size, soil fertility, soil moisture, irrigation, closing date, moisture stress, nectar secretion, seed yield components.**

INTRODUCTION

Consistent high seed yields from improved herbage-producing white clover (*Trifolium repens* L.) cultivars have been a point of conjecture for many decades (Lorenzetti, 1981). However, only in recent years have the distinctly different growth requirements needed to produce 'seed' rather than 'feed' been bought into focus (Clifford 1980, 1985a, 1985b, 1986a, 1986b). When growing a seed crop, most researchers and growers still fail to comprehend the innate sensitivity of the intimate relationships between both morphological and physiological characteristics and nutrient availability in this apical dominant species, and thereby gain inconsistent results. Therefore, this review will emphasise the principles of white clover growth as they affect management decisions to produce consistently high yielding seed crops.

VEGETATIVE GROWTH

White clover is an apical dominant plant. Growth is therefore synonymous with the continuing process at the apical meristem of cell formation and expansion, a leaf being associated with each newly expressed node (Thomas 1961). Because of this species' poor ability to support upward growth expression, particularly in pure seed crops, surface area available for stolon expression is an over-riding factor in maintaining uninterrupted vegetative growth. The reproductive phase occurs with the change from stolon to inflorescence initiation in leaf axils (Thomas 1961, 1980). Reproductive expression therefore depends on basic vegetative growth functions (Clifford 1980, 1985a, 1986b). All the stolons that have developed in leaf axils will contribute to edible herbage yield. However, throughout the reproductive phase, a proportion of stolons is insufficiently developed to produce inflorescences. Nevertheless they will still grow and compete for space with reproductive stolons. Therefore stand management during the 'from sowing to closing to flower period' aims to: (i) achieve a high ratio of reproductive to vegetative apical meristems, while (ii) maintaining sufficient space to ensure the most beneficial reproductive response possible, per unit area.

As such, consistent relationships between stolon tip densities at closing the crop to flower, and seed yield should be evident. However, the diversity of establishment and management (or mis-management) techniques, let alone site variability problems, frequently precludes the determination of any meaningful relationships (Clifford and McCartin 1985). In contrast, pure autumn-established 'Grasslands Huia' and 'Grasslands Pitau' crops to be taken for seed in the first productive season, which were 'precision' sown at row spacings of 15, 30 and 45 cm (at seeding rates equivalent to 6 kg ha^{-1} at 15 cm spacing), all at the same intra-row density, provided good information on the compensatory nature of the per-stolon reproductive resource (Table 1). Only in the reproductive function did a significant level of additional expression with each increase in row spacing become evident (Clifford 1985b). Both the percentage of stolons

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Table 1. Row spacing effects on stolon development and contribution to seed yield in autumn-sown Huia and Pitau crops taken for seed in the first productive season (from Clifford 1985b).

Measurements	Row spacing (cm)		
	15	30	45
Stolons/row m (mid Oct)	108	122	120
% increase in stolons/row m (Oct-end Jan)	56	143	148
% flowering stolons/row m	57	71	78
Inflorescences/flowering stolon	1.1	1.3	1.5
Crown inflorescence contribution to total infloresences/row m (%)	14	7	5
Total inflorescences/row m	123	294	368
Potential seed yield/row m (g)	18.0	42.2	53.3
Potential seed yield (kg ha^{-1})	1200	1410	1190

flowering and the inflorescence numbers borne by individual stolons were enhanced with each increase in row spacing. Although the contribution of crown stolons to total inflorescence numbers/row meter declined with increased spacing (Table 1), this feature had no effect on response to increase in distance between rows in both total inflorescence numbers and yield/row meter.

Of ultimate importance, however, is the use of these results to denote the relationship between stolon tip density and the level of reproductive exploitation and maximum seed yield per unit area. For these particular cultivars, 30 cm row spacings gave the most appropriate percentage of reproductive stolons (71%), at an individual level of contribution of 1.3 inflorescences/stolon. As a consequence 30 cm spacings gave the best harvestable seed yield potential (1400 v. 1200 kg ha^{-1} for the other two spacings). These results demonstrate that under the canopy formation limitations of a one-harvest-only commercial crop system, the crop flowering potential will be fully utilized only when stolon numbers are insufficient to completely utilize the available space. The results also show that maximizing seed yield potential for any particular cultivar requires knowledge of the 'uniformly-distributed' stolon tip density needed by time of closing the crop to flower and an understanding of how management affects speed of stolon formation and/or development, according to season and site variations.

To achieve these aims the New Zealand growers have adopted the following management practices, either singly or in combination (Clifford 1977, 1980, 1985a, 1985b, 1986a, 1986b).

1. Using autumn rather than previous spring sowings to curtail over-development of stolons.
2. Doubling the distance between rows (15 cm to 30 cm), to ensure sufficient and evenly distributed space for floral expression.
3. Retaining normal seeding rate (3 kg ha^{-1}) at 30 cm row spacings, to promote competition between primary meristems at the expense of secondary stolon development.
4. Correct any spring growth limitation by nitrogen rather than additional phosphorus application to ensure a more controlled response.
5. Control surplus spring growth by topping, silage or haying techniques rather than grazing up to closing, to further limit secondary stolon development, while protecting primary meristems from undue loss.
6. Adjust time of closing the crop to flower to ensure maximum reproductive utilization of space.

REPRODUCTIVE GROWTH

Reproductive limitations among cultivars initially fall into two categories, genetic and environmental.

Genetic limitations

Inflorescences form predominantly in leaf axils (Thomas 1961, 1980; Clifford 1985b 1986a), and subsequently these leaves have the dominant influence on seed yield (Zaleski, 1961; Clifford, 1977). Therefore, leaf size, as reflected in leaf numbers per unit area, will have a dominant effect on seed yield both among and within cultivars (Fig. 1). For example, the large-leaved cultivar ('Grasslands Kopu') needs fewer leaves to intercept the

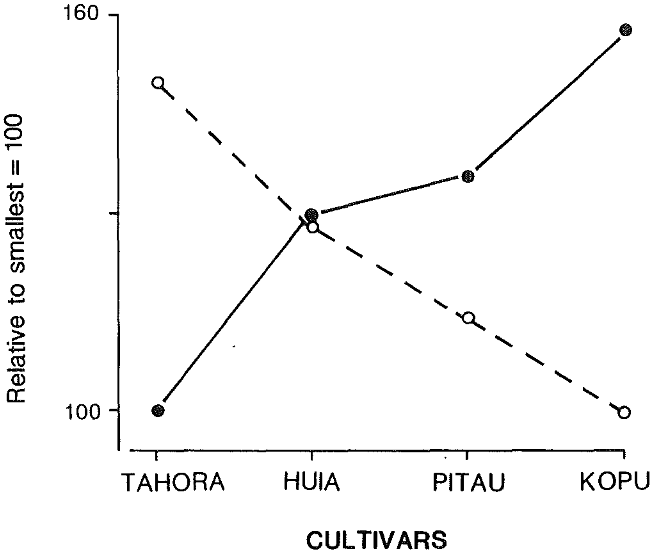
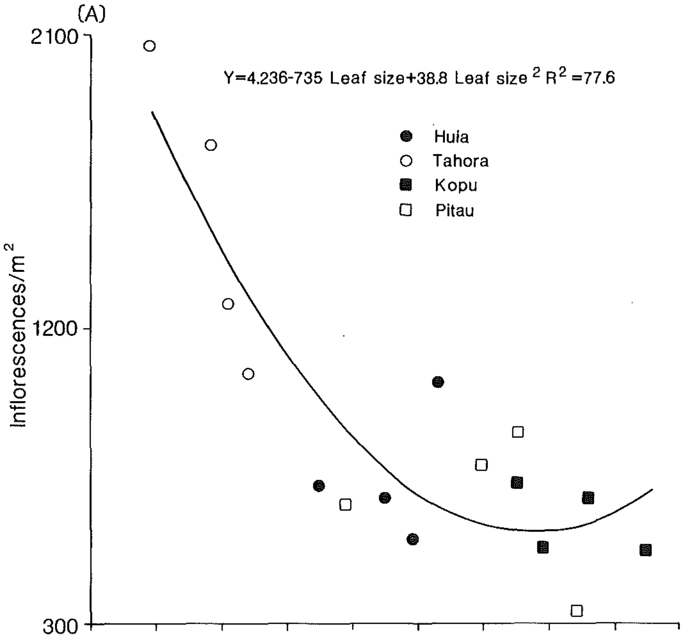


Fig. 1 **Relationships between leaf size and leaf number relationships for New Zealand white clover cultivars in the total canopy at flowering in the 1985-86 season. (● = size, ○ = numbers).**

total radiant energy available for photosynthesis than the small-leaved cultivar ('Grasslands Tahora'); the medium leaf-size cultivars, 'Grasslands Pitau' and 'Grasslands Huia' fall between these points. As a consequence, both inflorescence numbers (Fig. 2A) and seed yield per unit area (Fig. 2C) were lower for large-leaved than a small-leaved white clover, even though floret numbers were directly associated with leaf size (Fig. 2B) (Clifford 1985a).



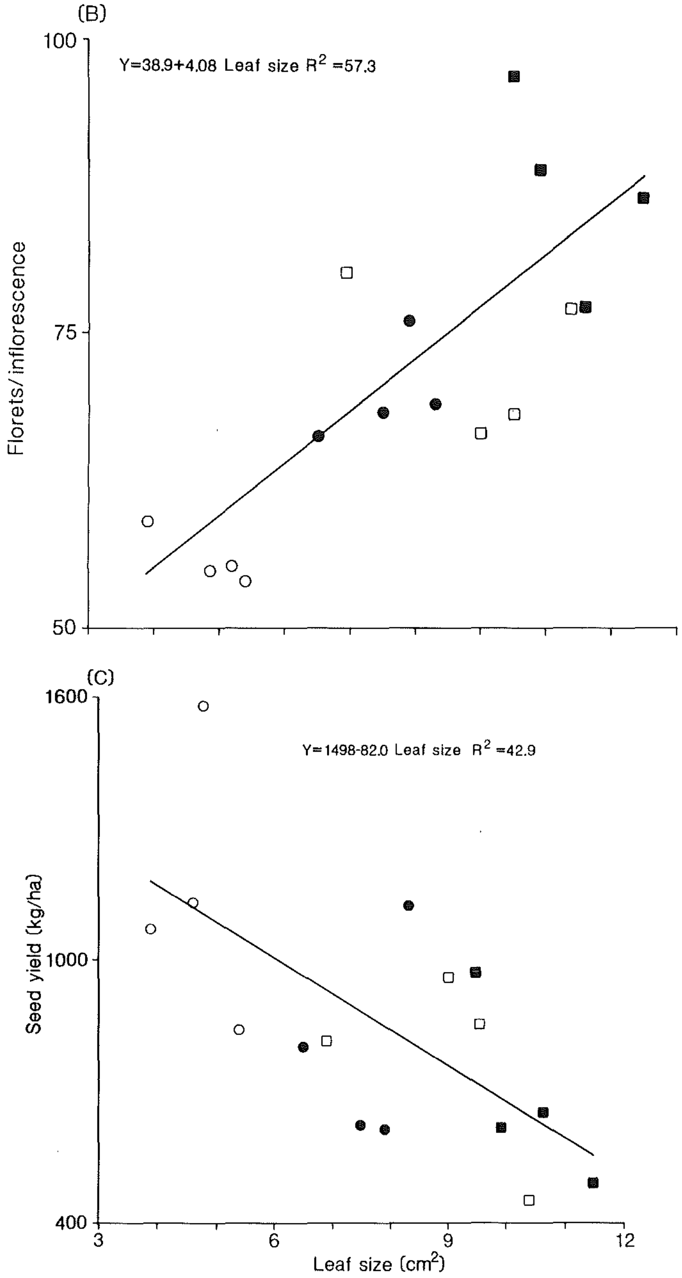


Fig. 2 **Effect of leaf size on (A) inflorescences m^{-2}, (B) floret/inflorescence, and (C) seed yield among NZ white clover cultivars (from Clifford 1985a)**

Sites compatible to the day length and temperature requirements for floral induction of all plants which constitute the cultivar are important for maintaining genetic purity and for seed yield potential. However, within the site range there is scope for increasing yield, particularly for early-initiating cultivars such as Pitau. This cultivar was bred for better cool season growth (Caradus, 1986). Therefore in an environment which limits its seasonal

Table 2. Effect of initiation pattern on seed yield potential at different latitudes. (Piau relative to Huia)

Harvest	Palmerston North New Zealand 40° 20'S	Lincoln New Zealand 43° 38'S	Idaho USA 46° 44'N
1	1.06	0.83	0.84
2	0.98	0.93	0.91

development, the reproductive to vegetative stolon ratio will also be lowered at the expense of seed yield, as is evident in seed yields of Pitau relative to Huia over a range of latitudes (Table 2). At Palmerston North expression of reproductive potential was superior than at Lincoln or Moscow, Idaho, U.S.A., and stolon number per unit area by the time of closing the crop to flower was more than twice as great. At Lincoln, even for spring sowings or second harvest crops, management of Pitau (medium-large leaved) to obtain similar or higher yields than for Huia (medium-small leaved) is more critical for this larger-leaved cultivar (Clifford 1977, 1979, 1985b).

Environment

This discussion is limited to environmental effects that influence plant nutrition and pollination. In the broad sense, crop nutrition is the sum of photosynthetic input from leaves, translocation from other plant parts, moisture and minerals. Therefore, the expression of seed production potential will depend on crop nutrition. As radiant energy is fixed, the constraining of leaf size over the reproductive phase to maximize inflorescence numbers will be a function of soil fertility as modified by moisture availability for plant uptake and subsequent vegetative growth (Clifford 1985a, 1986a, 1986b).

Again, seasonal effects among cultivars of different leaf size appear to be important (Fig. 3). Initial data for first-harvest crops growing on sites of similar fertility, showed that in a season when soil moisture was not limiting growth, relative to a season when it was, leaf size of a small-leaved cultivar was almost doubled and its seed yield halved. By contrast, leaf size of a large-leaved cultivar was increased by only 10% but its seed yield was also halved. As mean leaf size for this large-leaved cultivar growing with unlimited moisture was less than half that where soil fertility was also non-limiting, larger-leaved cultivars seem to be more disadvantaged by unlimited moisture than small-leaved cultivars, in relation to seed yield decline per unit of increase in leaf size. Further verifying this inference are the effects of delay in closing the crop to flower. In most seasons the delay coincides with reduced soil moisture availability for nutrient uptake (Table 3). Here one month's delay, for a medium to small-leaved cultivar, reduced leaf size by 25% and increased seed yield by 7% (Clifford 1985a). However the reduction in leaf size of a medium to large-leaved cultivar was only 11%, but seed yield increased by 14%. Therefore, conversely, large-leaved cultivars will give greater increases in seed yield per unit of reduction in leaf size than small-leaved cultivars.

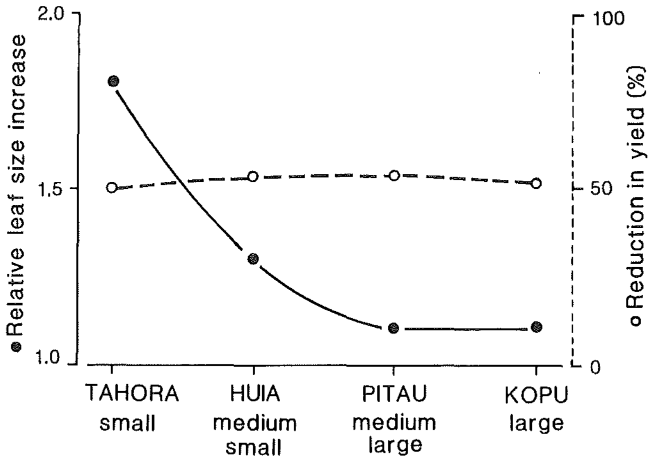


Fig. 3 **Effect of a moist relative to a dry season on the leaf size increase and seed yield reduction among NZ white clover cultivars. (● = size, ○ = yield).**

Soil fertility: Phosphorus (P), initially to assist in plant establishment and subsequently stimulate nitrogen (N) fixation, is a key element for clover growth. Therefore, if soil moisture is not limiting the amount of plant available P in the soil should be evident in both leaf size and subsequently seed yield (Fig. 4). For the cool moist 1985-86 New Zealand season, for autumn-sown crops of four cultivars ranging in leaf size from large to small, the following mean cultivar results were gained from a range of P x N treatments.

1) No P at sowing limited stolon production per unit area. As a consequence there was less competition among stolons for soil residual P. Therefore, leaves were larger and yield lower than when P at

Table 3. Effect of spring closing date on leaf size, subsequent inflorescence formation and seed yield of two medium leaf-sized cultivars (from Clifford 1985a)

Measurement	Cultivar leaf size			
	medium-small		medium-large	
	Mid spring	Late spring	Mid spring	Late spring
Leaf size (cm^2)	9.7*	7.3	11.2*	8.9
Infloresecenses/m^2	307*	432	327*	417
Seed yield (kg ha^{-1})	473	505	471	535

*P = 0.05

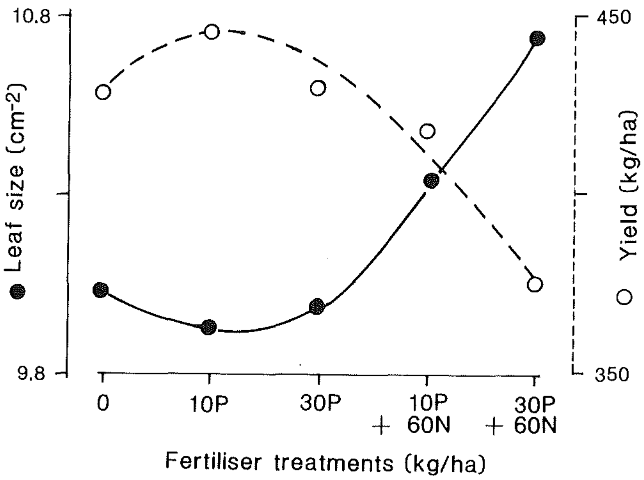


Fig. 4 **Fertilizer effects on leaf size and seed yield in conditions of unlimited soil moisture. (points = means of 4 cultivars x 4 replicates) (● = size, ○ = yield).**

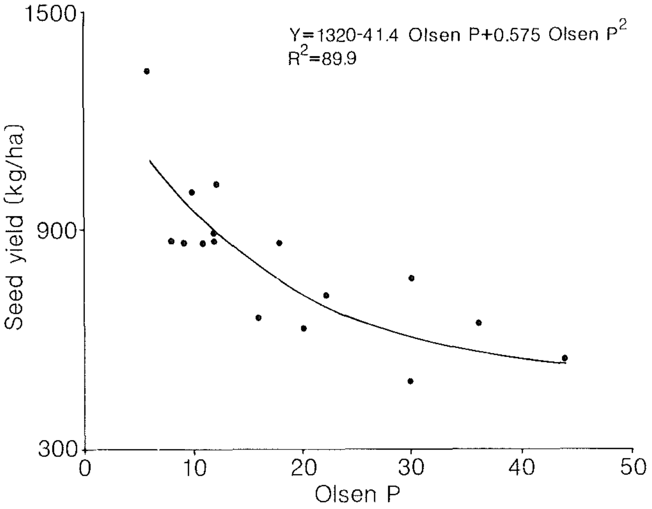


Fig. 5 **Effects of soil phosphorus on seed yield of commercially grown Huia white clover seed crops (from Clifford 1985a).**

10 kg ha^{-1} was applied at sowing.

2) P at 10 kg ha^{-1} gave the best level of competition among stolon numbers for available nutrients, to maximize use of the reproductive space.
3) P at 30 kg ha^{-1} reduced nutrient competition, and again led to poor utilization of space.
4) Addition of N (30 kg ha^{-1} late-autumn and again in early spring) to P treatments only, further increased luxury feeding to the detriment of seed yield.

The most outstanding result from a survey of commercial seed crops, established and grown on moisture-retentive soils under a wide range of management, was a general decline in harvestable seed yield potential as available soil P levels (Olsen P test) rose (Fig. 5, Clifford 1985a). This result for moisture-retentive soils, suggests that the managing of any additional phosphorus surplus becomes increasingly more difficult. Thus, choice of low P sites coupled with a sound knowledge of the likely response to amount and timing of P application in relation to 'time from sowing to closing the crop to flower' are key management criteria.

Soil moisture: The easiest way to control the seed yield problems in high fertility soils is to limit plant nutrient uptake by reducing soil moisture (Fig. 6). Any reduction in plant-available soil moisture directly reduces leaf size (Clifford 1985a). The results of growing a large-leaved cultivar on a soil of widely divergent moisture-holding characteristics are shown in Table 4. Regardless of irrigation crops growing on soils with the poorest compared with the best moisture retention characteristic trebled leaf numbers m^{-2} and doubled seed yield (Clifford 1986b). For smaller-leaved cultivars these differences in seed yield would have been less, as explained above.

Table 4. Effect of leaf number extremes on seed yield and its components for the large-leaved white clover cultivar (Kopu) (from Clifford 1986b)

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 x 10^6	1.57	0.84	1.86	0.89
1000-seed weight (g)	0.65	0.65	0.58	0.68

[1]leaf numbers to cover 1 m^2

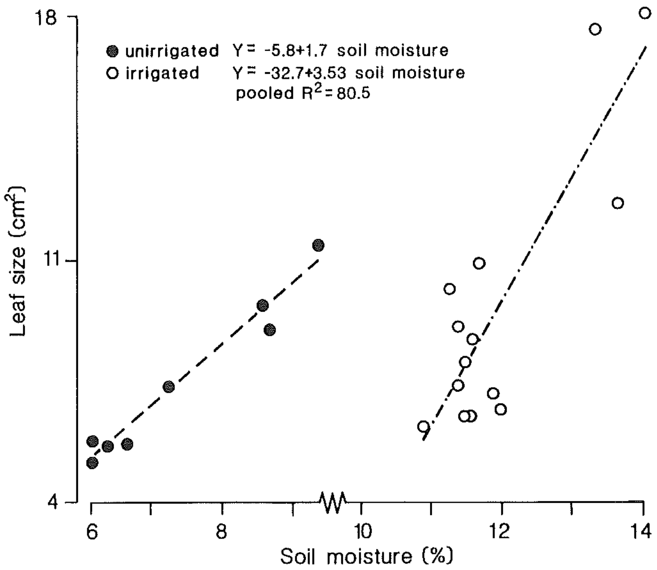


Fig. 6 **Soil moisture effects on leaf size in irrigated and unirrigated Kopu white seed crops (from Clifford 1985a).**

Irrigation: The function of irrigation for seed crops is to eliminate moisture stress over the reproductive phase. However in doing so, rate and frequency of application must be consistent with ensuring the best level of nutrient partitioning between reproductive and vegetative growth, in relation to space available for floral expression (Clifford 1986a, 1986b). In white clover photosynthetic efficiency is unaffected until the approximate time when the first visual symptoms of 'wilting' appear (Upchurch, 1955). Therefore wilting point is the lowest limit of exhaustion of plant available soil moisture. To find an effective upper limit, Clifford (1986a) used an irrigation system based on 'topping up' plant available soil moisture to 50% each time 'near wilting' was reached. In that season this amounted to six irrigations, at weekly intervals, from around peak flowering onwards. Thus this system maintained mean plant available soil moisture at about 25%. Compared with unirrigated treatments, irrigation increased seed yield by 53% (Table 5), as a result of a 22% increase in inflorescence density (additional growth) and a 27% reduction in ovule abortion (higher available nutrient level to maintain ovule development). Overall ovule development (1000-seed weight) increased only 4%. It is important to note that enhanced nutrition to individual inflorescences, as promoted by irrigation, predominantly increased the number of ovules taken

Table 5. Mean irrigation effect on seed yield components in the large-leaved white clover cultivar (Kopu) (derived from Clifford 1986a).

Measurement	Irrigated	Unirrigated
Seed yield (kg ha^{-1})	637	417
Inflorescences m^{-2}	729	598
1000-seed weight (g)	0.60	0.58
Seeds/inflorescence (calculated)	146	119

through to maturity (Clifford 1986a, 1986b), as shown by the differences in seed numbers/inflorescence between irrigated and unirrigated crops (Table 5).

That differences in growth *per se*, and of the same nature, accounted for the results in this comparison is evidenced in Fig. 7 (Clifford 1986b). Seed yield relationships with both (a) seed numbers and (b) inflorescence density gave a common linear response. In contrast, seed yield associations with leaf numbers gave an additional 119 kg ha^{-1} of seed for irrigated compared with unirrigated crops of the same leaf number. This difference is an artifact of equating measured leaf size with surface area. Had total leaf numbers within each size category also been counted then a common line denoting growth advantage to irrigation would have been gained. Irrigation points would then have dominated the upper end of this common response line.

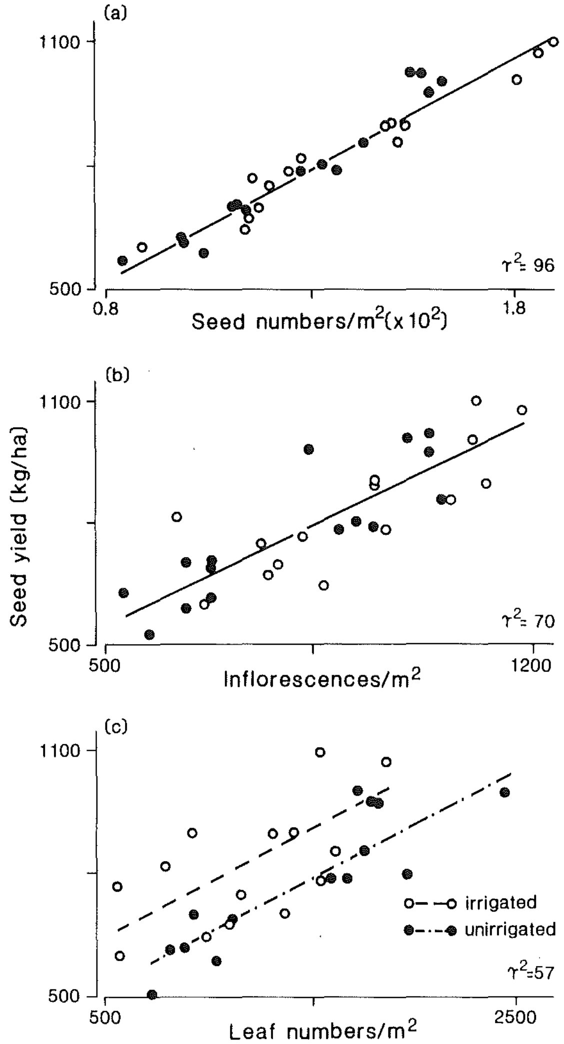


Fig. 7 **Irrigated and unirrigated seed yield relationships with (a) seed numbers m^{-2}, (b) inflorescences m^{-2}, and (c) leaf numbers for a large-leaved cultivar (Kopu) (from Clifford 1986b).**

In New Zealand, to fully implement the advantages of controlled moisture application, much of the white clover seed crop is now grown in 'free-draining' soils with irrigation, to offset the deleterious effects of any unforeseen heavy rainfalls.

Moisture stress: This review has emphasised the basic mean seasonal associations of leaf numbers, inflorescence numbers and seed yield. As such, the results do not identify the real effects on reproduction of any within season short fall in photosynthetic efficiency caused by moisture stress, particularly in unirrigated crops. The reproductive process is the obligatory sequence of floret formation, ovary, ovule and pollen grain formation, floret opening, fertilization, ovule maturation and provisioning through to mature harvestable seed (Thomas, 1961, 1980, 1981). This individual sequence, as observed through flowering, is repeated many times over the 3-month reproductive period. Therefore stress effects may not only be evident between inflorescences but also within the components of yield per inflorescence. In general the stages from floret to pollen grain formation occur under more beneficial environmental conditions (up to 10 weeks earlier) than the later stages from fertilization through to mature seed (Thomas 1981). Therefore it is assumed that the diminishing of nutrients available for partitioning between vegetative and reproductive requirements, over the later stages of inflorescence development, will totally preclude full exploitation of the reproductive potential of any inflorescence (Clifford 1986b). This is shown by the fact that, regardless of time of flowering, competition for nutrients occurs even between florets on individual inflorescences. The result is a reduction in seed numbers per floret formed, as floret opening proceeds on the inflorescence. Therefore, competition for nutrients exists within the reproductive process itself (Clifford 1986b).

With the onset of stress, nutrient partitioning will favor vegetative growth at the expense of supported reproductive growth (Fig. 8). Although severe moisture stress over the fortnight of peak flowering had no observable effect on floral expression, yield per inflorescence was affected in relation to stage of development on individual inflorescences at that time (Clifford 1986b). The combined effect on the seed yield available for harvest was a reduction of about 200 kg ha^{-1}. Of interest are the effects of moisture stress on variations in the components of yield per inflorescence in relation to stage of inflorescence development (Fig. 9). Inflorescences starting to flower had been tagged at weekly intervals over flowering. The decline in floret numbers/inflorescence with

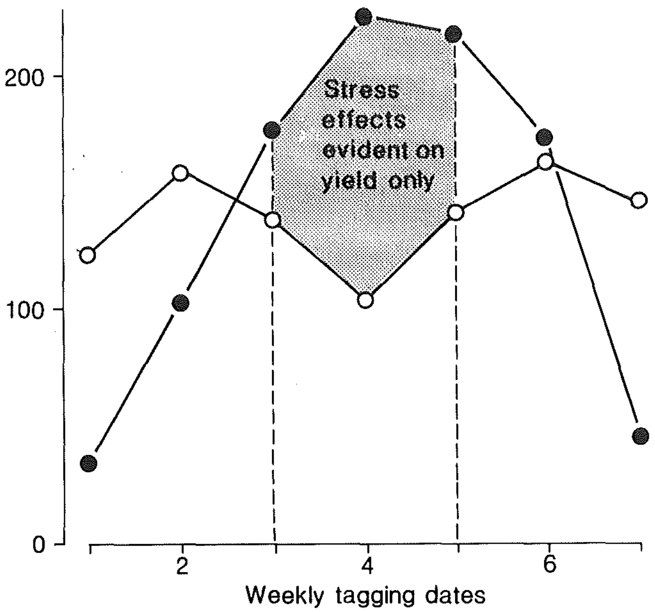


Fig 8. **Moisture stress effects on flowering and yield/inflorescence (from Clifford 1986b). (● = inflorescences m^{-2} available for pollination , ○ = seed yield (mg/inflorescence)).**

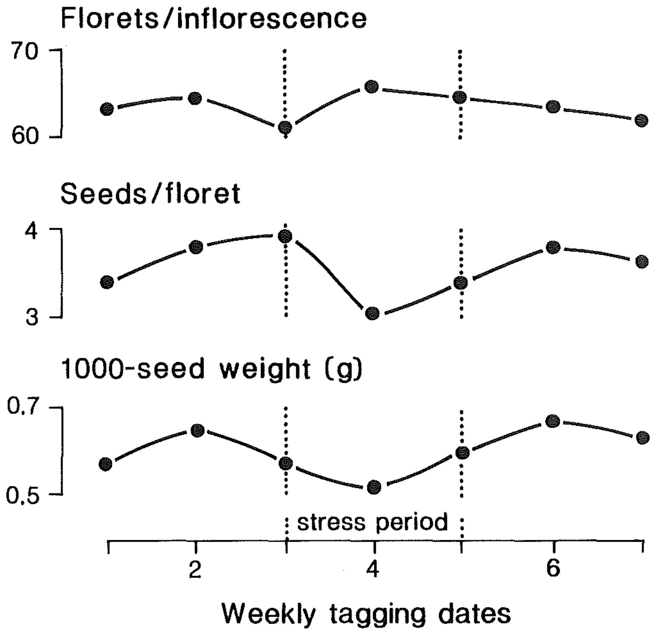


Fig. 9 **Moisture stress effects on the components of yield/inflorescence (derived from Clifford 1986b).**

the onset of stress is an artifact of floral expression, as shown by the high numbers in taggings 4 and 5. Nutrient privation for 3 would have occurred much earlier, at floret formation. Also unaffected were seed numbers per floret forming at the start of the stress period (tagging date 3). Therefore, there seems to be some time lag in the onset of nutrient privation once wilting is seen. For the two later taggings nutrient limitations either reduced fertilization or promoted early abortion, more so in 4 and 5. The ultimate effects of stress on limitations to ovule provisioning are seen in the resultant 1000-seed weights. Although seed numbers per floret for tagging 3 were unaffected, 1000-seed weight was diminished, and even further in 4. Although seed numbers that developed through to maturity in 5 were reduced, their level of provisioning was unaffected, because a timely rainfall ensured adequate nutrition over the subsequent 21 days. Thus lack of plant-available soil moisture, depending on the duration of the shortage, may affect one or all the components of yield per inflorescence, particularly from the fertilization stage onwards.

Delay in closing the crop to flower often reduces floret numbers per inflorescence because declining moisture availability causes nutritional privation at inflorescence formation (Fig. 10) (Clifford, 1979), and leaf size is thus constrained (cf. the relationships between leaf size and floret number among cultivars, Fig. 2). Ovule provisioning (1000-seed weight) also tends to be affected in a similar manner (Fig. 10). Even so, the 'managed' lowering of floret numbers is more than offset by the increase in inflorescence density (total floret numbers per unit area) to give higher seed yields (Table 6) (Clifford 1979, 1980). In contrast, luxury feeding gives high 1000-seed weights (early closing, Fig. 10; high soil moisture, Table 4 - irrigated highest-lowest leaf number comparison), low inflorescence populations and poor seed yields (Table 6) (Clifford, 1979, 1986b). Thus, closing date choice is a prime determinant of the seed yield.

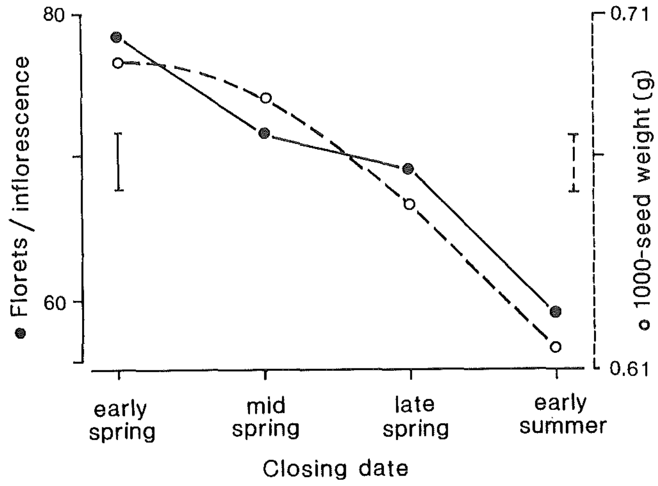


Fig. 10 **Closing delay effects on florets/inflorescence and 1000-seed weight (points = means of 2 cultivars x 4 seasons x 4 reps) (● = florets/inflorescence, ○ = 1000-seed weight). Bars P = <0.05.**

Pollination: Cross fertilization, as promoted by foraging bees, is fundamental to the reproductive process. Therefore it is important to understand how plant physiological processes affect nectar secretion and thereby bee visitation. In red clover, nectar secretion depends on a carbohydrate surplus over and above that needed for growth, respiration and other concurrent processes (Shuel and Peterson, 1952). Therefore the practices, already outlined, for maintaining a good balance in nutrient partitioning between reproductive and vegetative growth must also be conducive to nectar secretion. Thus crop attraction to pollinators is also a function of management practices to maximize inflorescence density and thereby yield, as verified by observations of Johnson 1946. He found that white clover growing on light, sandy and soils sloping to the sun gave superior nectar-flows than on clay or flat soils. Both cloud cover (low radiant energy) and cool winds also reduced nectar secretion.

In conclusion, it is hoped that this alternative approach, based on the fundamental growth sequences of this apical dominant species, promotes a better understanding of the management required to consistently produce high yielding seed crops.

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