Adaptation of Chickpea to Water-limited Environments

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ABSTRACT

In Mediterranean-type climates, seed filling of cool-season pulses frequently coincides with the onset of terminal drought. Studies over several seasons with chickpea have shown that leaf photosynthesis is low during seed filling. Pod gas exchange, which is also affected by terminal drought, is low even in well-watered chickpea. Studies in the glasshouse with isotopically-labelled carbon showed that the redistribution of carbon from vegetative parts was less than 20%, but did vary with genotype. Studies of the recycling of CO_2 inside the pod showed that the rate of internal photosynthesis was similar in water-stressed and well-watered pods and the rates were similar to those in well-watered leaves. This is in agreement with the observation that the water relations of the seed are unaffected by the dehydration of the remainder of the plant. The efficient re-use of respired CO_2 by the pod enables the low, but positive, rates of leaf photosynthesis to maintain seed filling under conditions of terminal drought.

KEY WORDS

Cicer arietinum, drought, photosynthesis, assimilate redistribution, water stress, seed filling.

INTRODUCTION

Cool-season pulses have been widely introduced into southern Australia over the past few years and chickpeas have been adopted as a profitable pulse crop by an increasing number of farmers in southern Australia. In Western Australia, chickpeas are grown on the neutral-to-alkaline fine-textured soils that are found predominantly in the low-rainfall eastern region of the cropping zone. The crops are frequently subjected to terminal drought which results in reduced seed yields and seed size (1,5). Agronomic studies have concluded that early podding and greater biomass at podding contribute to high yields in cool-season pulses (4,9). However, the lack of pod set at cool temperatures (3,7) delays podding until water deficits decrease the photosynthetic rate of leaves to low levels and therefore drought-resistance mechanisms to fill the seeds under terminal drought are required.

Over the past five years, there has been considerable research to determine the responses of chickpeas to terminal drought and the factors that contribute to yield under water-limited conditions. This paper summarises some of the key findings.

RESULTS

The rate of net photosynthesis of chickpea leaves was measured in the field over two seasons, one with below-average growing-season rainfall (173 mm) and one with above-average growing-season rainfall (313 mm). Leaf photosynthesis in a rainfed chickpea crop decreased to values below 5 ?mol m^{-2} s^{-1} at the onset of seed filling in both seasons, compared to values above 20 ?mol m^{-2} s^{-1} in an adjacent irrigated crop (4,5). Figure 1 shows that leaf net photosynthesis in rainfed chickpea reached a peak prior to podding and decreased rapidly during pod filling. The decrease in leaf photosynthesis occurred as the leaf water potential decreased with soil water depletion (4,5). In one year, the rates of leaf photosynthesis and leaf water potential were measured at the same time in six genotypes of chickpea. Figure 2 shows that there were no genotypic differences in the response of leaf photosynthesis to leaf water potential among the six genotypes (5). In this field study, the rate of pod photosynthesis was below the measurable rate for the instrument (5). In a subsequent glasshouse study, the rate of pod photosynthesis was shown

to be only 1 ?mol m^{-2} s^{-1} when well illuminated and well watered (6). When water stressed the pods respired CO_2 (6). Thus the pods do not appear to contribute significantly to the gas exchange of the canopy and are unlikely to provide additional carbon for seed filling under rainfed conditions.

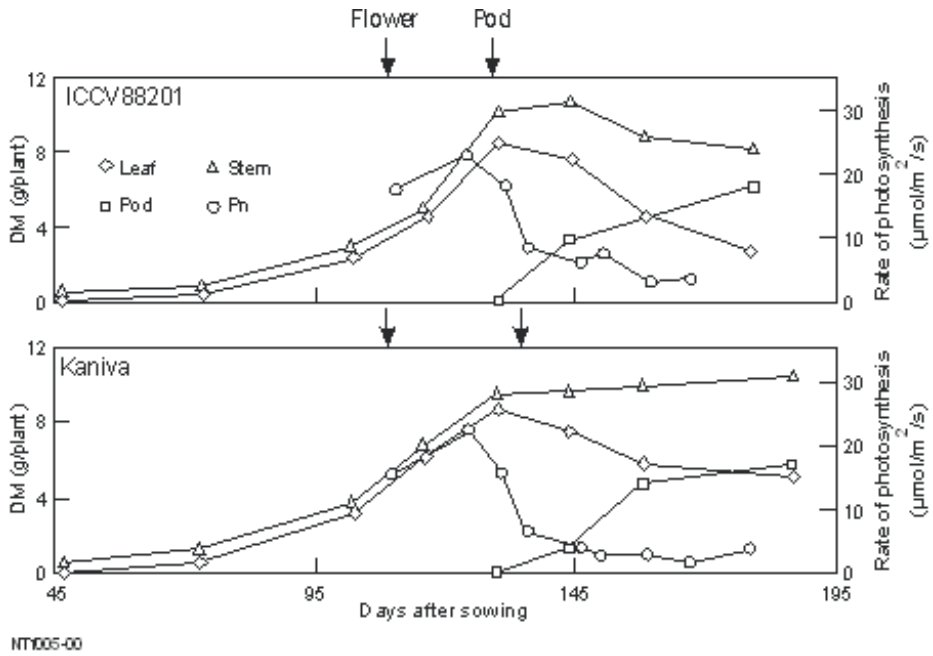

Figure 1. Changes with time in the rate of leaf photosynthesis (circles), and leaf (diamonds), stem (triangles) and pod (squares) dry weight in two rainfed chickpea genotypes in the field.

Table 1. Total seed C (mg/plant) and the C arising from post-podding fixation or from pre-podding remobilisation in glasshouse-grown Tyson and Kaniva chickpea under both well-watered (control) and water-stressed conditions. The percentage contribution of remobilised pre-podding C to total seed C is shown in brackets. Adapted from Davies et al. (2).

Genotype	Treatment	Total	Post-pod fixation	Pre-pod remobilised
TYSON	Control	3360	3058	302 (9)
	Stressed	1800	1508	292 (16)
KANIVA	Control	2284	2130	154 (7)
	Stressed	626	574	52 (8)

Figure 1 shows that the leaf and stem dry matter decreased during seed filling in one genotype, while only leaf dry matter only decreased in the second genotype. Studies in the field and glasshouse suggested that the losses of dry matter from leaves, stems and pod walls, which varied from 4 to 58% of that at peak biomass depending on genotype, could contribute significant dry weight to the developing seed (1,2,5). However, detailed studies with two chickpea genotypes labelled with isotopic carbon (^{13}C) during vegetative growth showed that the contribution of carbon from vegetative parts was less than 20% (2). Table 1 shows the total carbon in the seed of well-watered and water-stressed chickpea and the amount that was derived from vegetative parts labelled prior to podding and that which was derived from post podding assimilation and remobilisation.

When the level of CO_2 inside the pod was measured, it was found to be as high as 10,000 ?L L^{-1} shortly after sunset, nearly 30-fold higher than in the atmosphere external to the pod (6). However, during the day the concentration inside the pod decreased indicating that the CO_2 produced by respiration was being reused in internal photosynthesis. By alternately shading and exposing the pods to light and by measuring the CO_2 concentration inside the pod cavity, the rate of respiration and photosynthesis of the pods was measured. Figure 3 shows the rate of net and gross photosynthesis inside the chickpea pod. While net photosynthesis was positive during the middle of the day, both the gross and net photosynthesis were similar in the water-stressed pods and the well-watered pods (6).

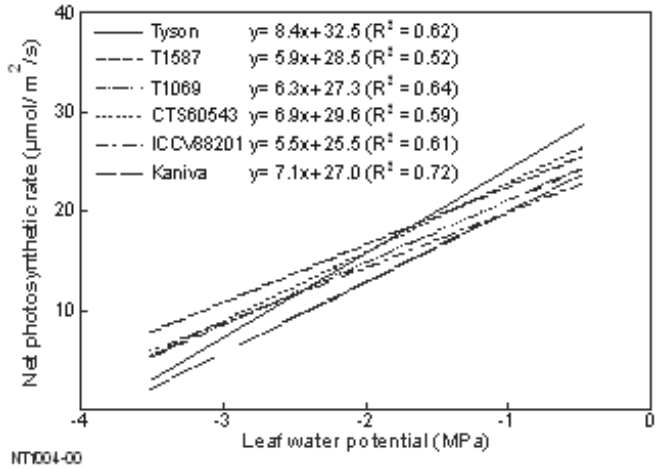

Figure 2. Relationship between the rate of leaf photosynthesis and leaf water potential for six genotypes of chickpea. Adapted from Leport et al. (5).

Table 2. Mean ? SD of the stem water potential (ψ_{stem}) and the turgor pressure (ψ_p) of pod wall cells and seed coat cells before and after irrigation. Adapted from Shackel and Turner (8).

Time Period	ψ_{stem} (MPa)	Cell ψ_p (MPa)	
		Pod Wall	Seed Coat
Before irrigation	-1.22 ? 0.24	0.25 ? 0.13	0.10 ? 0.04
2 to 4 h after irrigation	-0.37 ? 0.06	0.97 ? 0.20	0.12 ? 0.04
24 h after irrigation	-0.24 ? 0.03		0.13 ? 0.08

Detailed studies of the water relations of the seed and pod wall using the micropressure probe showed that the

turgor pressure and water status of the seed coat remained constant whether the plant and pod wall was adequately watered or water stressed (8). Table 2 shows that the turgor pressure of the seed coat was between 0.10 and 0.13 MPa irrespective of whether the plant water potential was -0.2 or -1.22 MPa.

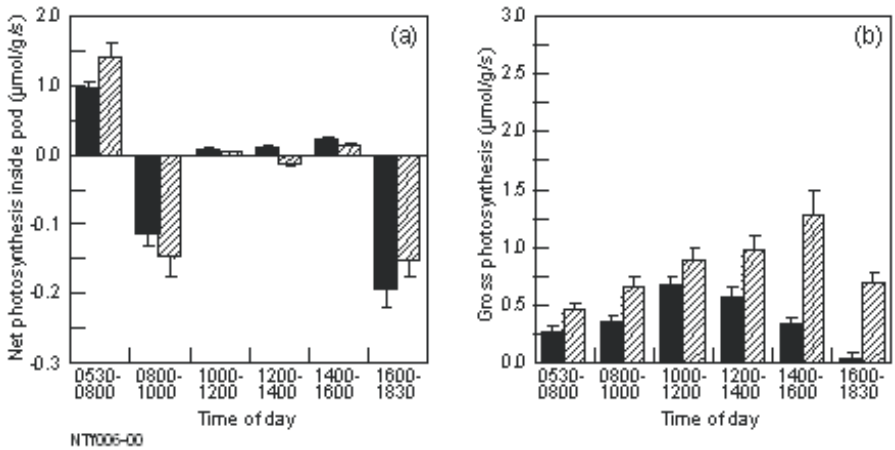

Figure 3. Net (a) and gross (b) photosynthetic rates inside 10- to 12-day-old pods of well-watered (solid bars) and water-stressed (hatched bars) chickpeas. Bars give the SE (n = 6). Adapted from Ma et al. (6).

DISCUSSION

This series of studies has shown that in chickpea subjected to terminal drought that leaf photosynthesis is markedly decreased as the soil dries and the leaf water potential decreases. Although the pod water status is higher (5) and the pods have about one-third the frequency of stomata as the leaves (6), the pods do not contribute significantly to the gas exchange of the plants during seed filling. Moreover, the remobilisation to the seed of carbon accumulated in vegetative parts of the plant prior to podding and from the pod wall prior to seed filling was shown to be small. However, the pods do contribute to seed filling by recycling respired carbon within the pod itself, thereby reducing carbon losses to the atmosphere. The rate of photosynthesis of respired carbon within the seed was the same in the water-stressed chickpeas as in the well-watered chickpeas and on a dry-matter basis was the same as the well-watered leaves.

While the recycling of CO_2 inside the pod provides a mechanism for the efficient use of carbon already fixed, it does not provide additional carbon for seed filling. We conclude that the low, but positive, rates of photosynthesis near midday in leaves of the chickpeas subjected to terminal drought, together with the efficient re-use of carbon respired by the seed and pod wall, contribute to the carbon for seed filling. Unlike other cool-season pulses, the rate of leaf photosynthesis did not decrease to zero at midday (4) and presumably was higher in the early part of the day before the leaf water potential decreased (10). Further, some genotypes of chickpea were able to accumulate solutes in the leaves and adjust osmotically to water deficits (4). This would enable the plants to maintain leaf photosynthesis, albeit at low rates, at low water potentials (5) and may aid in carbon accumulation for seed filling.

The high rate of internal recycling of CO_2 inside the pods of the water-stressed plants is consistent with the maintenance of turgor pressure in the seed coat of chickpea (Table 2). However, studies with isotopically-labelled carbon showed that the fixation of the carbon inside the pod occurred primarily in the pod wall (6), the turgor pressure of which decreased in concert with the water status of the rest of the plant (8). Thus the high rate of fixation of recycled carbon by the pod wall is worthy of further investigation to determine whether the water status of the inner pod wall is higher than that measured by Shackle and Turner (8) or whether the pod wall can refix carbon at lower water potentials than the leaves.

CONCLUSIONS

Chickpeas have mechanisms to refix CO_2 inside the pod, thereby minimising losses of carbon when leaf photosynthesis is decreased to low levels by terminal drought. The role of osmotic adjustment in the maintenance of low rates of photosynthesis and the genetic variability in the recycling of CO_2 inside the pod to improve the drought resistance of chickpea need further investigation.

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