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Cotton responses to different light–temperature regimes

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SUMMARY

A series of experiments investigating the interactive effects of light and temperature on vegetative growth, earliness, fruiting, yield and fibre properties in three cultivars of cotton, was undertaken in growth rooms. Two constant day/night temperature regimes with a difference of 4 °C (30/20 and 26/16·5 °C) were used throughout the growing season in combination with two light intensities (75 and 52·5 W m^{-2}).

The results showed that significant interactions occurred for most of the characters studied. Although the development of leaf area was mainly temperature-dependent, plants at harvest had a larger leaf area when high temperature was combined with low rather than with high light intensity. Leaf area was least in the low temperature–low light regime. However, the plants grown under the high temperature–low light combination weighed the least.

Variations in the number of nodes and internode length were largely dependent on temperature rather than light. Light did, however, affect the numbers of branches, sympodia and monopodia. The first two of these were highest in the high light–high temperature regime and the third in the low light–low temperature regime.

All other characters, except time to certain developmental stages and fibre length, were reduced at the lower light intensity. Variation in temperature modified the light effect and *vice versa*, in a character-dependent manner. More specifically, square and boll dry weights, as well as seed cotton yield per plant, were highest in high light combined with low temperature, where the most and heaviest bolls were produced. But flower production was favoured by high light and high temperature, suggesting increased boll retention at low temperature, especially when combined with low light. Low temperature and high light also maximized lint percentage.

Fibres were shortest in the high temperature–high light regime, where fibre strength, micronaire index and maturity ratio were at a maximum. However, the finest and the most uniform fibres were produced when high light was combined with low temperature.

Cultivar differences were significant mainly in leaf area and dry matter production at flowering.

INTRODUCTION

Nutritional stress in cotton, caused by decreased photosynthesis due to a reduction in intercepted solar radiation, by increased respiration as a result of high temperatures during long warm nights and by alterations in the demand for photosynthetic products as boll load changes during the growing season, may delay fruiting and increase shedding (Guinn 1976).

Light-stress effects may also result from interplant competition for light, caused by high plant population densities (Bhatt 1974; Kerby & Buxton 1978; Richardson & Wiegand 1988), excessive plant growth (Guinn 1974) or even inefficient row orientation (Walhood & Johnson 1976). Generally, during the development of a cotton crop canopy, net photosynthesis rates, apart from changing with CO_2 concentration (Idso *et al.* 1994), increase in the early part of the season, due to increases in plant size, with the peak occurring at *c.* 80–90 days after planting (Wells *et al.* 1988), and decrease later, due to a

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combination of factors, including (i) an increase in shading and the ageing of existing leaves (Peng & Krieg 1991), (ii) the appearance of new leaves of reduced photosynthesising ability (Wells 1988), (iii) an increase in non-photosynthetic biomass, e.g. stems and bolls (Boote *et al.* 1985) and (iv) a seasonal decrease in solar radiation (Guinn 1974; Puech-Suanzes *et al.* 1989).

Reduction in solar radiation (or experimental shading) usually results in reduced yield (Bhatt & Nathan 1977; Roussopoulos *et al.* 1978) by promoting vegetative growth at the expense of reproductive development. However, reduced light may also increase yield (Bhatt & Ramanujam 1975). These contradictory results are possibly due to complex light–temperature interactive effects in controlling the growth and development of cotton (Rajan *et al.* 1973; Mutsaers 1983).

Bhatt (1974) suggested that a smaller but more effective leaf area may result in greater plant efficiency. Reddy *et al.* (1991) found that net photosynthesis becomes maximal at certain (high) light intensity, temperature (25 °C) and leaf area index (3–4) values, whereas negative effects on net photosynthesis, with leaf area index increasing beyond its optimum, are temperature-dependent. Hesketh & Low (1968) reported that the optimum air temperature for boll production is a negative function of light intensity, whereas Low *et al.* (1969) noted that earliness (expressed as the position of the first floral branch) is a complex function of temperature and radiation. McMahon & Low (1972) observed that the thermal time required to reach a certain stage of plant development decreases with increasing radiation.

As the existing evidence is rather limited, experimental work in controlled environments was undertaken to establish a better understanding of the interactive effects of light and temperature on the whole process of growth and development in cotton as well as on cotton yield and fibre properties.

MATERIALS AND METHODS

Two temperature regimes and two light intensities were used to study the combined effects of light and temperature on cotton growth, yield and fibre properties. The four environments in the different growth rooms represented all possible combinations of high and low temperature and high and low light. Temperature regimes were: constant day/night temperatures of either 30/20 °C (high temperature, HT) or 26/16·5 °C (low temperature, LT). Irradiance, provided by fluorescent tubes, was either 'high light' (HL, 75 W m^{-2}) or 'low light' (LL, 52·5 W m^{-2}). Experiments were carried out in growth rooms (2·0 × 1·8 × 2·3 m) set to provide a 14 h day/10 h night and the selected temperature was generally maintained to an accuracy of $\pm 0{\cdot}5$ °C and was practically uniform throughout each room.

Three cotton (*Gossypium hirsutum*) cultivars (4S, Coker–210 and PU), which differed in earliness, were used. About five or six seeds were sown in each pot (18 cm in diameter and filled with John Innes No. 1 compost) and seedlings were thinned after emergence to three seedlings per pot. There were 20 pots for each of the cultivars arranged in four randomized blocks. Only one plant per pot was left by the time the first pair of permanent leaves had expanded. From this stage until flowering, approximately weekly harvests were made, during which plant height, leaf area and dry weight of leaves, stems and reproductive organs were measured, while internode length and numbers of nodes, sympodia (fruiting branches) and monopodia (vegetative branches) were determined at the final stage. Earliness components, namely position of the first floral or fruiting branch, time to certain developmental stages, flowering intervals and boll maturation period, were also determined. Usually four plants of each cultivar were used in each harvest. Plants were watered daily and fertilized ($7N:7P_2O_5:7K_2O$) fortnightly after the first 4 weeks. When maximum growth was reached, plants in each room had approximately the same density. Experiments were terminated when most of the bolls had opened.

The experiment was not replicated in the sense that the treatments were not repeated more than once. It is only an assumption, therefore, that significant differences between the rooms for any character were due to the conditions imposed. The results were submitted to analyses of variance and significant differences were determined by calculating least significant differences.

RESULTS

Vegetative growth

In this experiment it should be remembered that plants growing in low light and/or temperature took longer to reach specific growth stages than plants receiving high light and/or temperature. The two temperature regimes and two light intensities affected leaf area at squaring, flowering and harvesting. Compared with the HT–HL regime, leaf area was increased by either low temperature (LT) or low light (LL) in the first two stages, but the response to LT was reversed at harvest, while the light repsonse remained unchanged (Table 1). Effects of temperature and light on leaf area, although significant ($P < 0{\cdot}05$ and $P < 0{\cdot}001$), were less pronounced at flowering than at the other growth stages ($P < 0{\cdot}001$). Even at this stage, however, significant cultivar and temperature × cultivar differences were observed, with cv. 4S producing the greatest leaf area. Temperature ×

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Table 1. *Means, over three cotton cultivars, of the effects of two day/night temperatures (30/20 °C, HT; 26/16·5 °C, LT) combined with two light intensities (75 W* m^{-2}*, HL; 52·5 W* m^{-2}*, LL) on leaf area (*cm^2*/plant) at various stages of development*

	Regimes				S.E. (36 D.F.)	
Stage	HT–HL	HT–LL	LT–HL	LT–LL	T/L	T × L
Squaring	333	511	532	527	13·5	19·1
Flowering	2726	2881	2876	3093	48·1	67·9
Harvesting	5085	5686	3053	5163	157·7	222·8

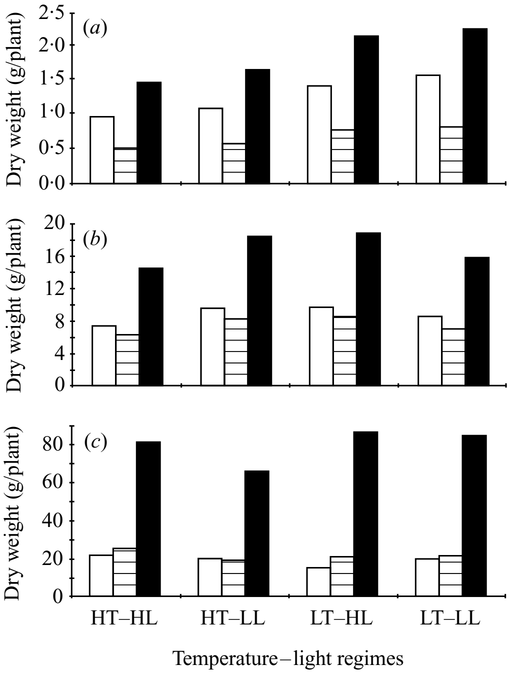

Fig. 1. Means, over three cotton cultivars, of the effects of two day/night temperatures (30/20 °C, HT; 26/16·5 °C, LT) combined with two light intensities (75 W m^{-2}, HL; 52·5 W m^{-2}, LL) on leaf dry weight (LDW ☐), stem dry weight (SDW ▤) and total dry weight (TDW ■) at (*a*) squaring, (*b*) flowering and (*c*) harvesting. (Respective S.E. values for T/L: 0·04, 0·16 and 0·57 for LDW, 0·02, 0·23 and 0·78 for SDW, 0·06, 0·35 and 1·98 for TDW. D.F. = 36.)

light × cultivar interactions were significant ($P < 0·05$) only at squaring.

At squaring, all dry weights (leaves, stems and total) were increased significantly ($P < 0·001$) by LT, while light reduction had less effect ($P < 0·05$) except for leaf dry weight which, as for leaf area, was increased by LL (Fig. 1*a*). Cultivar effects were noted for stem and total dry weight ($P < 0·05$). At flowering, neither temperature nor light variation caused significant main effects but a significant ($P < 0·001$) temperature × light interaction was found in all instances. The HT–LL regime increased dry weight, but LT–LL had the opposite effect (Fig. 1*b*). At this stage, leaf dry weight, like leaf area, showed significant cultivar differences. At harvesting, all characters were reduced ($P < 0·01$) by LL especially with HT, except leaf dry weight, which was increased by LT (Fig. 1*c*).

Dry weight of squares per plant, measured at flowering, was reduced only by LL, whereas boll dry weight per plant was increased by LT (Table 2), the effect of light being less important. The favourable LT effect on boll dry weight also influenced the value of the final total dry weight (Fig. 1*c*), which was higher at LT despite the significantly higher values of the other dry weight components at HT.

Plant final height, determined by the number of nodes and intermode length, was not significantly affected by either temperature or light (Table 2). Internode length was longer at LT but was unaffected by reduced light. The number of nodes was, however, higher at HT. Thus, plants at HT had more nodes with shorter internodes and plants at LT fewer nodes with longer internodes, producing no significant difference in the final height.

Table 2 also shows the numbers of branches, sympodia and monopodia produced in the various temperature–light regimes. The number of branches was similarly and significantly decreased by LT and LL. A temperature × light interaction ($P < 0·001$) was due to the fact that LL had a strong decreasing effect under HT but not at LT. Number of sympodia responded in the same manner, while the number of monopodia appeared to be more strongly affected by temperature decrease than by light reduction. However, both LT and LL increased the number of monopodia.

Earliness components

Although the node of the first floral or fruiting branch was significantly ($P < 0·001$) raised by HT, it was not affected by light (Fig. 2*a*) and there was no interaction.

Vertical flowering intervals were increased by both LT and LL (Fig. 2*b*). However, horizontal flowering intervals were signifcantly longer under LT only, although a temperature × light interaction ($P < 0·05$)

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Table 2. *Means, over three cotton cultivars, of the effects of two day/night temperatures (30/20 °C, HT; 26/16·5 °C, LT) combined with two light intensities (75 $\mathrm{W\,m^{-2}}$, HL; 52·5 $\mathrm{W\,m^{-2}}$, LL) on various cotton characters*

	Regimes				S.E. (36 D.F.)	
Character	HT–HL	HT–LL	LT–HL	LT–LL	T/L	T × L
Dry weight						
Squares (g/plant)	0·79	0·63	0·86	0·48	0·06	0·08
Bolls (g/plant)	28·7	25·3	51·2	43·5	1·56	2·19
Plant height (cm)	116·0	111·9	117·8	109·3	2·33	3·32
Internode length (cm)	3·95	3·98	4·95	4·68	0·09	0·13
Number of nodes	28·8	27·3	22·3	23·0	0·42	0·64
Branches	23·6	17·3	16·2	16·7	0·57	0·85
Sympodia	22·5	16·4	14·5	14·7	0·57	0·85
Monopodia	0·58	1·33	1·58	1·69	0·14	0·20

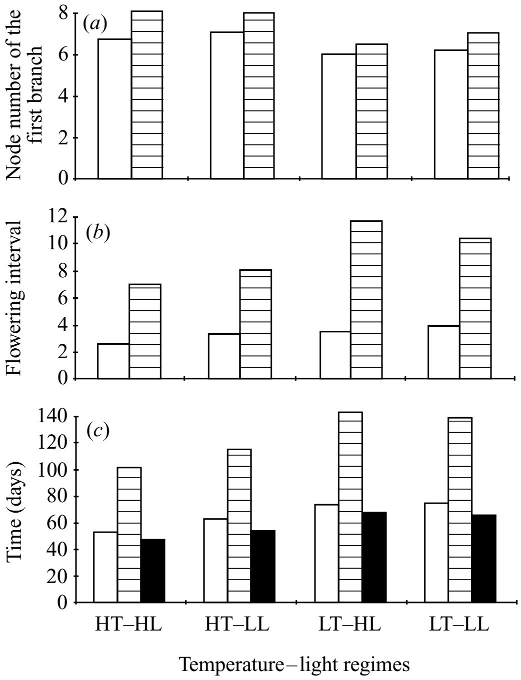

Fig. 2. Means, over three cotton cultivars, of the effects of two day/night temperatures (30/20 °C, HT; 26/16·5 °C, LT) combined with two light intensities (75 $\mathrm{W\,m^{-2}}$, HL; 52·5 $\mathrm{W\,m^{-2}}$, LL) on (*a*) node number of first floral (□) or fruiting (▤) branch, (*b*) vertical (□) and horizontal (▤) flowering intervals, (*c*) time from sowing to flowering (□) or boll opening (▤) and boll period (■). (Respective S.E. values for T/L: 0·14, 0·28 for (*a*), 0·07, 0·28 for (*b*) and 0·57, 0·85, 0·57 for (*c*). D.F. = 36.)

was observed, caused by a sharp decrease in the interval under the LT–LL regime, whereas there was a slight increase under HT–LL.

Periods from sowing to the beginning of flowering or opening of the first boll were increased by lowering either temperature or light, whereas boll period was affected only by temperature and was longer in the LT regime (Fig. 2*c*). Significant ($P < 0{\cdot}001$) temperature × light interactions occurred for all characters. For the time required to flowering, interaction occurred because LL resulted in a sharper increase of the period under a warmer than a cooler environment. Interactions in the other characters were due to a decreasing growth period under LL at LT, while LL increased periods under HT. Cultivar differences were significant ($P < 0{\cdot}05$) only for boll period, with PU having the shortest period.

Fruiting and yield components

Although most (*c.* 24) flowers appeared under the HT–HL regime (> 10 more than in the least favourable regime, HT–LL), the number of bolls per plant was reduced at HT and increased at LT. Light reduction decreased ($P < 0{\cdot}05$) the number of bolls (Fig. 3*a*). The number of open bolls per plant was only affected ($P < 0{\cdot}001$) by reduced light, becoming lower at LL (Fig. 3*a*). As a result, retention percentage relative to HT–HL (30·1 %) was increased (to 61·5 %) by both LT and LL because fewer flowers were produced under both conditions and more bolls were set under LT.

Total seed cotton yield per plant was significantly ($P < 0{\cdot}001$) affected only by temperature and, as expected, was higher at LT (Fig. 3*b*) because of the larger number of bolls set. The LL regimes slightly decreased total yield, hence the lowest yields were obtained under HT–LL. Yield from open bolls was influenced also by the number of open bolls and was thus increased by LT but decreased by LL (Fig. 3*b*).

Boll weight and lint percentage were significantly affected by both factors, although the temperature effect appeared to be much stronger than the light effect ($P < 0{\cdot}05$). Bolls were heaviest (4·6 g) in the

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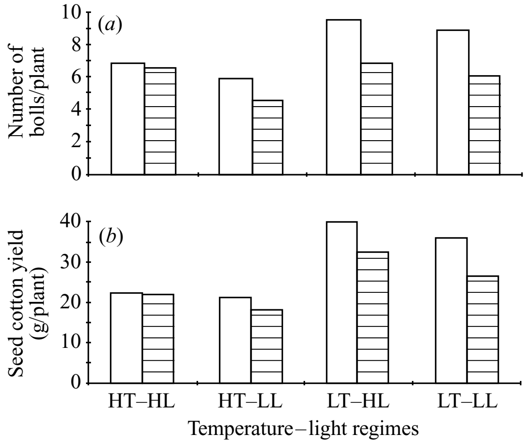

Fig. 3. Means, over three cotton cultivars, of the effects of two day/night temperatures (30/20 °C, HT; 26/16·5 °C, LT) combined with two light intensities (75 W m^{-2}, HL; 52·5 W m^{-2}, LL) on (*a*) number of bolls and (*b*) seed cotton yield (g/plant). (S.E. values for T/L: 0·28 for number of bolls, 1·34 and 1·41 for yield from total (□) and open (▤) bolls. D.F. = 36.)

LT–HL regime and lightest (3·2 g) in the HT–HL regime (S.E.D. ±0·15 g), because LL decreased boll weight at LT but increased it at HT. As with other yield components, LT favoured lint percentage, unlike LL, making lint percentage maximum (41·8) and minimum (35·9) at the same regimes as for boll weight. A temperature × light interaction ($P < 0{\cdot}001$) was observed. Cultivar differences were significant ($P < 0{\cdot}05$), with C–210 having the heaviest bolls and highest lint percentage.

Fibre properties

Long fibres (Fibrograph 2·5%) were longer at LL, while differences due to temperature were non-significant (Fig. 4*a*). Interactions, however, did occur ($P < 0{\cdot}01$) because fibres lengthened more at LL when combined with HT, while at LT no length increase (or even a slight decrease) occurred. On the other hand, the average fibre length (Fibrograph 50%) was affected only by temperature. Cultivar differences were significant ($P < 0{\cdot}05$) only for Fibrograph 2·5% measurements, with the longest fibres achieved by cv. 4S.

Length uniformity was affected by temperature only and was higher at LT (Fig. 4*b*), although significant ($P < 0{\cdot}001$) temperature × light interactions occurred. However, both factors significantly affected fibre strength ($P < 0{\cdot}001$) and micronaire index ($P < 0{\cdot}01$–$0{\cdot}05$). Both characters were decreased at LT and LL (Fig. 4*c*, *d*). Significant interactions appeared because of the sharp decrease by LL under HT only, while under LT no differences occurred.

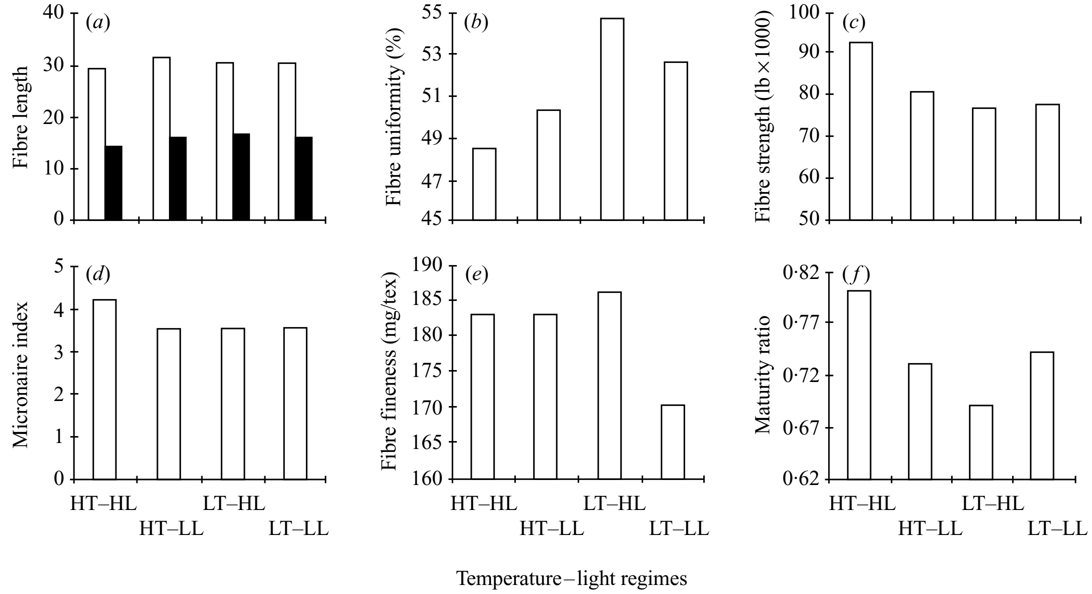

Fig. 4. Means, over three cotton cultivars, of the effects of two day/night temperatures (30/20 °C, HT; 26/16·5 °C, LT) combined with two light intensities (75 W m^{-2}, HL; 52·5 W m^{-2}, LL) on fibre properties, (*a*) fibre length, (*b*) fibre uniformity (%), (*c*) fibre strength, (*d*) micronaire index, (*e*) fibre fineness (mg/tex) and (*f*) maturity ratio. (S.E. values for T/L: 0·27 and 0·18 for long (□) and average (■) fibre length respectively, 0·5 for uniformity, 0·99 for strength, 0·09 for micronaire, 3·68 for fineness and 0·01 for maturity. D.F. = 36.)

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Fineness was not affected by either temperature or light, unless both were low (Fig. 4*e*), while HL combined with HT gave maximum, and with LT minimum, maturity ratios (Fig. 4*f*).

DISCUSSION

There is a considerable problem in relating the results from many growth room studies to those that might be found in the field. The benefit of having controlled conditions may be offset by the fact that these differ from those found in the field. This is particularly true for light intensity, where even the HL environment used here was only *c*. 20% of that likely outside. It is, however, thought, that the possible increase in CO_2 concentration within the rooms, which might influence leaf transpiration per unit area (Kimball & Idso 1983; Goudriaan & Unsworth 1990) or leaf stomatal conductance (Morison 1987; Harley *et al*. 1992; Nederhoff 1992; Nederhoff *et al*. 1992) and increase growth rate and finally plant size (usually offsetting the decrease in stomatal conductance, according to Hileman *et al*. (1994)), should not significantly affect the validity of the comparative results.

High light was found to improve growth and reproduction under a cooler environment. For most of the characters, significant interactions between temperature and light were evident, as the rather large difference between the values of the one factor did not overshadow the effects of the other. Although development of leaf area was mainly temperature-dependent, plants at harvest had a larger leaf area when high temperature was combined with light of low rather than high intensity. Leaf area was least in the low temperature–low light regime. However, the lightest plants were grown under the high temperature–low light regime. Light had no significant effect on plant height, as the number of nodes and internode length were largely dependent on temperature. On the other hand, light affected the numbers of branches, sympodia and monopodia, being highest for the first two in the high light–high temperature and for the third in the low light–low temperature regime.

All other characters, except time to certain developmental stages and fibre length, were reduced in low light. Temperature modified the light effects (and *vice versa*) but the effects differed between characters. This was not unexpected because it is known that both factors influence some of the basic functions of the plant such as photosynthesis, dark respiration, floral initiation, translocation of assimilates and particularly the accumulation of sugars in the developing bolls (Rajan *et al*. 1973; Guinn 1974). Further sources of variable response are likely to come from the effects of light and temperature on hormonal balance and its influence on cell division and elongation. The degree of response to either factor also depends on the magnitude of the other factor and synergistic or antagonistic effects can be produced, depending on the particular character.

There were no indications that high intensity light can compensate for a lower temperature, probably because plants were unable to maintain a satisfactory yield at the high temperature used under the growth room light intensities. (In comparison with the high temperature regime used, the low temperature could be considered to be almost normal, at least for the stages up to flowering.) However, it is very difficult to set limits for such a relationship because it is also possible that some activities, such as reproduction, are more sensitive to light reduction than to temperature, because cultivars such as the ones used in these experiments were developed in relatively cool environments (at least during the early and late parts of the growing season) but with high solar radiation (and long photoperiod).

Although reduced light adversely affected growth and productivity as well as most of the fibre properties, particularly fibre strength and maturity under HT, very long periods of light reduction are not very common even in an area marginal for cotton production. However, the results for the effects of LL and LT on the fibre properties are of practical importance because periods of overcast weather do occur during the late part of the season and results which have so far been reported are mainly concerned with boll weight and lint percentage. It would be interesting to examine the extent to which reduction in light intensity, under different temperatures, during the later stages of growth only (boll development and maturation) affects the fibre properties.

REFERENCES

Bhatt, J. G. (1974). Leaf growth and leaf area index in morphologically contrasting varieties of cotton. *Cotton Growing Review* **51**, 187–191.

Bhatt, J. G. & Nathan, A. R. S. (1977). Studies on the growth of *G. barbadense* cottons in India. II. Responses to environmental stresses. *Turrialba* **27**, 83–92.

Bhatt, J. G. & Ramanujam, T. (1975). Responses of the cotton plant to variations in the intensities of natural light. *Turrialba* **25**, 440–443.

Boote, K. J., Jones, J. W. & Bennett, J. M. (1985). Factors influencing crop canopy CO_2 assimilation of soybean. In *Proceedings of the Third World Soybean Research Conference* (Ed. R. Shibles), pp. 780–788. Boulder, CO: Westview Press.

Goudriaan, J. & Unsworth, M. H. (1990). Implications of increasing carbon dioxide and climate change for agricultural productivity and water resources. In *Impact of Carbon Dioxide, Trace Gases, and Climate Change on Global Agriculture. American Society of Agronomy Special Publication 53* (Eds B. A. Kimball, N. J. Rosenberg &

https://doi.org/10.1017/S0021859698005735 Published online by Cambridge University Press

L. H. Allen, Jr), pp. 111–130. Madison WI: American Society of Agronomy/Crop Science Society of America/Soil Science Society of America.

Guinn, G. (1974). Abscission of cotton floral buds and bolls as influenced by factors affecting photosynthesis and respiration. *Crop Science* **14**, 291–293.

Guinn, G. (1976). Nutritional stress and ethylene evolution by young cotton bolls. *Crop Science* **16**, 89–91.

Hesketh, J. D. & Low, A. J. (1968). The effects of temperature on components of yield and fibre quality of cotton varieties of diverse origin. *Cotton Growing Review* **45**, 243–257.

Harley, P. C., Thomas, R. B., Reynolds, J. F. & Strain, B. R. (1992). Modelling photosynthesis of cotton grown in elevated CO_2. *Plant, Cell and Environment* **15**, 271–282.

Hileman, D. R., Huluka, G., Kenjige, R. K., Sinha, N., Bhattacharya, N. C., Biswas, P. K., Lewin, K. F., Nagy, J. & Hendrey, G. R. (1994). Canopy photosynthesis and transpiration of field-grown cotton exposed to free-air CO_2 enrichment (FACE) and differential irrigation. *Agricultural and Forest Meteorology* **70**, 189–207.

Idso, S. B., Kimball, B. A., Wall, G. W., Garcia, R. L., LaMorte, R., Pinter, P. J., Mauney, J. R., Jr, Lewin, K. & Nagy, J. (1994). Effects of free-air CO_2 enrichment on light response curve of net photosynthesis in cotton leaves. *Agricultural and Forest Meteorology* **70**, 183–188.

Kerby, T. A., Buxton, D. R. (1978). Effect of leaf shape and plant population on rate of fruiting position appearance in cotton. *Agronomy Journal* **70**, 535–538.

Kimball, B. A. & Idso, S. B. (1983). Increasing atmospheric CO_2: effects on crop yield, water use and climate. *Agricultural Water Management* **7**, 55–72.

Low, A. J., Hesketh, J. D. & Muramoto, H. (1969). Some environmental effects on the varietal node number of the first fruiting branch. *Cotton Growing Review* **46**, 181–188.

McMahon, J. & Low, A. J. (1972). Growing degree days as a measure of temperature effects on cotton. *Cotton Growing Review* **49**, 39–49.

Morison, J. I. L. (1987). Intracellular CO_2 concentration and stomatal response to CO_2. In *Stomatal Function* (Eds E. Zeiger, G. D. Farquhar & I. R. Cowan), pp. 229–251. Stanford, CA: Stanford University Press.

Mutsaers, H. J. W. (1983). Leaf growth in cotton (*Gossypium hirsutum* L.). 2. The influence of temperature, light, water stress and root restriction on the growth and initiation of leaves. *Annals of Botany* **51**, 521–529.

Nederhoff, E. M. (1992). Effects of CO_2 on greenhouse grown eggplant (*Solanum melongena* L.). I. Leaf conductance. *Journal of Horticultural Science* **67**, 795–803.

Nederhoff, E. M., Rijsdijk, A. A. & de Graaf, R. (1992). Leaf conductance and rate of crop transpiration of greenhouse grown sweet pepper (*Capsicum annuum* L.) as affected by carbon dioxide. *Scientia Horticulturae* **52**, 283–301.

Peng, S. & Krieg, D. R. (1991). Single leaf and canopy photosynthesis response to plant age in cotton. *Agronomy Journal* **83**, 704–708.

Puech-Suanzes, I., Hsiao, T. C., Fereres, E. & Henderson, D. W. (1989). Water-stress effects on the carbon exchange rates of three upland cotton (*Gossypium hirsutum*) cultivars in the field. *Field Crops Research* **21**, 239–255.

Rajan, A. K., Betteridge, B. & Blackman, G. E. (1973). Differences in the interacting effects of light and temperature on growth of four species in the vegetative phase. *Annals of Botany* **37**, 287–313.

Reddy, V. R., Baker, D. N. & Hodges, H. F. (1991). Temperature effects on cotton canopy growth, photosynthesis and respiration. *Agronomy Journal* **83**, 699–704.

Richardson, A. J. & Wiegard, C. L. (1988). Modeling planting configuration and canopy architecture effects on diurnal light absorption changes in cotton. *International Journal of Remote Sensing* **9**, 710–714.

Roussopoulos, D. K., Gerakis, P. A., Gagianas, A. A. & Sficas, A. G. (1978). Autoecology of *Gossypium hirsutum* L. II. Relationship of solar radiation to fruiting, boll maturation and yield. *Scientific Annals, Thessaloniki University* **21**, 49–51.

Walhood, V. T. & Johnson, R. E. (1976). Interception of solar radiation by a constant population of cotton plants. *Beltwide Cotton Production Research Conference Proceedings*, pp. 70–71.

Wells, R. (1988). Response of leaf ontogeny and photosynthetic activity to reproductive growth in cotton. *Plant Physiology* **87**, 274–279.

Wells, R., Meredith, W. R., Jr & Williford, J. R. (1988). Heterosis in upland cotton. II. Relationship of leaf area to plant photosynthesis. *Crop Science* **28**, 522–525.

https://doi.org/10.1017/S0021859698005735 Published online by Cambridge University Press