Chapter 5

The influence of crop development and fruit retention on the timing of crop maturity in UNR and conventionally spaced cotton production systems

5.1 Aim

To identify and describe the differences in crop development and fruit retention for UNR and conventionally spaced cotton and to quantify how those differences influence maturity.

5.2 Introduction

Yield of cotton is ultimately determined by the number of fruit (bolls) per unit area and the amount of lint per boll (Hearn and Constable 1984). Similar yields can be reached over differing times and development rates depending on the pattern of boll production and the capacity of the plant to retain those bolls. Boll distribution and timing can also greatly affect crop maturity. The time for a crop to mature is dependent on a range of factors, but is ultimately determined by the time to boll initiation (node of first fruiting branch and time to first square), the rate of boll production (main-stem and sympodial node production), boll growth (retention and boll size), the time to cessation of initiation of new bolls (cut-out) and the time from anthesis to maturity of those bolls retained (boll period) (Harland 1929; Richmond and Radwan 1962; Ray and Richmond 1966; Munro 1971).

The rationale behind UNR cotton production being earlier and higher yielding than conventionally spaced cotton production is relatively simple:

- plants in a high population would be smaller and set fewer bolls per plant;

- yield is maintained as a higher number of plants m^{-2} compensates for smaller plants having fewer bolls per plant;
- a smaller plant has fewer fruiting branches and should cut-out earlier;

If these assumptions hold, the fruiting cycle on the smaller plants should be completed sooner than for larger more vegetative plants and the last bolls set and mature earlier (Lewis 1971).

In individual experiments investigating yield and maturity of UNR compared with conventionally spaced cotton no significant differences were found in maturity between the two row spacing treatments, but a combined analysis showed a significant increase in lint yield in the UNR system (Chapter 3). While yield in cotton is primarily linked to biomass development, growth analyses in three of these experiments showed that there were few significant differences in crop biomass accumulation. The increase in yield was most likely caused by increased boll numbers and increased partitioning of dry matter to fruit in the UNR plants (Chapter 4). Due to the effects of competition for light, water and nutrients among the higher number of plants in the UNR system, the growth and development of individual plants is likely to be different between the two row spacing treatments. Plants in the UNR system were observed to be shorter, with fewer nodes, fruiting branches and fewer mature bolls produced per plant (Chapter 3). Yield was at least maintained because the higher density of plants in the UNR treatments compared with the conventionally spaced treatments compensated for the lower number of bolls per plant. However, contradictory to the response to UNR proposed by Lewis (1971), these smaller plants did not mature earlier.

High rates of shedding in the lower fruiting branches have been reported to be the most likely cause of delays in maturity in UNR cotton (Constable 1975; Baker 1976). As Constable and Gleeson (1977) stated, "the success of narrow row spacing and other forms of crop manipulation aimed at rapid crop setting depends on the retention and rapid growth of early bolls". The UNR plants may compensate for early fruit loss by producing more fruit later in the growing season, thus delaying maturity.

Although differences in fruit retention were inconsistent between experiments, a combined analysis of the six experiments in Chapter 3 showed that overall boll retention per plant was significantly lower in the UNR crop compared with the conventionally spaced crop.

However, differences in fruit distribution or loss of early bolls can occur without differences in overall fruit retention. This chapter examines final fruit distribution and the timing of crop development stages in UNR plants compared with conventionally spaced plants to investigate whether the loss of early fruit caused delays in the crop maturity of UNR cotton.

5.3 Methods

5.3.1 Crop developmental stages

To determine the time when specific development phases occurred, four plants per plot were monitored in Exps. 1 and 5. Mapping was conducted twice weekly as it was possible to estimate events accurately a few days back in time by noting leaf, fruit or scar size and colour (Constable 1991). Four stages of fruit development were recorded for each fruit on sympodial branches (Figure 5.1):

- Date of squaring (flower bud appearance) was defined as when the subtending leaf unfolded (Constable 1991).

- Date of anthesis.

- Date of boll opening – when at least two sutures on the boll had cracked open.

From the detailed plant maps, timing of a number of developmental stages could be determined. For each plant the dates of first square, first flower, last effective flower (last flower that becomes an open boll), first open boll and last open boll were calculated. Fruit on monopodial branches were not recorded for this study. The days after sowing to each of these developmental stages was compared between row spacing treatments. Boll period (time from anthesis to mature boll) was calculated for each mature boll mapped and compared between row spacing treatments.

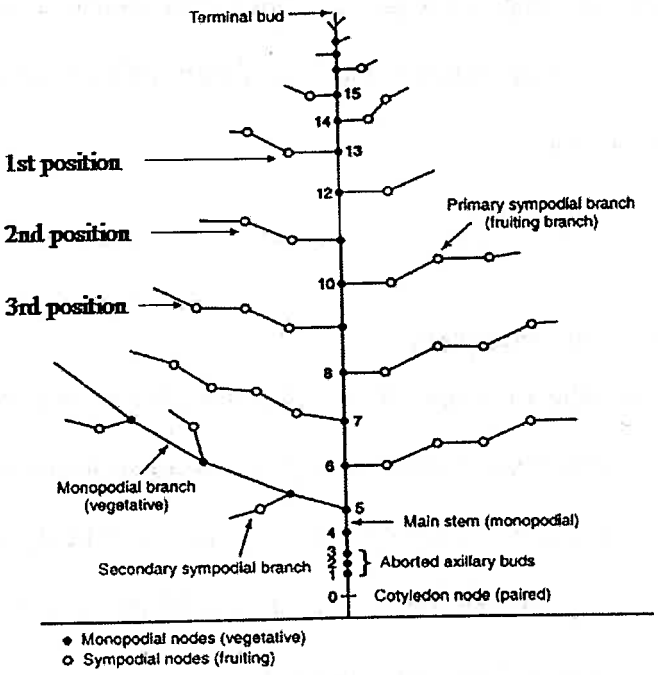

Figure 5.1 Representation of the cotton plant showing main-stem, monopodial and sympodial branch development (From Oosterhuis (1990))

5.3.2 Fruit retention

In Exps. 1, 2, 3 and 5 final fruit distribution and retention (the ratio of open bolls to each fruiting site (square) exerted) were determined through final plant maps. After all the bolls were open and the crop had been defoliated, four plants were harvested from each plot. The number of nodes on each plant was recorded. Each fruiting site was mapped and the presence or absence of fruit at each site was recorded (Figure 5.1).

Fruit retention for each sympodial branch (node) (Figure 5.1) was compared between the two row spacing treatments. Due to the high variation in fruit retention on individual nodes between plants, bolls were divided into different cohorts to examine boll distribution and retention vertically up the plant. As the plants in the conventionally spaced and UNR treatments had differences in the number of fruiting branches only the first 12 fruiting branches were compared: cohort 1 – fruiting branches 1 to 3, cohort 2 – fruiting branches 4 to 6, cohort 3 – fruiting branches 7 to 9 and cohort 4 – fruiting branches 10 to 12.

Statistical analyses

Analysis of variance (ANOVA) was used for comparing treatments effects for most parameters with data transformed where necessary. All statistical analyses were conducted using Genstat® software. Unless stated otherwise, significant differences were considered at 95% confidence intervals ($P < 0.05$).

5.4 Results

5.4.1 Crop development

There were few differences between row spacings in the time to reach definitive crop stages in Exp. 1 (Figure 5.2). Both row spacings reached first square, first flower and first open boll at the same time. The number of days after sowing to last effective

flower was 8.5 days earlier in the UNR treatment compared with the conventionally spaced treatment and the last open boll matured 6.4 days earlier in the UNR treatment compared with the conventionally spaced treatment. The average boll period was not significantly different between row spacings, with the average time from anthesis to maturity for the UNR plants being 65.1 days compared with 65.9 days in the conventionally spaced plants.

There were few differences between row spacings in the time to reach definitive crop stages in Exp. 5 (Figure 5.2). The number of days after sowing to first square was 1.8 days earlier in the UNR treatment compared with the conventionally spaced treatment ($P = 0.033$). Both row spacings reached first flower, first open boll and last open boll at the same time. The time to reach last effective flower was significantly shorter (by 5.9 days) in the UNR plants compared with the conventionally spaced plants ($P = 0.035$). The average boll period was significantly longer for the UNR plants with an average boll period of 63.7 days compared with 60.6 days in the conventionally spaced plants ($P < 0.001$).

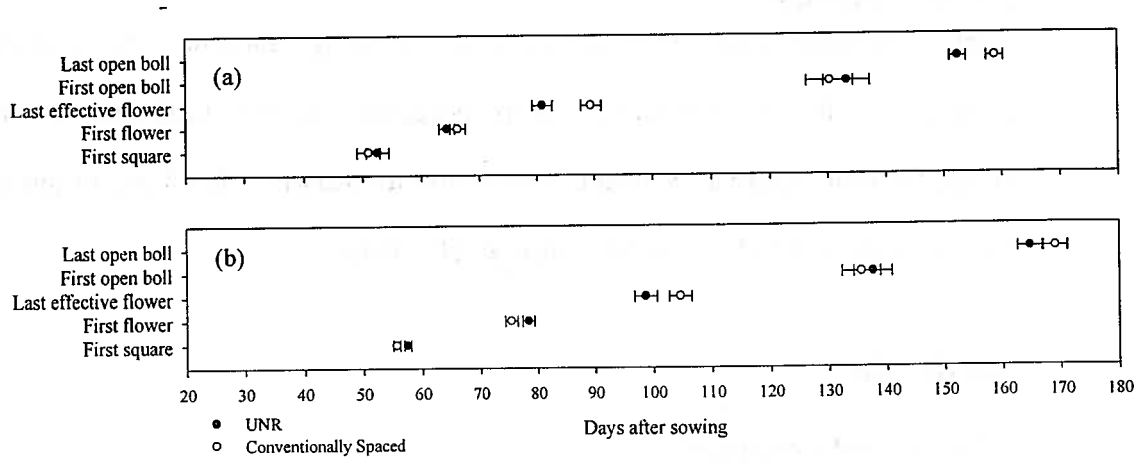

Figure 5.2 Days after sowing to first square, first flower, last effective flower, first open boll and last open boll in Exps. 1 (a) and 5 (b) for UNR and conventionally spaced treatments. Error bars are two standard errors of the mean

5.4.2 Fruit retention per plant

In Exps. 1, 2, 3 and 5 the plants mapped in the UNR spaced treatments had significantly fewer open bolls and fruiting sites than plants mapped in the conventionally spaced treatments (Table 5.1). Overall retention per plant was not significantly different between row spacings in Exps. 1, 3 and 5, but was significantly lower in the UNR plants compared to the conventionally spaced plants in Exp. 2 (Table 5.1).

Table 5.1 Number of fruiting sites, open bolls and retention per plant in Exps. 1, 2, 3 and 5 for UNR and conventionally spaced treatments. (Significant differences indicated by * = 95% confidence level; ** = 99% confidence level)

	Total fruiting sites per plant	Total open bolls per plant	Retention per plant (%)
Exp. 1			
UNR	14.60	3.64	24.7
Conventionally Spaced	24.20	6.22	25.4
L.S.D	**5.69	*2.17	6.3
Exp. 2			
UNR	16.90	5.17	31.3
Conventionally Spaced	30.40	14.75	49.2
L.S.D	**5.39	**2.55	**8.2
Exp. 3			
UNR	12.06	5.69	47.7
Conventionally Spaced	23.25	10.50	45.7
L.S.D	**2.97	**1.37	5.4
Exp. 5			
UNR	15.97	6.60	43.9
Conventionally Spaced	29.46	13.83	46.4
L.S.D	**4.11	**2.48	9.1

In Exp. 1, retention per node was only significantly different between row spacings on node 14 (Figure 5.3a). Node 14 had lower fruit retention in the UNR plants. In Exp. 2 retention per node was significantly lower in the UNR plants compared with the conventionally spaced plants on nodes 11, 13, 15, 16 and 17 (Figure 5.3b). In Exp. 3 retention per node was only significantly lower in the UNR plants compared with the conventionally spaced plants on nodes 15 and 16 (Figure 5.3c). In Exp. 5 on nodes 8,

13 and 16 the UNR plants had significantly lower fruit retention compared with the conventionally spaced plants (Figure 5.3d).

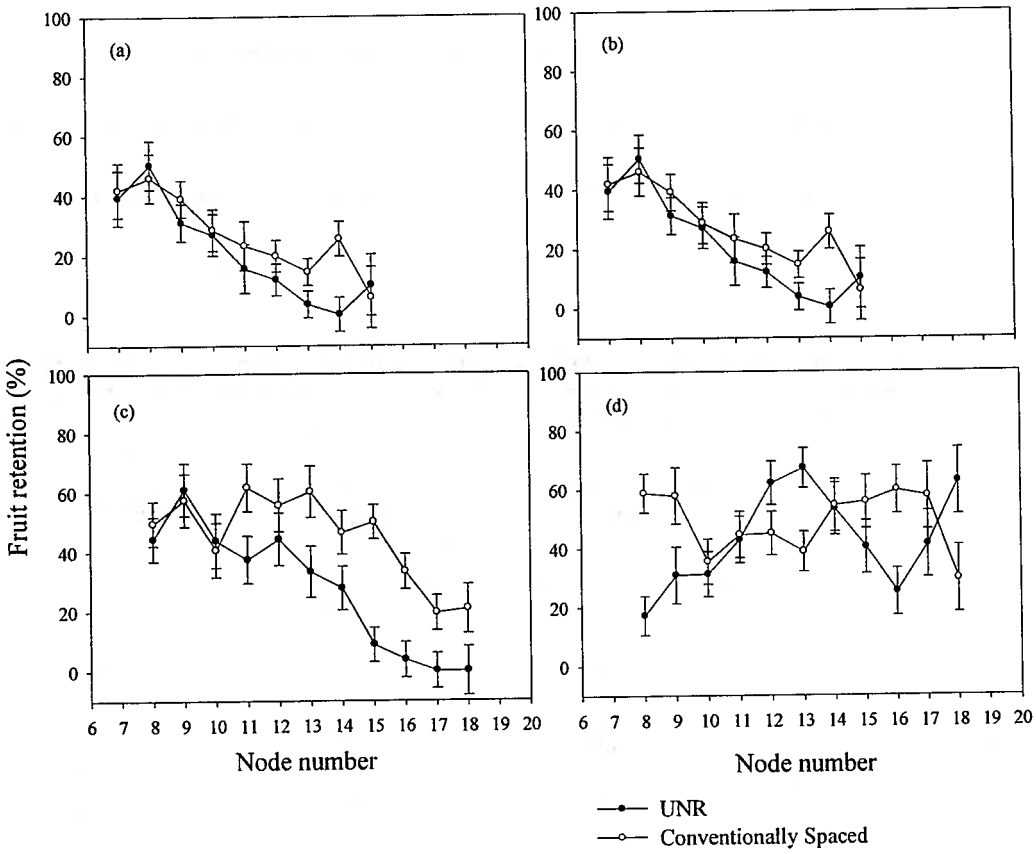

Figure 5.3 Average retention per plant on each node in UNR and conventionally spaced treatments for Exps. 1 (a), 2 (b), 3 (c) and 5 (d). Error bars are two standard errors of the mean.

To account for high variability between individual nodes on a plant, the plants were grouped into four cohorts (three sympodial nodes per cohort). There were few differences in retention per cohort for each cohort in UNR plants compared with conventionally spaced plants in Exps. 1, 2, 3 and 5 (Table 5.2). The only significant differences in retention in Exp. 1 and 3 were in cohort 3 where retention was significantly lower in the UNR plants than conventionally spaced plants (Table 5.2). In Exp. 5, retention of the UNR plants was significantly lower in cohort 1. Exp. 2 had significantly lower retention in cohorts 2 and 3. A higher proportion of bolls were on

the lower two cohorts (1 and 2) for the UNR plants compared with the conventionally spaced plants (Table 1.2b).

In Exps. 1, 2 and 5 the UNR plants had a significantly higher proportion of open bolls in cohort 2 compared with the conventionally spaced plants. In Exps. 2 and 3 the UNR plants had a significantly higher proportion of open bolls in cohort 1 but a significantly lower proportion in cohort 3 and 4. In Exp. 5, the UNR plants also had a significantly lower proportion of open bolls compared with the conventionally spaced plants in cohort 4.

Table 5.2 Retention and proportion of open bolls for cohorts 1 to 4 (3 fruiting branches per cohort) per plant for UNR and conventionally spaced treatments in Exps. 1, 2, 3 and 5. (Significant differences indicated by ** = 99% confidence level)

Experiment	Treatment	Cohort 1 (Fruiting branches 1-3)	Cohort 2 (Fruiting branches 4-6)	Cohort 3 (Fruiting branches 7-9)	Cohort 4 (Fruiting branches 10-12)
Retention (%)					
Exp. 1	UNR	41.3	14.3	1.8	4.6
	Conventionally Spaced	39.0	23.3	10.9	3.6
	L.S.D	15.0	12.0	*8.4	12.7
Exp. 2	UNR	51.7	37.9	15.1	0.0
	Conventionally Spaced	50.3	57.8	43.4	17.9
	L.S.D	18.7	*16.5	**12.1	**7.6
Exp. 3	UNR	65.1	59.4	20.3	14.0
	Conventionally Spaced	66.2	54.8	43:7	21.2
	L.S.D	17.21	10.4	**16.6	16.2
Exp. 5	UNR	31.8	53.5	45.9	40.3
	Conventionally Spaced	48.0	43.5	54.6	37.4
	L.S.D	*15.0	12.8	17.9	34.8
Proportion of open bolls in each cohort (%)					
Exp. 1	UNR	74.8	23.4	0.4	1.4
	Conventionally Spaced	55.2	33.4	9.8	1.6
	L.S.D	*14.5	7.6	**5.4	3.8
Exp. 2	UNR	51.1	35.8	11.0	0.0
	Conventionally Spaced	23.8	39.5	27.8	6.7
	L.S.D	**16.0	14.1	**9.4	**2.9
Exp. 3	UNR	38.2	49.2	10.2	2.5
	Conventionally Spaced	25.7	38.0	25.9	8.5
	L.S.D	*12.4	**7.9	**7.8	*5.4
Exp. 5	UNR	27.6	44.1	23.5	4.9
	Conventionally Spaced	29.2	28.3	29.3	12.1
	L.S.D	11.0	**7.8	7.2	*6.5

A combined analysis of fruit retention in each cohort found that there was no significant difference between UNR and conventionally spaced plants for cohort 1 and 2, but there was a significant difference between experiments ($P = 0.022$) and a significant interaction for fruit retention between row spacings and experiments ($P = 0.026$). Cohort 3 had significantly lower retention of fruit in the UNR plants compared with the conventionally spaced plants ($P < 0.001$), significant differences between experiments ($P < 0.001$) but no interaction. In cohort 4 fruit retention was not significantly different between row spacings, but was significantly different between experiments ($P < 0.001$) with no interaction between row spacings and experiments.

5.5 Discussion

In both Exps. 1 and 5 there were no large differences between row spacing treatments in time to fruit initiation (first square), time to anthesis (first flower) or time to first open boll. The UNR plants initiated their last effective flower 8.5 days earlier in Exp. 1 and 5.9 days earlier in Exp. 5 than the plants in conventionally spaced row spacings. In Exp. 1, this boll opened 6.4 days earlier but not any earlier in Exp. 5. These differences did not translate into a difference in overall crop maturity in UNR. The average boll period was not different between row spacings in Exp. 1 and only 3 days longer in UNR plants in Exp. 5, indicating that average time from anthesis to maturity for a boll was not greatly affected by row spacing. Hence, the smaller boll size in the UNR treatments was due to reduction in boll growth associated with limited assimilate supply. Even if the fruit is not abscised, boll size can be significantly reduced if assimilate supply to the developing boll is below optimum.

UNR plants were smaller and had fewer sites and bolls per plant. This change in plant architecture in response to narrow row spacings and higher plant populations had been found in other studies (Jost and Cothren 2001; Vories *et al.* 2001; Marois *et al.* 2004; Nichols *et al.* 2004). It had also been found that higher plant populations compensated for the smaller plants, and total boll number was usually the same or slightly higher (Witten and Cothren 2000). There were no differences in total retention per plant between row spacings in Exps 1, 3 and 5, but UNR plants had significantly lower retention in Exp. 2. A combined analysis of all six experiments showed significantly lower retention in the UNR plants compared with conventionally spaced plants (Chapter 3).

Fruit retention vertically up the plant was not consistently affected by row spacing, and there was no indication that the UNR plants lost more early bolls than the conventionally spaced plants in Exps. 1 to 3. Retention was not consistently different between experiments at different positions on the plant. The UNR plants had significantly lower retention in cohort 1 compared with the conventionally spaced plants in Exp. 5 but not in the other three experiments. It was in the upper part of the plant that boll retention was consistently lower in the UNR plants compared to the conventionally spaced plants (i.e. cohort 3). Retention for cohort 4 was not significantly different between treatments, except for Exp. 2, probably due to the high variability between plants in this section of the plant.

Fruit distribution differed between row spacings (in all experiments except Exp. 5) with the UNR plants having a significantly higher proportion of mature bolls located in the bottom part (cohort 1) of the plant compared with conventionally spaced plants.

UNR plants in Exp. 5 had a higher proportion of mature bolls in cohort 2 compared with conventionally spaced plants.

While differences in environmental conditions between years of these experiments had a far greater effect on fruit retention than the difference between row spacings, the patterns with less fruit at higher nodes in the UNR plants are probably related to the differences in final node number in the UNR plants compared with conventionally spaced plants (Chapter 3). Jenkins *et al.* (1990a, b) found that fruit retention was related to main-stem node position. They found that greater than 70% of the total yield was on the central part of the plant (in their case – main stem nodes 9 to 14) (Jenkins *et al.* 1990b; Jenkins *et al.* 1990a). These nodes coincide with maximum leaf area in the canopy (Oosterhuis and Wullschleger 1988). They also have the largest leaves and are the highest suppliers of carbon to fruit, as leaves produced on lower nodes export a greater proportion of assimilates to root development (Constable 1981).

In previous studies high rates of shedding in the UNR treatments have been thought to be the most likely cause of delays in maturity in UNR cotton (Constable 1975; Baker 1976). However, the results of this study show that a loss of bolls on the lower fruiting branches in the UNR plants was not responsible, so other factors must be slowing the time to crop maturity. In contrast to losing bolls in the lower part of the plant and compensating later and perhaps delaying maturity, the UNR plants actually set a higher proportion of bolls in the lower part of the plant than the conventionally spaced plants. Other researchers have also found that boll distribution of plants in UNR crops is different to conventionally spaced crops. Clawson and Cothren (2002) found a higher percentage of boll were on nodes 6-10 and a significantly lower

proportion of bolls were on higher fruiting branches in UNR cotton compared with conventionally spaced cotton. Gerik *et al.* (1998) found that UNR cotton set a higher percentage of bolls on the lower branches in one year of their study but not in the other.

Lower fruit retention in the bottom part of the UNR plants did not occur in these experiments and hence did not cause delays in maturity. Lower retention of bolls on the higher nodes on the plant and a higher proportion of bolls set on the lower part of the plant indicate that early in the development of the plants under UNR conditions there was sufficient assimilate available to support boll growth, but later in plant development when the fruit on higher nodes were produced, the plant did not have sufficient resources to support these later bolls. This lower retention of later fruit is reflected by last effective flower (last flower that was retained until maturity), being a flower set a few days earlier in the UNR plants, which corresponded with the last boll opening a few days earlier in the UNR crop in Exp. 1 but not Exp. 5. This was due to slight differences in boll period between the two experiments. In Exp. 1 boll period was similar between treatments, however, in Exp. 5 boll period was a few days longer in the UNR treatment, which explains why there were no differences in maturity in Exp. 5 even though the last effective flower was set a few days earlier.

In each experiment, the UNR plants were smaller, with fewer fruiting sites and bolls per plant. A smaller plant with fewer fruiting sites, that retains early bolls and sheds later bolls was hypothesised to have earlier maturity than a larger plant that has more fruiting sites and retains more fruit higher (later) in the plant. However, this was not the case in this study comparing UNR and conventionally spaced plants. One explanation as to why a smaller plant does not mature earlier would be later initiation

of fruit. However, both UNR and conventionally spaced plants started fruiting at the same time. If boll period was consistently longer this would also explain lack of difference in the timing of crop maturity. However, boll period was only different for bolls on UNR plants compared with conventionally spaced plants in Exp. 5.

Boll distribution and timing can greatly affect the timing of crop maturity. The time for a crop to mature is variable and dependent on a range of factors. Fruiting began on the same node as the node of first fruiting branch was not different between row spacings (Chapter 3). In this chapter it has been shown that differences in the time to first square, retention, time to last effective flower (last flower that was retained to maturity) and boll period do not explain why maturity was not earlier in the UNR crops.

For a small plant that starts fruiting at the same time, finishes fruiting at the same time, retains it's early fruit and has no change in boll development time compared to a larger plant with more fruiting sites, the rate of site production must be different. Chapter 6 will examine whether there are differences in the rate of boll production (site production) in UNR plants compared with conventionally spaced plants and how any differences might influence maturity in the two row spacings. Unlike determinate crops, these development processes are not driven primarily by temperature and day length, but by the balance of demand for, and supply of, assimilates to the developing fruit and growing points (Bange and Milroy 2000). To help ascertain why any differences are occurring, the impact of carbon supply on site production will also be examined in Chapter 6. Smaller boll size (Chapter 3), lower retention and lower biomass accumulation (Chapter 4) in UNR plants indicate a reduction in assimilate

supply, which might also be contributing to the lack of differences in the maturity of the UNR crop compared to the conventionally spaced crop.

5.6 Conclusion

A smaller plant with fewer bolls did not set and mature these bolls over a shorter period than the larger plants in the conventionally spaced crop. There were few differences in the timing of the crop to reach development phases between row spacings, and the influence of the environment on differences in the pattern of retention in the crops had a greater impact than row spacing. UNR plants tended to have higher fruit retention at the bottom of the plant and less at the top of the plant compared with conventionally spaced plants. These differences in fruit distribution were likely due to differences in plant size. The lack of difference in maturity between plants in UNR and conventional treatments in this study cannot be explained by loss of early bolls or differences in time to reach crop development stages.

Chapter 6

Site production in UNR and conventionally spaced cotton

6.1 Aim

To identify differences in the rate of site production between UNR and conventionally spaced cotton and determine how those differences influence yield and maturity in UNR and conventionally spaced cotton.

6.2 Introduction

As cotton is an indeterminate plant there is no morphological limit to its size and development. As long as conditions are favourable, vegetative production of new main-stem and fruiting branches could continue indefinitely (Hearn and Constable 1984). However, the plant stops producing new leaves and fruiting sites (this stage is termed 'cut-out') due to the demand on the resource supply by developing bolls leaving none for the initiation of new fruiting sites (Mason 1922; Hearn 1994).

The time for a cotton crop to mature is dependent on a range of factors, but is ultimately determined by the time to fruit initiation (node of first fruiting branch and time to first square), the rate of boll production (main-stem and sympodial node production), boll growth (retention and boll size), the time to cessation of initiation of new bolls (cut-out) and the time from anthesis to maturity of those bolls retained (boll period) (Harland 1929; Richmond and Radwan 1962; Ray and Richmond 1966; Munro 1971)

In previous studies high rates of shedding in the UNR treatments have been thought to be the most likely cause of delays in maturity in UNR cotton (Constable 1975; Baker

1976). As Constable and Gleeson (1977) stated, "the success of narrow row spacing and other forms of crop manipulation aimed at rapid crop setting depends on the retention and rapid growth of early bolls". In this study, however, an examination of retention patterns in Chapter 5 showed that there was not a loss of bolls on the lower fruiting branches in the UNR plants, so other factors must be slowing the time to crop maturity. Node to first fruiting branch was not found to differ between row spacings in Chapter 3. In Chapter 5 it was also shown that time to first square, time to last effective flower (last flower that was retained to boll maturity) and boll period were not affected by row spacing and those measures did not explain why maturity was not earlier in the UNR crop.

Due to the effects of competition for light, water and nutrients between the higher numbers of plants in the UNR system, the development of individual plants may be different between the two row spacing treatments. Plants in the UNR system were shorter, with fewer nodes, fruiting sites and had fewer mature bolls per plant. However, contradictory to the response to UNR proposed by Lewis (1971), these smaller plants did not have earlier crop maturity.

Time to crop maturity in the experiments in this study does not appear to have been delayed through loss of early bolls, delayed time to cut-out or a longer boll period. This chapter will examine whether there are differences in the rate of fruit production through investigating main-stem and sympodial node (site) production in UNR plants compared with conventionally spaced plants and how any differences might influence the maturity of the two row spacings.

If there are differences in site production rates between UNR and conventionally spaced plants, this chapter will also examine the relationship between carbon supply and site production between the two row spacings.

6.3 Methods

6.3.1 Node production

Node production was compared between row spacing treatments to identify differences in site development. In Exps. 1, 2 and 5, nine plants per plot were tagged and monitored weekly to record node development. In the conventionally spaced plots these plants were in the same row but for UNR plots three plants in three parallel rows were monitored (row 1 – row adjacent to furrow; row 2 – adjacent to row 1; row 3 – adjacent to row 2 in centre of 2 m wide bed (Plate 3.1)). Plant height and number of main stem nodes were recorded. A node was recorded as present when the main stem leaf had unfolded. Cotyledons were counted as node zero (Figure 5.1).

6.3.2 Site production

To determine site development, four plants per plot were monitored in Exps. 1 and 5. Mapping was conducted twice weekly as it was possible to estimate events accurately a few days back in time by noting leaf, fruit or scar size and colour (Constable 1991). Vegetative sites were not recorded for this study. Four stages of fruit development were recorded for each main stem fruiting site:

- Date of squaring (flower bud) – when the subtending leaf on the same node unfolded (Constable 1991).

- Date of anthesis.

- Date the fruit was shed – if at all. On some occasions, a square was shed before it had been recorded as appearing.

- Date of boll opening – when at least two sutures on the boll had cracked open.

To determine differences in fruiting site production and fruit retention over time at both an individual plant and at crop level between row spacing treatments, total sites produced, total fruit shed and total fruit present per plant were converted to a per m^2 basis using average plant number per plot. To enable a comparison with growth analyses of Exps. 1 and 5 in Chapter 4, site production, and the number of fruit shed and present were grouped into approximately 10-day intervals corresponding to the biomass harvests for Exps. 1 and 5.

6.3.3 Relationship between site production and available carbon production

To determine whether differences in site production were linked to carbon production, the relationship between the number of sites per plant was compared with total dry matter production (average per plant) using regression analysis. This relationship was compared for the period from first flower to cut-out as this is the time of peak demand from developing bolls (59 DAS to 118 DAS in Exp. 1 and 60 DAS to 112 DAS in Exp. 5). Before first flower, there is little demand from developing bolls and the slowing of site production rate before this time is likely to be due to other factors impacting on carbon supply, such as competition for light, water and nutrients. Cut-out generally occurs when supply of assimilates from the leaves equals demand from developing bolls and as there are no new sites after this time the crop can be considered "finished" as there are no new sites and negligible changes in total dry matter production after this time (Bange and Milroy 2000).

6.3.4 Statistical analyses

Analysis of variance (ANOVA) was used for comparing main-stem node and site production between row spacings at each date. Analysis of covariance was used to test for differences in the regressions between *ln* site production and *ln* total dry matter production between row spacings. All statistical analyses were conducted using Genstat® software. Unless stated otherwise significant differences were considered at 95% confidence intervals ($P < 0.05$).

6.4 Results

6.4.1 Main-stem node production

In Exp. 1 weekly main-stem node counts commenced at 35 DAS and there were no significant differences in the number of nodes per plant between row spacing treatments until 49 DAS when the conventionally spaced treatment had an average 9.2 nodes per plant and the UNR treatments 8.1 nodes per plant ($P < 0.001$) (Figure 6.1). From 49 DAS there were fewer nodes per plant in the UNR plants compared with the conventionally spaced plants and final node numbers were 18.7 for conventionally spaced and 14.8 for UNR plants.

In Exp. 2 weekly main-stem node counts commenced at 69 DAS and there were no significant differences in the number of nodes per plant between row spacing treatments until 89 DAS when the conventionally spaced treatment had an average 19.6 nodes per plant and the UNR treatments 16.8 nodes per plant ($P = 0.046$) (Figure 6.1). From 89 DAS there were fewer nodes per plant in the UNR plants compared with the conventionally spaced plants and final node numbers were 21.8 for conventionally spaced and 18.4 for UNR plants.

In Exp. 5 weekly main-stem node counts commenced at 59 DAS and there were no significant differences in number of nodes per plants between row spacing treatments until 72 DAS when the conventionally spaced treatment had an average 15.0 nodes per plant and the UNR treatments 13.6 nodes per plant ($P = 0.003$) (Figure 6.1). From 72 DAS there were fewer nodes per plant in the UNR plants compared with the conventionally spaced plants and final node numbers were 20.8 for conventionally spaced and 18.3 for UNR plants.

6.4.2 Site production, fruit shedding and number of fruit present

When site production, fruit numbers and shedding were analysed over time for Exps. 1 and 5 there were some distinct trends in the fruit production and shedding in UNR compared with the conventionally spaced treatments.

Site production, fruit shedding and number of fruit present per plant

In Exp. 1 site production per plant was significantly lower in the UNR plants compared with conventionally spaced plants from 69 DAS ($P = 0.008$) (Figure 6.2a). From 69 DAS the number of sites produced per plant was significantly lower in the UNR plants compared with conventionally spaced plants; new sites stopped being produced after 137 DAS in both row spacings. In Exp. 5 site production per plant was significantly lower in the UNR plants compared with conventionally spaced plants from 69 DAS ($P = 0.014$) (Figure 6.3a). From 69 DAS the number of sites produced per plant was significantly lower in the UNR plants compared with conventionally spaced plants; new sites stopped being produced after 134 DAS in both row spacings.

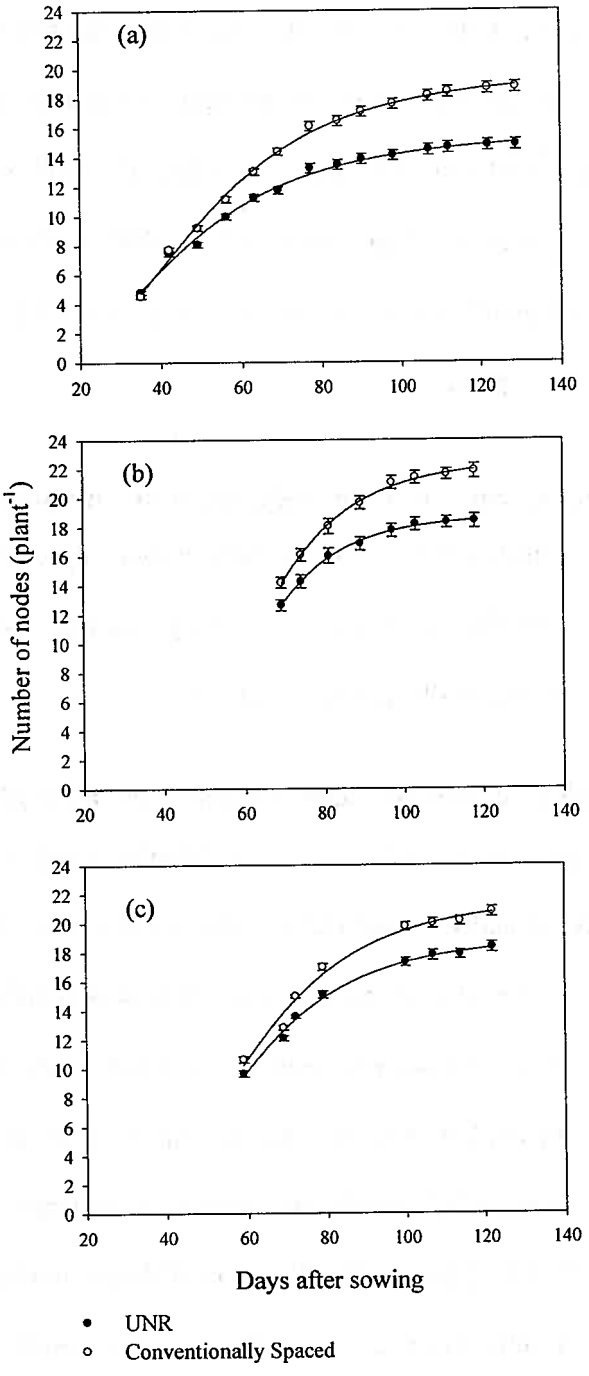

Figure 6.1 Mean number of main-stem nodes per plant for UNR and conventionally spaced treatments in Exps. 1 (a), 2 (b) and 5 (c). Error bars are two standard errors of the mean.

In Exp. 1 fruit shedding per plant was significantly lower in the UNR treatments from 109 DAS ($P = 0.018$) (Figure 6.2c). In Exp. 5 fruit shedding per plant was lower in the UNR treatments compared with the conventionally spaced treatments. This difference was significant at 78 DAS ($P = 0.01$) but not at 89 or 103 DAS. Shedding, however, continued to be numerically lower in the UNR treatments and was again significantly lower from 112 DAS ($P = 0.044$) (Figure 6.3c).

In Exp. 1 fruit present per plant was consistently numerically lower in the UNR plants compared with conventionally spaced plants; however, this difference was not significant except at 90, 96 and 109 DAS ($P = 0.035$; $P = 0.014$; $P = 0.045$ respectively) (Figure 6.2e). In Exp. 5 fruit present per plant was consistently numerically lower in the UNR treatments compared with the conventionally spaced treatments, this difference was significant from 69 DAS ($P = 0.027$) (Figure 6.3a).

Site production, fruit shedding and number of fruit present per m^2

In Exp. 1 cumulative site production per m^2 was only significantly higher in the UNR treatments compared with conventionally spaced treatments at 81 DAS ($P = 0.044$). However, average cumulative site production per m^2 was always higher in the UNR treatments and, except for 47 DAS and 69 DAS, was significant at the 90% confidence intervals (Figure 6.2b). In Exp. 5, average cumulative site production per m^2 was again consistently numerically higher in the UNR treatments compared with the conventionally spaced treatments. This difference, however, was only significant at 69 and 78 DAS ($P = 0.038$; $P = 0.041$ respectively) and at the 90% level at 89 DAS ($P = 0.055$) (Figure 6.3b).

In Exp. 1 cumulative fruit shedding per m^2 was always higher in the UNR treatments. From 90 DAS this difference was significant at the 90% confidence intervals, but only for 96, 109, 118 and 137 DAS was $P < 0.05$ (Figure 6.2d). In Exp. 5 fruit shedding per m^2 was again consistently numerically higher in the UNR treatments compared with the conventionally spaced treatments; this difference was significant from 103 DAS ($P < 0.05$) (Figure 6.3d).

In Exp. 1, fruit present per m^2 was not significantly different between row spacings, however, it was consistently numerically higher in the UNR treatments, but only at 59, 81 and 90 DAS was $P < 0.10$ (Figure 6.3f). In Exp. 5, fruit present per m^2 was numerically higher in the UNR treatments compared with the conventionally spaced treatments until 112 DAS. From 112 DAS the conventionally spaced treatments had higher fruit present per m^2 than the UNR treatments (Figure 6.3f). These differences were not significant and only at 69 and 78 DAS was $P < 0.10$.

6.4.3 Relationship between site production and available carbon production

Regression analyses of sites per plant and total dry matter per plant showed there was a significant positive linear relationship between the number of sites produced and total dry matter per plant (Figure 6.4). This relationship was not significantly different between row spacings for Exps. 1 or 5 ($P = 0.488$; $P = 0.968$ respectively).

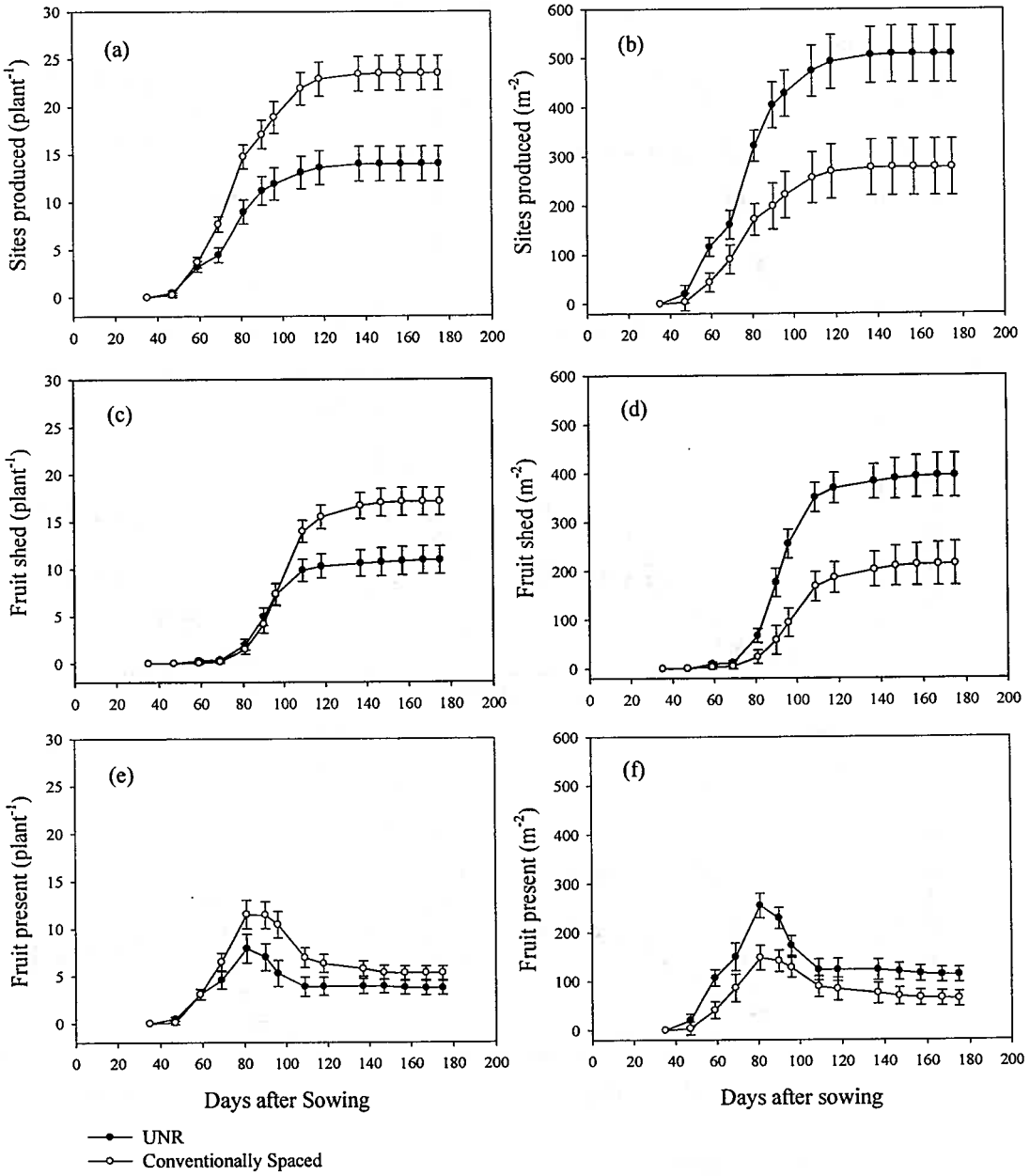

Figure 6.2 Cumulative site production per plant (a) and per m^2 (b), cumulative fruit shedding per plant (c) and per m^2 (d) and fruit present per plant (e) and per m^2 (f) at dates corresponding to biomass harvests in Exp. 1 for UNR and conventionally spaced treatments. Error bars are two standard errors of the mean.

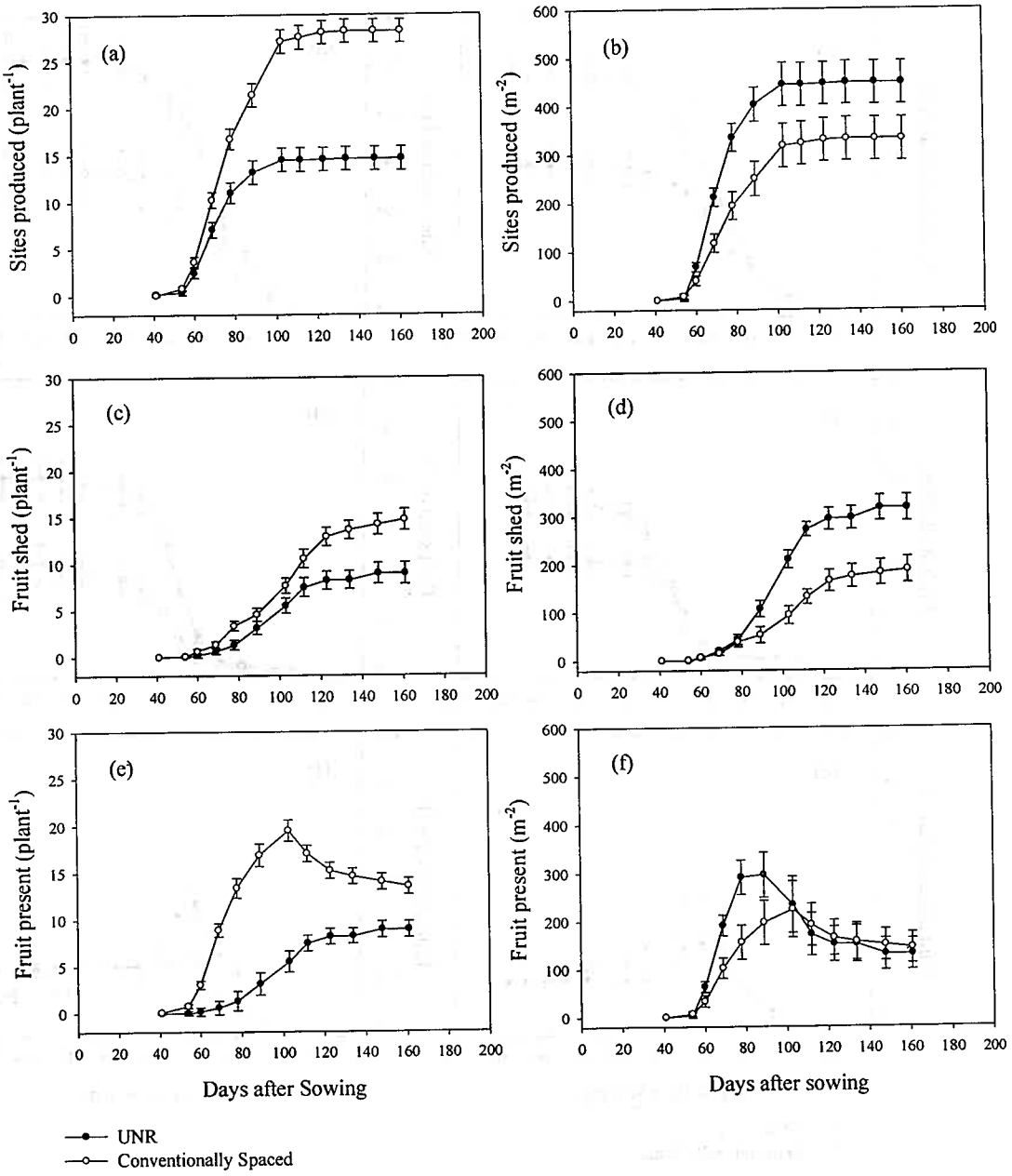

Figure 6.3 Cumulative site production per plant (a) and per m^2 (b), cumulative fruit shedding per plant (c) and per m^2 (d) and fruit present per plant (e) and per m^2 (f) at dates corresponding to biomass harvests in Exp. 5 for UNR and conventionally spaced treatments. Error bars are two standard errors of the mean.

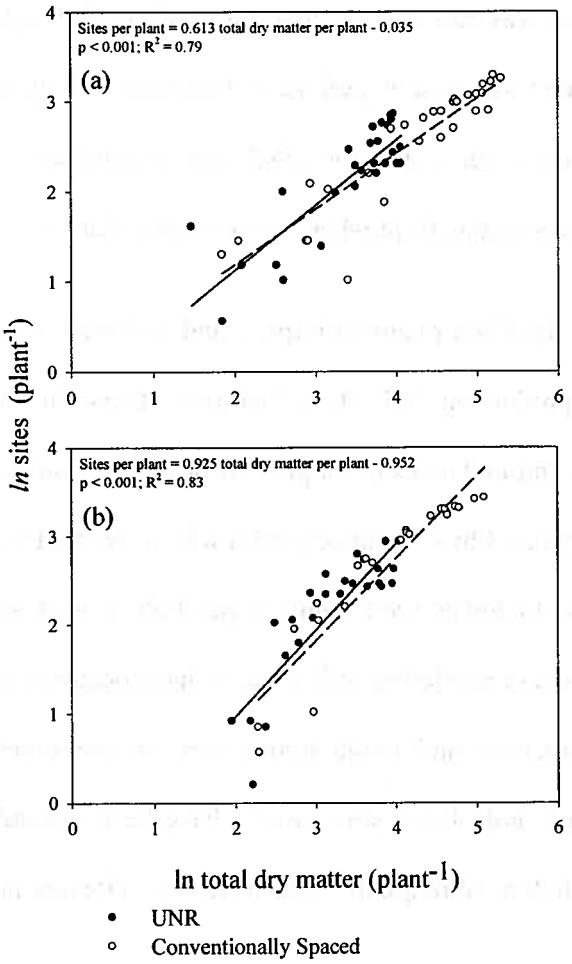

Figure 6.4 Relationship between sites and total dry matter per plant for UNR (solid line) and conventionally spaced (broken line) treatments in Exps. 1 (a) and 5 (b).

6.5 Discussion

Node production and site production was significantly slower in the UNR plants in the experiments from early in the growing season. Main-stem node production was less in the UNR crop even before site production was influenced by demand from developing fruit.

In Exp. 1 by 49 DAS node production was significantly less in the UNR plants compared with the conventionally spaced plants. This date corresponded to approximately first square appearance in the crop. In Exp. 2 node production in the UNR plants was significantly less than the conventionally plants from 69 DAS and 72

DAS in Exp. 5. This was between the appearance of the first square (flower bud) and anthesis (first flower) for those experiments; however, in both of those experiments the number of nodes per plant for UNR was numerically lower than for the conventionally spaced plants from when measurements started.

Site production in the UNR plants in Exps. 1 and 5 slowed around the same time as main-stem node production indicating that restrictions on the plants' ability to produce new sites and nodes occurred prior to flowering. Early competitive stress in UNR cotton is supported by Constable (1975) who found that the smaller boll size in his study was due to lower seed numbers per boll. Lower seed number per boll indicated that the stress restricting seed set must have occurred at flowering or earlier as flower bud formation and ovule fertilisation are important in determining the number of seeds per boll. Later stress would have been evident through impacts on seed size, lint per boll or fibre quality, which were not affected in Constable's study.

Slower node and site production meant that the UNR plants produced fewer bolls per plant over the same time period as the larger conventionally spaced plants. In Exp. 1 the UNR plants had produced only 13.1 sites before cut-out whereas in the same time period the conventionally spaced plants had produced 21.9 sites. In Exp. 5, the UNR plants produced 14.5 sites before cut-out compared with 27.1 in the conventionally spaced plants over the same period of time.

Shedding per plant was proportional to the number of sites per plant and the number of fruit present reflected this. In Exp. 1, the conventionally spaced plants had significantly more fruit present than the UNR plants between 96 and 109 DAS and numerically higher fruit for the rest of the season. In Exp. 5, this difference in fruit present per plant occurred much earlier with the conventionally spaced plants having

significantly more fruit per plant compared with the UNR plants from 69 DAS. In Chapter 5, the plants in the UNR crop had lower retention on the upper part of the plant compared with the conventionally spaced plants, but there was no difference in whole plant fruit retention in Exps 1 or 5.

Although the rate of site production and number of fruit present was lower in the UNR plants compared with conventionally spaced plants, the higher number of plants in the UNR crop led to higher numbers of fruit initiated per unit area with the number of sites per m^2 rapidly increasing from 47 DAS in Exp. 1 and 54 DAS in Exp. 5. Total number of sites per m^2 remained higher for the rest of the growing season, with cut-out occurring at about the same time in both row spacing treatments (approx. 103 DAS for Exp. 1 and 118 DAS for Exp. 5). The number of fruit shed was proportional to the number of sites produced and resulted in only slighter higher final boll numbers in the UNR treatment in Exp. 1 and hardly any difference in final boll numbers in Exp. 5. Most studies comparing site production between UNR and conventionally spaced cotton have compared site production on a unit area rather than a per plant basis, finding the UNR crops have greater early site production per unit area (Constable 1975); however, for early maturity to occur the rate of site production must be also be maintained on a per plant basis as well as at crop level.

The timing of increased shedding in the UNR crop occurred around the same time as increased shedding in the conventionally spaced crop and hence was probably linked to changes in environmental conditions or increased demand from developing bolls rather than any fundamental changes in the UNR crop causing differences in shedding.

The number of fruiting sites and the rate of production of fruiting sites are primarily dependent on vegetative growth and the ratios and position of monopodial to sympodial branches (Mauney 1986). Unlike determinate crops, these processes are not driven solely by temperature and day length, but by the balance of supply and demand of resources to the developing bolls and growing points (Bange and Milroy 2000). Slower site production and increased shedding of bolls indicates a restriction in assimilate supply in the UNR treatments in these experiments.

Regression analyses examining the relationship between the number of sites per plant and total dry matter per plant showed that the number of sites produced is highly dependent on the amount of dry matter per plant in both UNR and conventionally spaced crops. This relationship was not different between row spacings; however, site production was reduced in the UNR crop because each plant produced less total dry matter and hence slowed plant development.

These results explain why crop maturity of the UNR spaced cotton was not earlier than the conventionally spaced cotton. The rationale behind UNR cotton production being earlier and higher yielding than conventionally spaced cotton production relies on a few simple assumptions:

- plants in a high population would be smaller and set fewer bolls per plant;
- yield is maintained as a higher number of plants m^{-2} compensates for smaller plants having fewer bolls per plant;
- a smaller plant has fewer fruiting branches and should cut-out earlier;

therefore, the fruit on the smaller plants should be set and mature over a shorter period than a larger more vegetative plant (Lewis 1971).

This study has shown that the plants were smaller due to competition for between plants restricting dry matter production per plant. As a result, site production in the UNR plants was slowed and fruit were set over the same time period as larger more vegetative plants in the conventionally spaced system resulting in cut-out occurring at the same time.

For UNR plants to mature earlier, early node production and fruiting site production must be produced at a similar rate to conventionally spaced crops. However, in these experiments the slowing of site and main-stem node production occurred early in plant growth. Node and site production were significantly slower before anthesis, which was strongly linked to dry matter production. In some other crops the opposite response to higher plant population has been found, with individual plant growth similar to that of lower plant populations during the early stages of growth leading to rapid early CGR with individual plant growth slowing as competition between plants slow growth (Loomis and Connor 1992).

6.5.1 Conclusion

Node and site production per plant was slower in the UNR plants compared to the conventionally spaced plants. Slower node and site production explains why the UNR plants did not mature earlier than conventionally spaced plants as the fruit were set over the same time period in both row spacings. Node production slowed before flowering indicating that restrictions on the plants' ability to produce new sites and nodes occurred prior to flowering. Site production was highly dependent on dry matter production and site production was reduced in the UNR crop because each plant produced less total dry matter and hence slowed plant development.

Chapter 7

The physiological determinants of yield and maturity in UNR cotton

General discussion and concluding remarks

There is strong interest to develop cotton production systems that reduce the time from planting to harvest without a yield penalty. In addition to avoiding cool temperatures, reducing the time to maturity may also lead to savings in irrigation water and production costs.

Ultra-narrow row (UNR) cotton, a production system with rows spaced less than 40 cm apart, has been proposed as a system for earlier maturity without substantial yield loss (Low and McMahon 1973). The rationale for ultra-narrow row production being earlier and higher yielding than conventionally spaced cotton (1 m row spacing) is relatively simple. Plants grown in a high population should be smaller and set fewer fruit (bolls) per plant (Lewis 1971). Yield should be maintained as a higher plant population compensates for smaller plants having fewer bolls per plant (Lewis 1971). A smaller plant, with fewer bolls should mature earlier than a larger, more vegetative plant as the bolls are set earlier on the lower parts of the plant (Lewis 1971). The closely spaced cotton closes the canopy faster than conventionally spaced cotton, leading to greater light interception earlier in the season (Kerby *et al.* 1996b; Kreig 1996).

These assumptions, however, have not been consistently met in trials comparing UNR and conventionally spaced rows in Australia and the United States of America (Constable 1977b; Constable 1977a; Jost and Cothren 2000b; Jost and Cothren 2000a;

Jost and Cothren 2001). In Australia UNR cotton is grown commercially in high yielding, high-input systems in areas with a shorter growing season.

This study was a first step in understanding the performance of cotton in UNR production systems in Australia, by comparing its growth, development and yield to conventionally spaced high-input production systems. There was limited understanding of cotton's growth response to different row configurations in the Australian production environment. Research into UNR in Australian cotton production systems has been limited with few studies into the detailed physiological responses of cotton to high plant population UNR production systems (Low and McMahon 1973; Hearn and Hughes 1975; Constable 1977b; Constable 1977a).

Yield and maturity did not differ significantly between row spacings in any of the six experiments in this study. However, yield was numerically higher in the UNR crop in all of the experiments and the combined analysis showed that the mean lint yield of the UNR treatments was 15.9% higher than the conventionally spaced treatments. In this chapter, the differences found in the growth and development of UNR cotton compared with conventionally spaced cotton will be summarised, the influence on yield and maturity of these differences will be discussed and opportunities to optimise yield and maturity of UNR cotton will be considered.

Contrary to Lewis' (1971) rationale for earliness in UNR, a smaller plant with fewer bolls did not set and mature these bolls over a shorter time period than the larger plants in the conventionally spaced crop.

UNR plants were smaller, had fewer fruiting sites and bolls per plant. This change in plant architecture in response to narrow row spacings and higher plant populations

had been found in other studies (Jost and Cothren 2001; Vories *et al.* 2001; Marois *et al.* 2004; Nichols *et al.* 2004).

Maturity was not influenced by differences in the time to reach crop development stages between row spacings or by loss of early bolls in the UNR plants. Node of first fruiting branch did not differ between row spacings. Time to first square, retention, time to last effective flower (last flower that was retained to boll maturity) and boll period were also not consistently different between row spacing treatments, which was consistent with maturity not occurring any earlier in the UNR crop.

Loss of early bolls can delay maturity, but there was no indication of consistent differences in boll loss in the lower part of the plants between row spacings. In contrast to losing bolls in the lower part of the plant and compensating later and perhaps delaying maturity, the UNR plants actually set a higher proportion of bolls in the lower part of the plant than the conventionally spaced plants. It was in the upper part of the plant that boll retention was consistently lower in the UNR plants compared to the conventionally spaced plants. The timing of shedding in the UNR crop occurred around the same time as increased shedding in the conventionally spaced crop. The percentage of total fruit shed was higher in the UNR crop, indicating that shedding events occurred at the same time in both crops. Hence, the loss of fruit was probably linked to changes in environmental conditions or increased demand from developing bolls rather than any fundamental changes in the UNR crop causing differences in shedding. In previous studies, high rates of shedding in the UNR treatments have been thought to be the most likely cause of delays in maturity in UNR cotton (Constable 1975; Baker 1976).

For UNR plants to mature earlier, early node production and fruiting site production must occur at a similar rate to conventionally spaced crops. However, in these experiments the slowing of site and main-stem node production occurred from early in plant growth with node and site production being significantly slower before anthesis. This was strongly linked to dry matter production per plant.

Table 7.1 outlines node production, site production and shedding and how this relates to the percentage of yield present over the growing season for Exp. 1. Exp. 5 had similar development patterns as Exp. 1 (data not shown).

Node production and site production were significantly slower in the UNR plants in the experiments from early in the growing season (Table 7.1 and Figures 6.1 to 6.3). Site production in the UNR plants in Exps. 1 and 5 slowed around the same time as main-stem node production, indicating that restrictions on the ability to produce new sites and nodes occurred prior to flowering (Table 7.1 and Figures 6.1 to 6.3). Early competitive stress in UNR cotton is supported by findings from the study of Constable (1975), who found that the smaller boll size was due to lower seed numbers per boll. The lower seed numbers per boll indicated that the stress restricting seed set must have occurred at flowering or earlier as flower bud formation and ovule fertilisation are important in determining the number of seeds per boll. Later stress would have been evident through effects on seed size, lint per boll or fibre quality, which were not affected in Constable's study.

Slower node and site production meant that the UNR plants produced fewer bolls per plant over the same time period as the larger conventionally spaced plants (Table 7.1). The proportion of the realised yield set over the growing season was almost identical for the two row spacings (Figure 7.1a). Overall fruit retention was generally lower in

the UNR plants compared to the conventionally spaced plants. For the example in Table 7.1 lower retention between 90 and 110 DAS meant that the UNR crop was slower in yield development for this period (Figure 7.1a). Boll size was smaller in most of the experiments in this study. Smaller boll size is commonly reported in UNR studies (Baker 1976; Constable 1977a; Bednarz *et al.* 1999; Witten and Cothren 2000; Boquet 2005) although not always (Hawkins and Peacock 1973; Gerik *et al.* 1999).

Figure 7.1b shows hypothetical yield development of UNR when site production and boll size are assumed to be equal to that in of the conventionally spaced plants in Exp. 1 but with differences in final node number retained. Simulating this scenario where the UNR plants are smaller with fewer bolls per plant, but with the same boll growth and development as conventionally spaced plants, would lead to earlier maturity in the UNR crop as suggested by Lewis (1971). In this scenario, 60% of final yield was present eight days earlier and 90% of final yield was present 14 days earlier in the UNR crop compared to the conventionally spaced crop. Hence, for UNR plants to cut-out and mature earlier, early node production and fruiting site production must occur at a similar rate to conventionally spaced crops and boll size must be similar. However, in the experiments in this study the slowing of site and main-stem node production occurred from early in plant growth with node and site production being significantly slower before anthesis (Table 7.1).

Although the rate of site production and number of fruit present per plant was lower in the UNR crop compared with conventionally spaced plants, the greater number of plants in the UNR crop led to a greater number of fruit initiated per unit area with the number of sites per m^2. Most studies comparing site production between UNR and conventionally spaced cotton have compared site production on a unit area rather than

a per plant basis, finding the UNR crops have greater early site production per unit area (Constable 1975). However, for this to lead to increased yield or early maturity the rate of site production must be greater on a per plant basis as well as at crop level.

The number of sites produced was highly dependent on the amount of dry matter per plant in both UNR and conventionally spaced crops. This relationship did not differ between row spacings. Site production was reduced in the UNR crop because each plant produced less total dry matter, and hence slowed plant development.

The three experiments in 2001-02, 2002-03 and 2003-04 showed a trend to higher yield in the UNR treatment and a combined analysis showed an average 13.1% increase in UNR yield compared to conventional spacing across the three experiments. While early season crop growth, fruit production and light interception tended to be higher in the UNR crop this did not translate into greater final crop biomass production. There was a trend to greater partitioning of carbohydrates to fruit in the UNR crop. Final boll numbers per m^2 were higher in the UNR treatments compared to the conventionally spaced treatments. This was accompanied by a decrease in boll size. However, the 9% reduction in boll size in the UNR treatments was more than compensated for by the 21% increase in boll number. Other studies have also found that higher plant populations compensated for smaller plant size, and total boll number was usually the same or slightly higher (Witten and Cothren 2000).

Table 7.1 Average node production, site production, retention, boll size and proportion of yield over the growing season for UNR and conventionally spaced plants in Exp. 1

Days after sowing	Number of nodes per plant		Number of sites per plant		Retention (%)		Boll size (boll dry matter g boll^{-1})		Yield per plant (g) (sites x retention x boll size)		Proportion of yield present (%)	
	UNR	Conventionally Spaced	UNR	Conventionally Spaced	UNR	Conventionally Spaced	UNR	Conventionally Spaced	UNR	Conventionally Spaced	UNR	Conventionally Spaced
0	0	0										
10	0	0										
20	1	1										
30	4	3										
40	7	7										
50	9	10	0.90	1.29	99	100	0.00	0.00	0.00	0.01	0.01	0.01
60	11	12	2.67	3.92	98	99	0.02	0.03	0.05	0.11	0.15	0.12
70	12	15	5.63	8.53	93	97	0.09	0.12	0.47	1.03	1.36	1.13
80	13	16	8.76	13.77	79	91	0.33	0.45	2.28	5.63	6.58	6.21
90	14	17	11.07	17.88	53	75	1.00	1.33	5.80	17.76	16.70	19.58
100	14	18	12.37	20.30	33	52	2.27	3.00	9.26	31.81	26.67	35.06
110	14	18	13.16	21.81	25	36	4.36	5.72	14.16	44.37	40.79	48.91
120	15	19	13.59	22.63	23	29	6.57	8.61	20.39	57.21	58.72	63.06
130	15	19	13.82	23.09	23	28	8.23	10.79	25.89	69.23	74.57	76.30
140	15	19	13.95	23.34	23	28	9.22	12.12	29.63	77.96	85.34	85.93
150	15	19	14.02	23.48	23	28	9.73	12.81	31.74	83.10	91.40	91.59
160	15	20	14.07	23.58	23	28	10.03	13.21	33.08	86.47	95.27	95.31
170	15	20	14.10	23.64	24	28	10.19	13.42	33.85	88.44	97.48	97.48
180	15	20	14.12	23.67	24	28	10.27	13.54	34.30	89.61	98.78	98.77
190	15	20	14.13	23.70	24	28	10.32	13.60	34.57	90.31	99.55	99.55
200	15	20	14.14	23.71	24	28	10.34	13.64	34.72	90.73	100.00	100.00

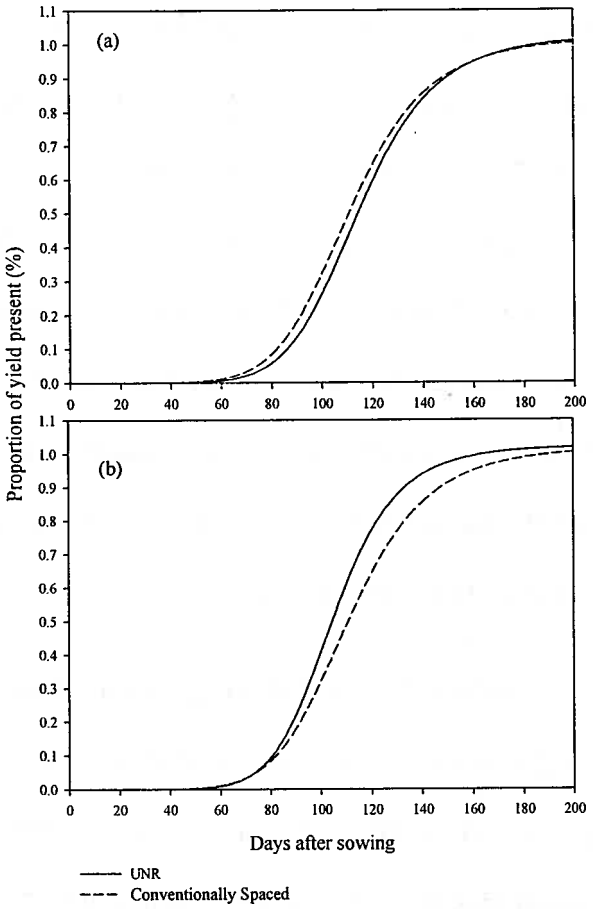

Figure 7.1 Proportion of yield present over the growing season in UNR and conventionally spaced treatments in Exp. 1. (a) shows the actual yield present (b) presents a calculation where site production and boll growth is the same in both row spacings but the UNR plants final node number and boll size remains the same (14 nodes per plant and 10 g boll^{-1} as presented in Table 7.1)

The major factors affecting crop growth and development of the UNR crop in this study were differences between the two row spacings in light interception and conversion efficiency. The higher crop light extinction coefficient (k) in the UNR crop, and hence, greater light capture at low LAI, did not increase final total biomass production, most likely because of a compensating reduction in RUE. Higher k generates less uniform light distribution in the canopy so that overall conversion efficiency is reduced, especially at high LAI. The higher k in UNR crops would be advantageous to light capture in early canopy development and generate greater earlier crop growth, thus supporting early fruit

production, leading to the higher early fruit numbers at the crop level in the UNR crop (Figure 6.2 and Figure 6.3). However, the associated reduction in RUE would generate reduced crop growth at the higher LAI found after canopy closure, thus reducing retention of later fruit later in the UNR crop. Hence, the similar total final biomass of the two systems is a consequence of two compensating factors. Limitations in assimilates to individual plants in the UNR crop due to lower RUE and increased shading of the lower part of the canopy may also explain why boll size was smaller in the UNR treatments as boll size is related closely to carbohydrate supply, especially from nearby leaves. At a crop level, even though boll size was reduced in the UNR crop, the setting of more fruit may have stimulated enhanced partitioning to fruit.

As the UNR and conventionally spaced treatments have different spatial arrangements, differences in the light extinction coefficient (k) may be related to differences in canopy structure. Most of the light in the UNR canopy was intercepted in the top part of the canopy with less penetrating through the canopy. Although peak LAI was not significantly different in the three experiments, LAI continued to develop in the UNR crop after maximum light interception had been reached, whereas in the conventionally spaced treatments, peak LAI was more aligned with maximum light interception. This means that the UNR crop was continuing to develop leaves that were not increasing light interception, and were shading earlier leaves, which probably contributed to reduced RUE. Elevated LAIs can be detrimental if the lower canopy receives excessive shading reducing assimilate production to support boll development (Hake *et al.* 1996). Jost and Cothren (2001) found that crop maturity was earlier, and yield was higher in UNR cotton crop in the year that no excessive vegetative growth occurred. Constable (1975) found that higher early leaf area did not favour rapid crop setting and that control of vegetative growth might be necessary to achieve earliness.

Both a reduction in boll size and the slowing of site production indicates that competition for resources occurs very early in the growth of UNR cotton. Many of the measurements made in this study began at first square, by which time individual plant growth had already begun to slow in response to competition between plants. Further research is needed into whether increasing inputs or making other modifications early in the season could prevent the slowing of growth and development in the UNR system, or whether the plants are responding to other indicators such as root competition or changes in the light environment and adjusting their growth on detection of neighbouring plants (Ballare and Casal 2000). Cotton (*Gossypium* spp.) is a perennial plant found in the wild in isolated or in very open types of vegetation and its growth is highly plastic in response to its environment (Fryxell 1986). However, this adaptation may result in slowing growth in response to competition from other plants much more quickly than found in other determinant, annual crops.

This study has shown that in UNR crops competition between plants restricts dry matter production per plant very early in the crop cycle and as a result site production in the UNR plants is slowed and the fewer fruit per plant are set over the same time period as the greater number of fruit on the larger, more vegetative plants in the conventionally spaced system.

7.1 Concluding Remarks

This study found no differences in crop maturity and an increase in yield in UNR spaced cotton compared with conventionally spaced cotton in high-input production systems in Australia.

The UNR plants in this study were smaller and set fewer bolls but maintained or increased yield through a higher plant population; however, a smaller plant with fewer fruiting

branches did not cut-out earlier and the fewer fruit on the smaller plant were set and matured over the same time period as the greater number of fruit on the larger, more vegetative plant in the conventionally spaced treatments. These effects were related to competition between plants restricting dry matter production per plant and changing its distribution in the crop cycle in the UNR system via modifications to light interception and radiation use efficiency. The plant growth restriction occurs early in the life cycle before anthesis and leads to smaller boll size and lower overall retention in the UNR plants. However, early fruit production is enhanced at a crop level, most likely because of increased light interception and plant growth early in the crop cycle leading to enhanced partitioning to fruit in the UNR crop.

For UNR plants to mature earlier, early node production and fruiting site production must occur at a similar rate to conventionally spaced crops. However, in these experiments the slowing of site and main-stem node production occurred from early in the crop cycle with node and site production being significantly slower before anthesis. Further research is needed into whether increasing inputs early in the season will prevent slower growth and development in UNR crop grown under high-input conditions, or whether the plants are responding to other indicators such as root competition or changes in the light environment that might lead them to adjust their growth on detection of neighbouring plants. In the case of the latter, either genetic or environmental manipulations might be required to influence plant growth and development in UNR crops grown under high-input conditions.

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Appendices

Appendix 1 – History of crop management for each experiment

Table 1. Crop management for Exp. 1: 2001-2002 Narrabri growth analysis

Fertiliser History	*Amount*	*Date*
Anhydrous Ammonium	100 kg N ha^{-1}	18/07/2001
Herbicide Application		
Diuron	2.5 L ha^{-1}	23/07/2001
Treflan	480 g L^{-1} @ 2.3 L ha^{-1}	23/07/2001
Irrigation Management		
Irrigation Dates		19/12/2001
		5/01/2002
		22/01/2002
		8/02/2002
		22/02/2002
		14/03/2002
Pest Management		
Tracer	0.7 L ha^{-1}	12/01/2002
Affirm	0.55 L ha^{-1}	19/01/2002
Steward	0.8 L ha^{-1}	26/01/2002
	0.85 L ha^{-1}	01/03/2002
Talstar 100 RC	0.8 L ha^{-1}	06/02/2002
P.B.O.	0.4 L ha^{-1}	06/02/2002
Rogor	0.85 L ha^{-1}	01/03/2002

Table 2. Crop management for Exp. 2: 2002-2003 Narrabri growth analysis

Fertiliser History	*Amount*	*Date*
Anhydrous Ammonium	120 kg N ha^{-1}	27/08/2002
Herbicide application		
Diuron	1.0 L ha^{-1}	19/09/2002
Stomp	3.0 L ha^{-1}	19/09/2002
Irrigation Management		
Irrigation Dates		24/9/2002
		30/10/2002
		13/12/2002
		1/01/2003
		17/1/2003
		30/1/2003
		14/2/2003
Pest Management		
Regent	1.0 L ha^{-1}	12/01/2003

Table 3. Crop management for Exp. 3: 2002-2003 Hillston growth analysis

Fertiliser History	*Amount*	*Date*
Anhydrous Ammonium	135 kg N ha^{-1}	11/06/2002
MAP + 1% Zinc	150 kg ha^{-1}	9/08/2002
Zinksul (ground app)	2.0 L ha^{-1}	4/11/2002
Irrigation Management		
Irrigation Dates		6/10/2002

		4/12/2002
		22/12/2002
		10/01/2003
		24/01/2003
		7/02/2003
		4/03/2003
Pest Management		
Endosulfan	2.1 L ha^{-1}	4/11/2002
Regent	0.063 L ha^{-1}	12/12/2002
Amino Feed	1.0 L ha^{-1}	23/12/2002
		01/01/2003
		06/01/2003
		11/01/2003
Co Star OF	0.9 L ha^{-1}	23/12/2002
		01/01/2003
		18/01/2003
Tracer	0.2 L ha^{-1}	01/01/2003
MVPII	1.5 L ha^{-1}	06/01/2003
Agrimec	0.6 L ha^{-1}	06/01/2003
Pegasus	0.6 L ha^{-1}	11/01/2003
Gemstar	0.5 L ha^{-1}	11/01/2003
Tracer II	0.8 L ha^{-1}	18/01/2003
Intrepid 360 SC	0.55 L ha^{-1}	31/01/2003

Table 4. Crop management for Exp. 4: 2002-2003 Breeza row configuration experiment

Fertiliser History	***Amount***	***Date***
Urea	110 kg N ha^{-1}	21/09/2002
Irrigation Management		
Irrigation Dates		19/01/2003
Pest Management		
Nil		

Table 5. Crop management for Exp. 5: 2003-2004 Narrabri growth analysis

Fertiliser History	***Amount***	***Date***
Anhydrous Ammonium	120 kg N ha^{-1}	19/08/2003
Herbicide Application		
Treflan	2.2 L ha^{-1}	10/09/2003
Cotoran	4 L ha^{-1}	03/11/2003
Irrigation Management		
Irrigation Dates		04/11/2003
		16/12/2003
		31/12/2003
		09/02/2004
		05/03/2004
Pest Management		
Prodigy	2.5 L ha^{-1}	13/12/2003
Affirm	0.7 L ha^{-1}	10/01/2004
Regent	0.063 L ha^{-1}	10/01/2004
Steward	0.85 L ha^{-1}	28/01/2004
P.B.O	0.4 L ha^{-1}	05/03/2004
Talstar 100 EC	0.8 L ha^{-1}	05/03/2004

Table 6. Crop management for Exp. 6: 2003-2004 Hillston growth analysis

Fertiliser History	*Amount*	*Date*
Anhydrous ammonium	132 kg N ha^{-1}	22/08/2003
MAP & 1% zinc (	150 kg ha^{-1}	22/09/2003
Water run urea (50 K/ha)	50 kg N ha^{-1}	22/09/2003
Herbicide Application		
Roundup Max	1.2 L ha^{-1}	03/09/2003
Goal	0.07 L ha^{-1}	03/09/2003
Stomp	4.5 L ha^{-1}	30/09/2003
Cotogard	1.7 L ha^{-1}	30/09/2003
Roundup ready	1.5 L ha^{-1}	04/11/2003
Roundup ready	1.0 L ha^{-1}	14/11/2003
Irrigation Management		
Irrigation Dates		16/10/2003
		02/12/2003
		15/12/2003
		29/12/2003
		12/01/2004
		23/01/2004
		05/02/2004
		14/02/2004
		26/02/2004
		10/03/2004
Pest Management		
Dimethoate	0.200 L ha^{-1}	13/11/2003
Agrimec	0.600 L ha^{-1}	13/12/2003
Regent	0.06 L ha^{-1}	13/12/2003
Tracer II	0.400 L ha^{-1}	18/12/2003
	0.400 L ha^{-1}	24/01/2004
Endosulfan	2.1 L ha^{-1}	7/01/2004
Ovasyn	2.0 L ha^{-1}	23/12/2003
	2.0 L ha^{-1}	7/01/2004
Predator	5.0 L ha^{-1}	21/02/2004

Appendix 2 – Example GLM analysis

Response variate: Lint m^2
Fixed model: Constant + Exp + Treatment + Exp.Treatment
Random model: Rep + Exp.Rep
Number of units: 44

Residual term has been added to model

Sparse algorithm with AI optimisation

Estimated variance components

Random term	component	s.e.
Rep	6.	100.
Exp.Rep	0.	bound

Residual variance model

Term	Factor	Model(order)	Parameter	Estimate	s.e.
Residual		Identity	Sigma2	1261.	330.

Wald tests for fixed effects

Sequentially adding terms to fixed model

Fixed term	Wald statistic	d.f.	Wald/d.f.	chi pr
Exp	79.08	5	15.82	<0.001
Treatment	11.29	1	11.29	<0.001
Exp.Treatment	7.12	5	1.42	0.212

Dropping individual terms from full fixed model

Fixed term	Wald statistic	d.f.	Wald/d.f.	chi pr
Exp.Treatment	7.12	5	1.42	0.212

Appendix 3 – Specific leaf area for Exps. 1, 2 and 5

In Exp. 1 SLA in the UNR treatments was significantly higher than the conventionally spaced treatments at 35 DAS (P = 0.003) and significantly higher at 59 DAS (Figure 1). The only significant difference in SLA in Exp. 2 was significantly lower in the UNR treatments compared to the conventionally spaced treatments at 55 DAS (P = 0.024) (Figure 1). In Exp. 5 in SLA was significantly lower in the UNR treatments compared to the conventionally spaced treatments at 54 and 60 DAS (P = 0.018; P = 0.001 respectively) (Figure 1).

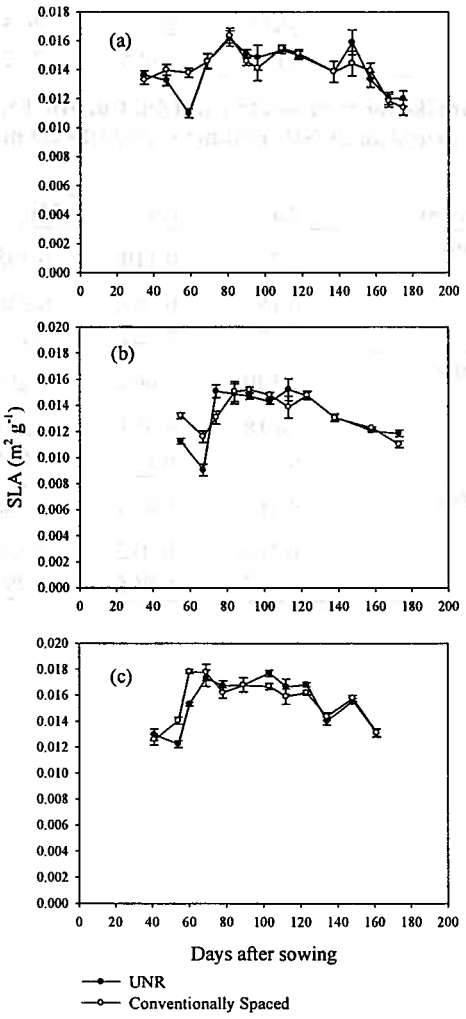

Figure 1. Mean specific leaf area for UNR and conventionally spaced treatments in Exps. 1 (a), 2 (b) and 5 (c). Error bars are two standard errors of the mean.

Appendix 4 – Nutrient uptake of macro- and micro-nutrients for Exps. 1, 2 and 5

Table 1. Mean nutrient uptake for macro-nutrients (N, K, P, S, Ca and Mg (kg ha^{-1})) in Exps. 1, 2 and 5 for conventionally spaced and UNR treatments (Significant differences indicated by * - 95% confidence level).

Exp.	Treatment	N	K	P	S	Ca	Mg
1	Conventionally Spaced	278.0	355.0	58.2	67.6	229.0	53.8
	UNR	149.0	240.0	37.8	44.3	146.0	36.4
	LSD	137.9	*104.7	*17.8	*15.4	*66.1	26.2
2	Conventionally Spaced	168.0	209.0	33.2	34.2	106.6	37.7
	UNR	175.0	206.0	36.0	28.9	82.4	36.2
	LSD	239.1	303.4	45.6	24.1	79.1	42.5
5	Conventionally Spaced	254.0	229.0	34.6	49.5	199.0	52.0
	UNR	263.0	248.0	39.5	50.8	199.0	51.3
	LSD	210.5	152.5	23.2	29.2	115.8	35.6

Table 2. Mean nutrient uptake for micro-nutrients (Zn, Cu, Mn, Fe, B and Na (kg ha^{-1})) in Exps. 1, 2 and 5 for conventionally spaced and UNR treatments (Significant differences indicated by ** - 99% confidence level).

Exp.	Treatment	Zn	Cu	Mn	Fe	B	Na
1	Conventionally Spaced	0.246	0.110	0.395	0.931	0.571	11.20
	UNR	0.155	0.063	0.258	0.507	0.391	11.20
	LSD	0.108	**0.021	0.153	0.439	*0.173	9.53
2	Conventionally Spaced	0.149	0.068	0.264	2.500	0.311	10.50
	UNR	0.18	0.083	2.83	3.700	0.255	10.50
	LSD	0.173	0.105	0.025	10.330	0.229	17.04
5	Conventionally Spaced	0.160	0.073	0.388	1.670	0.467	13.20
	UNR	0.169	0.072	0.383	1.015	0.489	12.80
	LSD	0.115	0.068	0.291	**0.253	0.272	11.38