

Electron Transport as a Limitation to Photosynthesis of Tea (*Camellia sinensis* (L.) O. Kuntz): A Comparison with Sunflower (*Helianthus annuus* L.) with Special Reference to Irradiance

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ABSTRACT. Some photosynthetic processes in tea (*Camellia sinensis* (L.) O. Kuntz) were compared with those of sunflower (*Helianthus annuus* L.) to identify factors limiting photosynthetic CO₂ exchange rate (A) in tea. Two experiments were done under controlled environmental conditions at IACR-Rothamsted, Harpenden, UK. Young tea plants (clone TRI 2025) and sunflower (cv. Printasol) were grown in two photosynthetically active radiation (PAR) photon fluxes (PPF), 150 and 650 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Rate of A and chlorophyll a fluorescence were measured simultaneously. Tea had significantly slower A (1–2.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR and 360 $\mu\text{mol mol}^{-1} \text{CO}_2$) than sunflower (16–21 $\mu\text{mol m}^{-2} \text{s}^{-1}$). This was related to smaller efficiencies of photosystem II (PSII) in excitation energy capture and transporting electrons and smaller rates of linear electron transport. A smaller proportion of electrons was used in tea for ribulose-bisphosphate (RuBP) carboxylation, the rate of RuBP carboxylation was slower than in sunflower. Stomatal conductance (g_s) to CO₂ and hence CO₂ inside the leaf (C_i) were also much smaller in tea than in sunflower. Tea dissipated a greater proportion of the absorbed excitation energy by non-photochemical quenching than sunflower. Shade during growth increased A in tea by increasing the efficiency of PSII, linear electron transport and increased the proportion of the electrons used in photochemistry supporting carboxylation of RuBP, but not in sunflower. Hence, tea can be considered as a shade plant with inherently small capacity for photosynthetic CO₂ assimilation owing to poor stomatal conductance and carboxylation capacity, which has a large capacity for energy dissipation. Tea is often regarded as a 'sink limited' crop but the inherent limitations in photosynthesis show it is also 'source limited'. As tea photosynthesis improves under shade, optimizing the light environment by shading may contribute to increased productivity.

INTRODUCTION

Total biomass production of tea is 15–18 t ha⁻¹ year⁻¹, compared to 25–40 t ha⁻¹ year⁻¹ typical of tropical crops (Magambo and Cannell, 1981). There is controversy as to why tea is so low yielding (Squire, 1985). Smaller harvest index (Magambo and Cannell,

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1981) and the low efficiency with which energy is used to make dry matter (Othieno, 1976; Squire, 1985) are possible reasons. Tea is often thought to be 'sink' limited, unable to use the assimilates produced (Magambo and Cannell, 1981; Squire, 1985; Rahman, 1988). The very small A in tea could be a major limitation to biomass and harvestable yield production. The light saturated rate of photosynthesis of tea is 2–14 $\mu\text{mol m}^{-2} \text{s}^{-1}$ compared with many other tropical plants (20–40 $\mu\text{mol m}^{-2} \text{s}^{-1}$) (Barua, 1960; Squire, 1977; Roberts and Keys, 1978; Smith *et al.*, 1993). Shade is important in determining the photosynthetic capacity of tea, but how it affects photosynthetic mechanisms is unclear (Carr and Stephens, 1992).

Regulation of A in tea is poorly understood, with no clear evidence as to why the rates are so low; relatively little work has addressed the fundamental processes. Hence, this study examined the possible causes for the low rates of A and to elucidate the effects of shade. This paper examines some photosynthetic processes in tea in comparison with that of sunflower, a 'sun' plant, which has large A and productivity.

MATERIALS AND METHODS

Two experiments were done using tea (*Camellia sinensis* (L.) O. Kuntz; clone TRI 2025) and sunflower (*Helianthus annuus* L.; cv. Printasol) grown at controlled environment (CE) cabinets at IACR-Rothamsted, Harpenden, UK, during July 1997–March 1998. The conditions were, 25°C day and 18°C night temperature respectively, 85% relative humidity and 13 h day length. Approximately 5 month old tea plants were grown at 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR for 3 months, then transferred to high light CE cabinets. Half of the plants were kept at 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and the other half gradually exposed to increasing light and acclimatized to the maximum light intensity of 650 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for 4 weeks. The light treatment was not replicated. Sunflower plants were grown in pots under each PPF (150 and 650 $\mu\text{mol m}^{-2} \text{s}^{-1}$). In tea, fully matured leaves that unfurled during the treatment were used for the measurements. In sunflower, fully developed 3rd, 4th and 5th leaves from the bottom were used. The sunflower plants were in vegetative phase during the time of measurement.

Measurement of photosynthesis

Photosynthetic CO_2 exchange was measured with an open, infra-red gas exchange system with 6 chambers and automatic data handling for continuous monitoring (ADC, model 225MK3, Hoddesden, UK). Rate of A was measured over a range of PPF (0–1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and CO_2 concentrations (360 and 0–1000 $\mu\text{mol mol}^{-1} \text{CO}_2$) at 25°C. Rate of respiration in the light (R_d), and the concentration of CO_2 in the chloroplast (Γ^*) at which the rate of carboxylation equals the rate of photorespiration were estimated from the relation between A and C_i (Brooks and Farquhar, 1985), made at low CO_2 concentrations, 25°C, 210 $\text{mmol mol}^{-1} \text{O}_2$ and three different light intensities; 70, 108 and 226 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for tea and 86, 176 and 285 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for sunflower.

Measurement of fluorescence

Chlorophyll *a* fluorescence was measured simultaneously with photosynthesis measurements at room temperature with a portable fluorescence meter (model OS-100, OSLOG, PP Systems, UK). Before dark-adapted measurements, the leaves were left in complete darkness ($0 \mu\text{mol m}^{-2} \text{s}^{-1}$) for at least 45 minutes. Using the fluorescence data the following were calculated (as in reference given): F_v/F_m , (efficiency of excitation capture of the fully oxidized PSII reaction centres (RC)) = $(F_m - F_o) / F_m$ where F_m = maximum fluorescence after dark adaptation of leaves, F_o = basal fluorescence; Φ_{EXC} (efficiency of excitation energy capture by 'open' PSII RC's) = $(F_m' - F_o') / F_m'$ where F_m' and F_o' are maximum and basal fluorescence respectively under actinic light (Genty *et al.*, 1989); Φ_{PSII} (relative quantum yield of PSII electron transport under actinic light) = $(F_m' - F_s') / F_m'$; q_p (photochemical quenching) = $(F_m' - F_s') / (F_m' - F_o')$; q_{NP} (non-photochemical quenching) = $1 - (F_m' - F_o') / (F_m - F_o)$ (Schreiber *et al.*, 1986); J_1 (rate of total linear electron transport) = $\Phi_c \times$ incident quantum flux $\times 4$ (Ghashghaie and Cornic, 1994) where, Φ_c is the maximum Φ_{CO_2} ($\Phi_{\text{CO}_2} = (A + \text{respiration}) / \text{photon flux}$) obtained from a calibration line constructed from the linear relationship between Φ_{PSII} and Φ_{CO_2} measured under non-photorespiratory conditions ($2300 \mu\text{mol mol}^{-1} \text{CO}_2$ and $20 \text{mmol mol}^{-1} \text{O}_2$); J_A (allocation of electron-transport products to CO_2 fixation) = $4(A + R_d)$ (Ghashghaie and Cornic, 1994); J_L (allocation of electron-transport products to photorespiration) = $J_1 - J_A$; V_o (rate of Rubisco oxygenation) = $J_L / 6$, V_c (rate of Rubisco carboxylation) = $A + R_d + 0.5 V_o$ (Brooks and Farquhar, 1985) and g_m (mesophyll conductance to CO_2) = $A / \{C_i - [(T^* (J_1 + 8(A + R_d))) / (J_1 - 4(A + R_d))]\}$ (Harley *et al.*, 1992).

RESULTS AND DISCUSSION

Photosynthesis

Photosynthesis of sunflower grown in $650 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR was saturated (A ca. $20 \mu\text{mol m}^{-2} \text{s}^{-1}$) about $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR (Fig. 1) and that of shade-grown leaves (A of ca. $15 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$) at about $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR. Tea was light saturated at $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR when grown at both high and low PPF, where the rates of A were very small: 1.5 and $3 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, very small indeed. When grown under shade, A of tea was consistently higher than that of unshaded. Tea grown at $150 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR had greater A than that grown at $650 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR, (2.51 cf. $0.93 \mu\text{mol m}^{-2} \text{s}^{-1}$), compared to sunflower grown at 150 and $650 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR (15.85 cf. $20.57 \mu\text{mol m}^{-2} \text{s}^{-1}$). The apparent quantum yield (mol CO_2 assimilated per mol of incident PAR) was greater in sunflower than tea (0.046 cf. 0.011, respectively, in bright light, and 0.048 cf to 0.026 in shade). In addition, the carboxylation efficiency (CO_2 fixed per unit change in C_i , at limiting C_i) of sunflower was greater in sunflower than tea (0.089 cf. 0.0179 grown without shade, 0.069 cf. 0.0097 when grown with shade). Thus, tea has many features of a shade plant (Percy, 1998), including reduced photosynthetic ability when grown in bright light, whereas sunflower behaves as expected of a sun species.

The g_s of tea was very small under all PPFs (Fig. 2), consequently its C_i was consistently small despite the very small A , both in marked contrast to sunflower (data not shown). Also shaded tea had slightly higher g_s than unshaded, although was not

significant. The g_s of sunflower increased with increasing PPF during measurements, reaching a maximum above about $600 \mu\text{mol m}^{-2} \text{s}^{-1}$, however, g_s of shaded plants decreased drastically above PAR $600 \mu\text{mol m}^{-2} \text{s}^{-1}$. Intense light during growth thus allows stomata to adjust in sunflower. Tea, in contrast, had increased g_s when grown in shade.

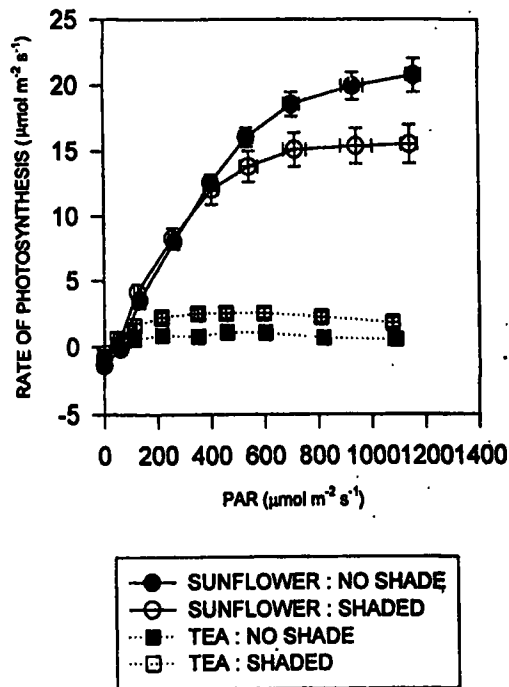


Fig. 1. Response of the rate of photosynthesis (A) to increasing quantum flux in CE grown, young tea and sunflower.

[Note: The vertical and horizontal bars indicate the standard errors of means].

Light reactions and electron transport

The F_v / F_m values were significantly larger in sunflower than in tea (Fig. 3). In sunflower the F_v / F_m value was 0.81 and did not change with the light treatment. In tea grown under higher light intensity, the F_v / F_m value was 0.70 and in shade grown tea, it was 0.75. F_v / F_m estimates the efficiency of excitation energy capture by 'open' PSII reaction centres and provides a rapid method for determining changes in the maximum quantum efficiency of PSII photochemistry (Andrews *et al.*, 1995). The ratio of F_v / F_m for dark-adapted healthy plants is normally close to 0.83. Photoinhibition and other non-photochemical quenching mechanisms lower the F_v / F_m value from this optimal level. Hence, tea is inherently low in its capacity in capturing light energy than sunflower. However, the shade grown tea has a larger value of F_v / F_m , showing a greater proportion of absorbed energy used in photochemistry, thus the importance of using shade in tea.

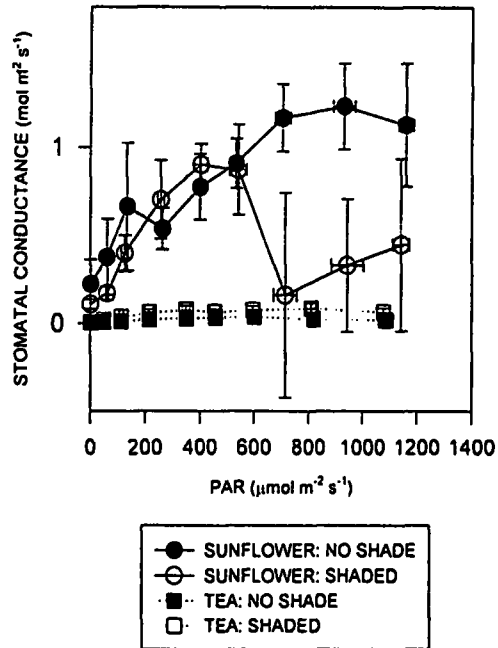


Fig. 2. Response of the stomatal conductance to increasing quantum flux in CE grown, young tea and sunflower. [Note: The vertical and horizontal bars indicate the standard errors of means].

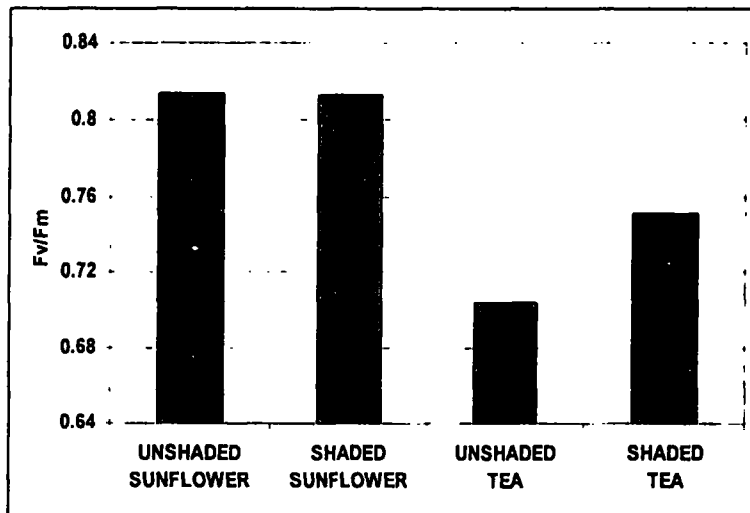


Fig. 3. F_v / F_m values of CE grown, young tea and sunflower plants.

Sunflower had much greater Φ_{EXC} than tea at a given photon flux (Fig. 4A), irrespective of light during growth; the decrease in tea was very great. The Φ_{EXC} of tea was similar, tending to be greater in shade-grown than unshaded plants. Hence, heavy shading of sunflower decreased the proportion of 'open' RC's under actinic light but, in contrast, increased that of tea. A similar response of Φ_{PSII} to that of Φ_{EXC} was observed: sunflower had much larger Φ_{PSII} than tea and it decreased less with increasing PPF (Fig. 4B). Unshaded tea tended to have lower Φ_{PSII} than the shaded. Sunflower had much greater capacity for electron transport and was less affected by increasing PPF than tea; also heavy shading decreased PSII efficiency in transporting electrons in sunflower, but increased that of tea.

Sunflower had larger q_p , which decreased less markedly with increasing PPF, than that of tea (Fig. 4C). Growth in low light decreased q_p of sunflower when measured in bright light; shaded tea increased q_p compared to unshaded, particularly above 400 $\mu\text{mol PAR m}^{-2} \text{s}^{-1}$. The q_p relates to the redox state of Q_A (Laasch, 1987; Seaton and Walker,

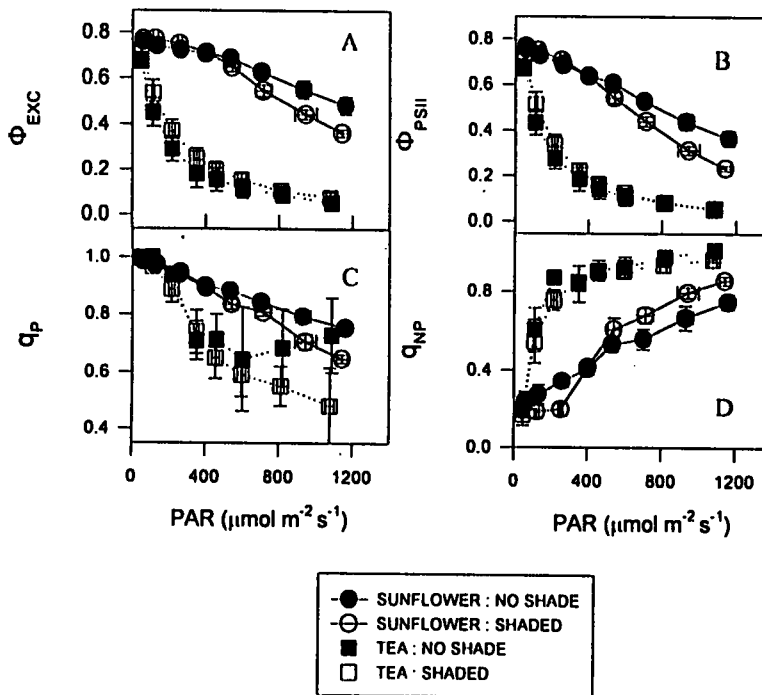


Fig. 4. Response of Φ_{EXC} (A), Φ_{PSII} (B), q_p (C) and q_{NP} (D) to increasing quantum flux in CE grown, young tea and sunflower. The Φ_{EXC} indicates the efficiency of 'open' PSII reaction centres in excitation capture, Φ_{PSII} , the relative quantum yield of PSII electron transport, q_p , photochemical quenching and q_{NP} , the non-photochemical quenching.

[Note: The vertical and horizontal bars indicate the standard errors of means].

1992), and indicates the proportion of open PSII RC's and of electron transport products used in photochemistry. Hence, sunflower had more open RCs than tea, and used a larger proportion of electron transport products for photochemistry.

Tea had much greater q_{NP} than sunflower with PAR > 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 4D), with that of shaded plants slightly smaller than unshaded. However, shaded sunflower had smaller q_{NP} than unshaded in dim light during measurements, but larger q_{NP} in bright light. At high light, particularly if stresses restrict CO_2 assimilation, energy capture exceeds utilization (Pearcy, 1998), and the imbalance may cause over-reduction of the electron transport chain, photoinhibition and photooxidation (Biehler and Fock, 1996). Plants prevent these in several ways. Firstly, by increased conversion of absorbed light into heat. Secondly, by reversibly decreasing PSII efficiency and thus the rate of electron transport. Thirdly, by using excess electrons in pathways other than the Calvin cycle: this is shown by q_{NP} . Tea dissipated more energy than sunflower under all light intensities. Shade-grown sunflower dissipated more energy than unshaded in bright light as less CO_2 is fixed (Fig. 1). The slightly larger q_{NP} of unshaded cf. shaded tea indicates greater energy dissipation.

The estimated R_d for (average for shaded and unshaded) tea and sunflower was 0.222 and 1.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ respectively (characteristic for shade and sun plants) and Γ^* was 58.7 and 20.7 $\mu\text{mol mol}^{-1} \text{CO}_2$, respectively. Allocation of total linear electron transport (J_t), to CO_2 fixation (J_A), to photorespiration (J_P) and to RuBP carboxylation and oxygenation (J_C) related to incident PPF (Figs. 5A, 5B, 5C and 5D), show that sunflower always had much higher rates of J_t , J_A , J_L and J_C than tea. Sunflower grown in shade had smaller J_t , J_A , J_L and J_C than unshaded, and J_t , J_A and J_L increased linearly with increasing PAR when not shaded. However, when shaded, it saturated above 600–700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR. Unshaded tea had smaller J_t and J_C than shaded, but higher J_L and similar J_P . In both shaded and unshaded tea, neither J_t nor J_A increased above 200–300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR. Unshaded tea had higher J_L than shaded; J_L was similar to that of sunflower below 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF, but at greater PPF, J_L of sunflower exceeded tea. J_L was similar in unshaded tea and shaded sunflower, indicating that a high proportion of electrons was used for oxygenation of RuBP.

Sunflower has substantially larger J_t and J_A than tea, indicating greater electron transport capacity, and slightly higher J_L , demonstrating greater capacity for use carboxylation. Larger J_t and J_A indicate larger pools of NADPH, ATP and RuBP in sunflower, perhaps related to higher A . The capacity of photosynthetic electron transport is considerably higher in chloroplasts of sun than shade plants (Boardman, 1977) due to increased electron carriers, e.g., cytochrome *b/f* complex, plastoquinone and ferredoxin. Shading decreased J_t , J_A and J_L in sunflower hence the effects on A . In tea, J_t did not change with shading, but J_L decreased. Hence, the photosynthetic system of tea grown in high light, utilized proportionately more electrons in oxygenation than carboxylation.

Different ways of calculating J_L , J_P and J_C indicate there are alternative sinks to RuBP oxygenation and carboxylation, e.g., the Mehler-peroxidase reaction (Biehler and Fock, 1996) and N reduction pathway (Loreto *et al.*, 1994). There are several sources of error in determining the different parameters to calculate use of electrons and further work is needed in order to establish how tea regulates the balance between energy capture and use.

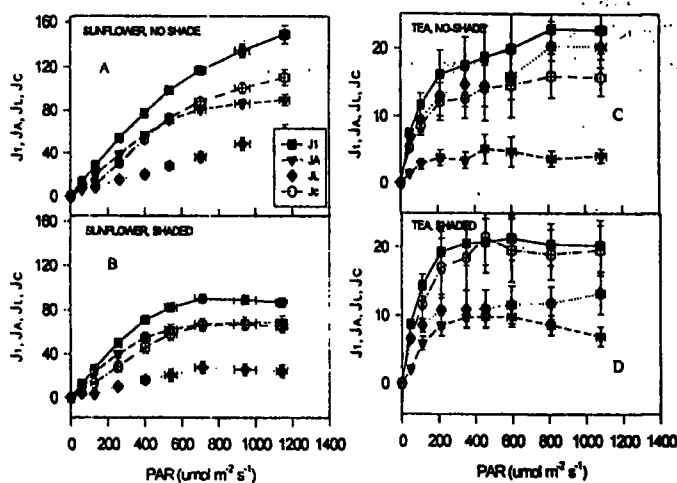


Fig. 5. The calculated rate of total linear electron transport (J_t), allocation of electron transport products to CO_2 fixation (J_A), allocation of electron transport products to photorespiration (J_l) and total electron transport supporting RuBP carboxylation and oxygenation (J_c) for shaded and unshaded sunflower and tea, as a function of the quantum flux. [Note: The units of measurement of J_t , J_A , J_l and J_c are $\mu\text{mol m}^{-2} \text{s}^{-1}$. Vertical and horizontal bars indicate standard errors of means].

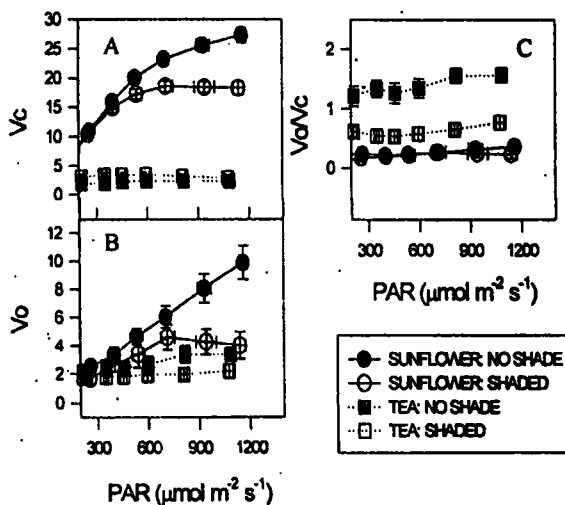


Fig. 6. The calculated V_c (A), V_o (B) and V_o/V_c (C) in tea and sunflower, as a function of the quantum flux. The V_c denotes the rate of RuBP carboxylation and V_o , rate of RuBP oxygenation. [Note: The units of measurement of V_c and V_o are $\mu\text{mol m}^{-2} \text{s}^{-1}$. Vertical and horizontal bars indicate standard errors of means].

Calculated rates of RuBP carboxylation (V_c), oxygenation (V_o) and ratio V_o/V_c are presented in Figs. 6A, 6B and 6C respectively. Both V_c and V_o were greater in sunflower than in tea under all light intensities. The V_c was higher in unshaded than shaded sunflower above $500 \mu\text{mol PAR m}^{-2} \text{s}^{-1}$, showing relatively greater carboxylation than oxygenation capacity. In contrast, tea had relatively more oxygenation than carboxylation capacity. This has large implications for photosynthetic efficiency and productivity of tea under shade.

CONCLUSIONS

Higher rates of A in sunflower than in tea were related to its larger capacity of excitation energy capture and electron transport leading to greater electron transport. Also, C_i was smaller in tea than sunflower, because of the lower g_s . Thus, there are several limitations to A in tea, as expected from analyses of 'shade' versus 'sun' plants (Boardman, 1977), and the impact of irradiances during growth on light saturated rates of A (Besford, 1986). Sunflower, is adapted to high light. In contrast, tea is shade adapted, with inherently small capacity for CO_2 assimilation. Tea must dissipate more of the captured light energy than sunflower and its ability to do so is affected by irradiance during leaf growth. As photosynthesis of tea improves under shade, optimizing light may increase productivity of tea.

ACKNOWLEDGMENTS

Authors wish to thank Mr. Simon Driscoll IACR-Rothamsted, Harpenden, UK for help in gas exchange measurements, Dr. (Mrs.) Dimah Habash and Dr. Alfred Keys for helpful discussions.

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