Tropical Agricultural Research Vol. 20: 376 – 387 (2008)

Impact of Long Term Shade on Physiological, Anatomical and Biochemical Changes in Tea (*Camellia sinensis* (L.) O. Kuntz)

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ABSTRACT. *This study examined physiological, anatomical and biochemical changes of mature tea when subject to long-term exposure to three different levels of shade, i.e. NS (receiving 100% incident photosynthetically active radiation [PAR]), MS (receiving 65% incident PAR) and HS (receiving 35% incident PAR). The changes in leaves were also examined at different depths of the tea canopy. On bright, clear days, NS leaves at the top of the canopy received PAR in excess of the requirement and hence showed signs of photoinhibition. MS leaves received desirable levels of PAR, therefore had the highest rates of photosynthesis (A) (12.2% higher than NS). HS leaves received much less PAR than the requirement, hence had the lowest rates of A. The MS plants also operated under favourable leaf temperature and had the highest stomatal conductance. The leaves inside the canopy received much lower radiation than the saturating intensities and resultantly had lower rates of photosynthesis. Radiation use efficiency was lowest in NS, which increased with shade, showing flexibility in adaptation to different light environments. Specific leaf weight was significantly higher in unshaded leaves exhibiting typical sun leaf characteristics. Similar characteristics were seen in terms of leaf and palisade layer thickness. The stomatal density and photosynthetic pigments did not significantly differ between treatments. Tea shows considerable flexibility in its adaptation and acclimation to different light environments as shown with physiological, anatomical and biochemical changes. Therefore this study clearly emphasizes the importance of regulation of shade in tea plantations.*

INTRODUCTION

Tea (*Camellia sinensis* (L.) O. Kuntze) is a plantation crop having a wide distribution extending from low elevations to levels exceeding 2000 m (Wijeratne *et al*., 2007). It is a shade loving plant which had originated in the forest under-story. Varying responses in terms of productivity under shade have been reported (Barua, 1969; Sakai, 1975; Rajkumar *et al*. 1999; Mohotti *et al*., 2000; Mohotti and Lawlor, 2002; Rajkumar *et al*., 2002; Karunaratne *et al,*. 2003; Mohotti, 2004; Wen-jin *et al*., 2004), leading to controversy over the need of shade in tea plantations. Tea shows comparatively lower photosynthetic rates than many other crops (Mohotti *et al*., 2000; De Costa *et al*., 2007). However, many recent reports on beneficial effects on the physiological aspects and yield suggest the requirement of shade in tea plantations. Barua and Gogoi (1979) found that the removal of shade caused a 50% drop of tea yield when compared to that of shaded tea plants in North East India. Barua (1969) reported that the yield of tea shoots under 35% light intensity was higher than

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that in plants grown with full sun. This is also supported by the findings of Mohotti and Lawlor (2002) and Karunaratne *et al*. (2003) where they reported that the net photosynthetic rate was significantly lower ($p<0.05$) in unshaded tea compared to that of shaded tea in higher elevations of Sri Lanka. This justifies further investigation on how different levels of shade influence net photosynthetic rates and related parameters of tea leaves.

Although tea plants grow to a height of 10-12 m in its natural habitat, in commercial cultivation, it is maintained as a bush with a closed canopy. Moreover, young leaves that are photosynthesizing, but acting as strong sinks to assimilate are harvested regularly along with the buds, significantly altering the physiology of the tea bush. Due to the nature in which the bush is managed, the leaves at the bottom of the canopy receive a very low intensity of light, which can also create undesirable effects on the physiology of the bush. Therefore, the changes in management of the bush can cause significant changes in the photosynthetic characteristics at leaf and canopy level.

In a tea canopy, the leaves present in the upper strata of the canopy receive full sunlight, and hence behave as sun leaves. The leaves present in the lower strata of the canopy receive filtered light, and hence behave as the shade leaves. However, the photosynthetic characterization of leaves in different canopy strata is not well understood in the case of tea although it has been studied in other tropical trees such as *Theobroma cacao* (Miyaji *et al*., 1997). For enhancing canopy photosynthesis, which is mandatory for further yield improvement, knowledge on physiological and anatomical variations of leaves is important. Such information will help to identify superior traits that could be incorporated in future genetic improvement programmes, and also to develop proper canopy management strategies. In this regard, it is important to find out how the photosynthetic characterization of leaves change with the canopy position. Therefore, the objectives of this study were to examine the photosynthetic behavior and some related physiological, anatomical and biochemical parameters of mature tea bushes under different levels of shade and also to study the same at different heights of the mature tea canopy.

MATERIALS AND METHODS

Experimental site

The experiment was carried out in field No. 8 at St Coombs Estate, Tea Research Institute, Talawakele, Sri Lanka (Latitude 6 ^{0} 55 ’ N, longitude 80 ^{0} 40 ’ E and altitude 1382 amsl) during the period June 2007 - January 2008. The long term mean annual rainfall, minimum and maximum temperatures in the region are 2250 mm, 14.2 ºC and 22.8 ºC respectively.

Treatments

The measurements were made in an on-going, long term shade experiment on mature tea bushes (cultivar TRI 2025), adapted to different shade levels for more than three years.
The three levels of shade tested were,

1. Artificial shade, providing approximately 35% of incident photosynthetically active radiation (PAR) (HS)

2. Artificial shade, providing approximately 65% of incident PAR (MS)
3. Unshaded treatment receiving 100% of incident PAR (NS)

Each shade treatment consisted of five replicates with each experimental plot consisting of approximately 20 bushes. Shade was provided by green nylon netting, which was mounted on a metal frame, leaving about 1 m clearance from top of the tea canopy.

Measurements

Three bushes were selected from each replicate (15 bushes per treatment). At a particular canopy position, 5 leaves were sampled per bush.

Canopy depth

The depth of the canopy (D) of each treatment was measured as depth from the top most leaf to the bottom-most leaf in the canopy, using a meter ruler. Five measurements at different places in the canopy were taken in each bush.

Photosynthesis

Mature healthy leaves of similar physiological maturity having similarly grown axillary buds were selected from two heights in the canopy, i.e., top of the canopy (top) and 15 cm below the canopy (inside) for the measurements. To overcome site heterogeneity leaves were sampled from randomly selected bushes, which were well dispersed in each experimental plot.

A portable infrared gas analyzer (model: LI-COR 6200, Li-Cor Inc., USA) with a quarter liter leaf chamber was used to determine the net photosynthetic rate (A), stomatal conductance (G_s), leaf temperature (T_L) and photosynthetically active radiation (PAR) on bright, clear days as well as overcast days, from 10 am to 12 noon each day. The measurements were repeated several times during the experimental period. Radiation use efficiency (RUE) was calculated as the net photosynthesis rate per unit of PAR.

Pigment concentration

Leaves that were used for photosynthesis measurements were harvested for pigment analysis. Chlorophyll a, b and total carotenoide pigments were extracted using 80% acetone, measured using spectrophotometer (model: GBC UV/VIS 911A) against a blank and the respective concentrations were calculated by using the following equations (Lichtenthaler and Welburn, 1983).

$$\text{Chlorophyll a (Ca) } \mu g/ml = 12.21 \times A_{663} - 2.81 \times A_{646}$$

$$\text{Chlorophyll b (Cb) } \mu g/ml = 20.13 \times A_{646} - 5.03 \times A_{663}$$

$$\text{Total Carotenoides (Cc) } \mu g/ml = (1000 \times A_{470} - 3.27 \times Ca - 104 \times Cb) / 229$$

where A_{663}, A_{646} and A_{663} are the solution absorbances at 470 nm, 646 nm and 663 nm respectively.

Leaf anatomy

Leaf cross sections were made by using free hand sections and were mounted on glass slides. Total thickness and palisade layer thickness were measured using a light microscope

(Model: Leica 020-518.500 DM/LS 11/01, Germany) with an eye piece graticule and a stage micrometer (LX # 68010-21, 01A21001, Graticules Ltd., England).

Specific leaf weight (gm^{-2}) was measured using leaf discs from the middle of the leaf, avoiding the mid-rib and major veins, and weighing using a four decimal electronic balance (Model: Denver M-220, USA).

Stomatal impressions were taken by applying nail varnish in the lower surface of the leaves similar to that used for photosynthesis measurements. It was then peeled off and mounted on a glass slide. Stomatal density was calculated as follows by using the stomatal impressions by counting the number of stomata of a known leaf area under the light microscope (Model: Leica 020-518.500 DM/LS 11/01, Germany).

Stomatal density = Number of Stomata / Area

Data analysis

Data were analyzed using General Linear Model in SAS statistical package and the means were separated using Duncan's Multiple Range Test.

RESULTS AND DISCUSSION

Photosynthetic rates and related parameters

The topmost leaves (top) in the canopy received full sunlight and leaves 15 cm below the canopy (inside) received only 8-12% of the PAR received by the topmost leaves (Table 1). On bright, clear days, the 'top' leaves in the unshaded (NS) treatment received about 1800-1900 $\mu mol\ m^{-2}\ s^{-1}$ PAR, but 'inside' leaves received only 150-170 $\mu mol\ m^{-2}\ s^{-1}$ PAR. The 'top' leaves in MS treatment received about 1000-1100 $\mu mol\ m^{-2}\ s^{-1}$ PAR, while 'inside' leaves received only about 110-120 $\mu mol\ m^{-2}\ s^{-1}$ PAR. The 'top' leaves in HS treatment received about 420-440 $\mu mol\ m^{-2}\ s^{-1}$ PAR, but 'inside' leaves received only about 50-70 $\mu mol\ m^{-2}\ s^{-1}$ PAR.

The situation of shaded leaves was further aggravated on overcast days. The unshaded leaves on top of the canopy received around 180 $\mu mol\ m^{-2}\ s^{-1}$ PAR, while leaves inside the canopy received around 44 $\mu mol\ m^{-2}\ s^{-1}$ PAR (Table 2). There was no significant difference in the PAR received by leaves on top of the canopy between different shade treatments, but the leaves inside the canopy of the HS treatment received only around 20 $\mu mol\ m^{-2}\ s^{-1}$of PAR.

In this experiment a light response curve was not done, but the results suggest that the light compensation point of the leaves inside the canopy of HS plants could be even lower than 20 $\mu mol\ m^{-2}\ s^{-1}$ PAR.

Table 1. Comparison of photosynthetically active radiation (PAR) distribution, leaf photosynthetic rates (A), radiation use efficiencies (RUE), leaf temperature (T_L), stomatal conductance (G_s) and canopy depth (D) in of tea under different levels of shade and canopy positions on bright clear days

Shade level	Leaf position	PAR μmol m^{-2} s^{-1}	A μmol m^{-2} s^{-1}	RUE *	T_L °C	G_s μmol m^{-2} s^{-1}	D cm
No Shade	Top	1836	7.9	0.004	31.00	0.1606	33.6
	Inside	158	3.7	0.062	29.46	0.1077	
Medium Shade	Top	1089	8.8	0.008	30.51	0.2603	23.1
	Inside	112	2.7	0.096	30.03	0.1774	
High Shade	Top	419	7.6	0.024	27.98	0.2290	18.7
	Inside	50	2.2	0.194	27.57	0.1390	
p (TRT)		<0.01	0.5850	0.359	<0.01	<0.01	<0.01
p (HT)		<0.01	<0.01	.0489	<0.01	<0.01	

* units of RUE = μmol m^{-2} s^{-1} CO_2/μmol m^{-2} s^{-1}PAR, TRT = Shade treatment, HT = Leaf position in the canopy

The rate of photosynthesis was not significantly different between shade treatments, but significantly different ($P<0.01$) between different depths of the canopy (Table 1). The differences in rates of photosynthesis were statistically significant on overcast days, both between treatments and different depths of the canopy (Table 2). The rate of photosynthesis of leaves on top of the canopy of NS and MS treatments were not significantly different, but that of HS was significantly lower. These results also support the findings of Mohotti and Lawlor (2002), Rajkumar *et al.* (2002) and Karunarathne *et al.* (2003). Rajkumar *et al.* (1999) found that under South Indian conditions, tea plants grown under MS conditions showed a 12.2% increase in the rate of photosynthesis than that of NS conditions under full sunlight conditions.

On overcast days too, although the PAR was quite low, all treatments had positive values of photosynthesis (Table 2). When photosynthesis values were plotted against PAR, at all levels of shaded and unshaded treatments the differences in the treatments were clearly evident (Figures 1 and 2). The MS leaves on top of the canopy showed the highest rate of photosynthesis, between 900-1400 μmol m^{-2} s^{-1} PAR. The NS leaves on top of the canopy, which received more than 1800 μmol m^{-2} s^{-1} PAR showed a photoinhibition and the rate of photosynthesis was lower. Leaves in other treatments did not show saturated rates of photosynthesis. On overcast days, all the leaves showed photosynthesis in the unsaturated range of PAR (Figure 2).

Light penetration was related to canopy depth of the tea bushes (Table 1). The bushes receiving full sunlight had deeper canopies than shaded bushes. The differences in the canopy depths were highly significant (P<0.01). The NS plants had the deepest canopy (33.6 cm), followed by MS plants (23.1 cm) and HS plants (18.7 cm).

Table 2. Comparison of distribution of photosynthetically active radiation (PAR), leaf photosynthetic rates (A), radiation use efficiencies (RUE), leaf temperature (T_L) and stomatal conductance (G_s) in tea under different levels of shade and canopy positions on overcast days

Shade level	Leaf position	PAR µmol m^{-2} s^{-1}	A µmol m^{-2} s^{-1}	RUE *	T_L (ºC)	G_s µmol m^{-2} s^{-1}
No Shade	Top	179.5	9.6	0.024	25.5	0.3285
	Inside	43.6	3.5	0.073	23.9	0.4206
Medium-Shade	Top	170.2	7.3	0.045	24.3	0.8643
	Inside	39.9	2.0	0.080	24.3	0.5334
High Shade	Top	177.3	7.1	0.041	23.4	0.6918
	Inside	20.0	1.6	0.125	24.7	0.2985
p (TRT)		<0.01	0.026	0.211	0.023	<0.01
p (HT)		<0.01	<0.01	<0.01	0.909	<0.01

* units of RUE = µmol m^{-2} s^{-1} CO_2/µmol m^{-2} s^{-1}PAR, TRT = Shade treatment, HT = Leaf position in the canopy

The radiation use efficiency (RUE) was highest in the MS plants (Table 1), followed by HS and NS. RUE increased significantly with the depth of the canopy. It was higher on overcast days (Table 2) than on clear days. The efficiency of radiation utilization is known to be higher under low light intensities than under higher intensities (Mohotti *et al*., 2000). In this experiment, the highest RUE in tea is shown in the MS treatment. The benefits of shade are also shown with the leaf temperature measurements (Tables 1 and 2), which were statistically significant between the shade treatments as well as the depth. The NS plants had significantly higher leaf temperature, followed by MS and HS treatments. Even on overcast days, the differences in leaf temperature among the shade treatments were significantly different, but there was no difference between different depths. The stomatal conductances were significantly different between the treatments (P<0.01) and canopy depths (P<0.01) (Tables 1 and 2). They were highest with the MS leaves on top of the canopy and lowest with the NS leaves inside the canopy on clear days. On overcast days, they were highest with the MS leaves on top of the canopy and lowest with the HS leaves inside the canopy.

Photosynthetic light saturation in tea is known to occur around 600 – 800 µmol m^{-2} s^{-1} PAR (Mohotti, 2004). Photoinhibition is known to occur at PAR above 1500 µmol m^{-2} s^{-1} (Smith *et al*., 1993; Mohotti and Lawlor, 2002; Karunaratne *et al*., 2003; De Costa *et al*., 2007). The light compensation point (LCP) in tea is around 50-60 µmol m^{-2} s^{-1} PAR. The LCP is known to decrease with shading. Due to the above, on clear days, the unshaded leaves on top of the canopy had received light intensities in excess of required PAR, whilst the leaves inside the canopy had received PAR, which is far below the saturating intensities. This shows that the leaves in the top few centimeter depths would be contributing the most by net photosynthesis for productivity. The leaves inside the canopy of the HS treatment received PAR which is just above the light compensation point. However, all the leaves under both clear and overcast conditions showed positive rates of photosynthesis, indicating the flexibility of photosynthetic apparatus of tea leaves under changing light environments. Further, the trees have the ability to reject leaves which are not contributing to growth. In addition, with regard to photosynthesis, the tea bush seems to be more adaptable under low light intensities than under high light intensities. The leaves inside the canopy of the HS treatment received PAR as low as only 20 µmol m^{-2} s^{-1}, but had rates of photosynthesis around 1.6 µmol m^{-2} s^{-1} suggesting that even at very low light intensities, they do not become parasitic. This agrees with earlier observations, where the top 10 cm of the tea canopy is known to contribute mostly towards productivity of the tea bush (Hadfield, 1975b; Rahman, 1988). However, the HS canopy depth was about 18 cm, indicating the leaves at this depth would be receiving PAR around the light compensation point.

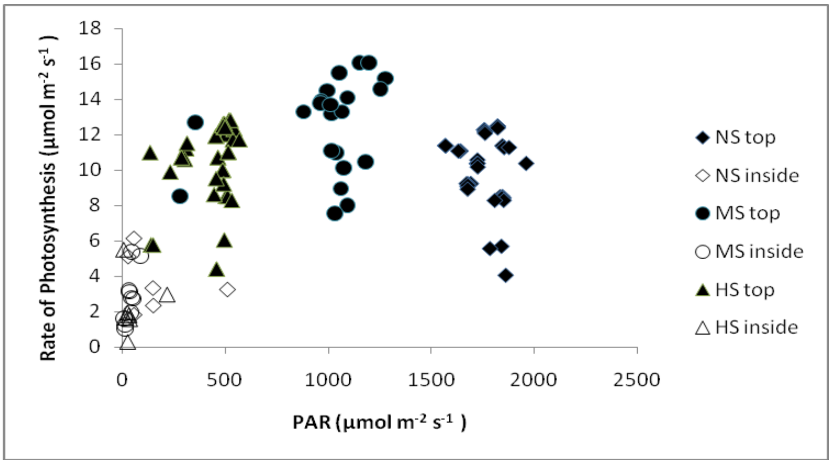

Figure 1. Rate of photosynthesis under different levels of shade on a bright clear day

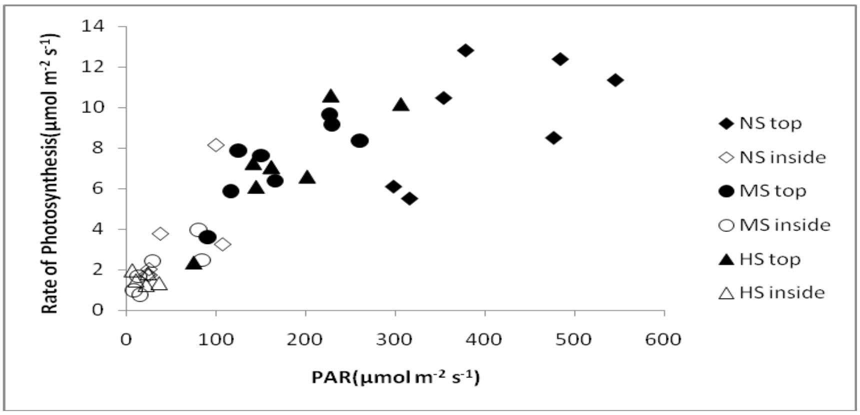

Figure 2. Rate of photosynthesis under different levels of shade on an overcast day

The high light intensity received by leaves on top of the canopy in NS treatment increases its leaf temperature significantly, which may ultimately reduce the stomatal conductance through stomatal closure. The rate of photosynthesis of tea leaves is known to decline at leaf temperatures exceeding 30 ºC (Hadfield, 1975a). Such high leaf temperatures also may contribute to lowered rates of photosynthesis observed in leaves on top of the canopy of NS treatment. Leaf temperatures as high as 33 ºC have been reported in upcountry conditions of Sri Lanka previously (Mohotti and Lawlor, 2002). The favourable light intensity, leaf temperature and resultant high stomatal conductance prevailing in the MS treatment would have resulted in the highest rate of photosynthesis in the leaves of the MS canopy. These findings are in agreement with the findings of the Hadfield (1975a), Barman *et al*. (1993) and De Costa *et al*. (2007). However the stomatal index calculated by the stomatal impressions was not significantly different amongst treatments and it may be a character determined by the genetic component rather than the environmental component.

Anatomical changes

Tea leaves grown under different light intensities showed significant changes in terms of the anatomical features (Table 3).

Table 3. Effect of shade and canopy position on the anatomy of tea leaves.

Shade level	Leaf position	Leaf thickness (mm)	Specific leaf weight ($g\ cm^{-2}$)	Palisade layer thickness (mm)	Stomatal Density (No./ mm^2)
No Shade	Top	0.314	0.027	0.166	173
	Inside	0.276	0.021	0.15	158
Medium Shade	Top	0.396	0.027	0.15	150
	Inside	0.28	0.017	0.13	160
High Shade	Top	0.30	0.020	0.144	157
	Inside	0.258	0.018	0.138	140
CV		8.77	15.06	14.84	22.7
p (TRT)		<0.01	0.0524	0.1350	0.91
p (HT)		<0.01	<0.01	0.1005	

TRT = Shade treatment, HT = Leaf position in the canopy

The shaded tea leaves and leaves inside the canopy of both shaded and unshaded treatments showed typical shade leaf characteristics. The leaf thickness decreased significantly with increased shade level and canopy depth. Shade leaves are known to have thinner leaves in general (Boardman, 1977). Further it is known that they lack a well organized palisade layer and the mesophyll cells are primarily spongy, with much more air spaces than found in sun-developed leaves (Pearcy, 1998). As a consequence, shade-developed leaves are generally much thinner with a lower mass per unit area. These were evident in tea leaves in this experiment too. The specific leaf weight decreased with increased shade and it was significantly higher (CV = 15.06, P <0.01) in leaves on top of the canopy than in leaves inside the canopy in all three treatments. A similar trend was observed in the palisade layer thickness as shown in the Table 3, which tended to decrease with the increased shade and depth of the canopy. Similar anatomical differences have been observed with tea (Wen-jin *et al*., 2004) and other species such as Pear (Xie and Luo, 2003), conifers (Richardson *et al*., 2000), and ivy (Bauer and Bauer, 1980).

The differences in leaf structure of sun and shade developed leaves have important consequences for light gradients and light absorption within leaves (Pearcy, 1998). Spongy mesophyll is quite effective in scattering light within the leaf, making light absorption more effective. The palisade function in light piping properties for direct beam sunlight is not needed in diffused light in shade environments. Therefore the above mentioned anatomical changes in tea leaves under shade conditions favour light absorption in such environments.

In contrast to the stomatal conductance (Tables 1 and 2), the stomatal index (Table 3) did not show a significant difference among the shade treatments or leaf position in the canopy. The stomatal conductance was the highest with MS leaves on top of the canopy and the lowest with NS leaves. These results may indicate that the number of stomata per unit area is not a factor that can be changed due to environmental conditions. However, the number of opened stomata and the stomatal pore size might have shown adaptations to the light environment.

Pigment analysis

None of the photosynthetic pigments analyzed, namely chlorophyll a, chlorophyll b and total carotenoides showed a significant difference amongst the shade treatments or leaf position in the canopy (Table 4). However, there was a tendency for the pigments to be high in MS leaves on top of the canopy than in other leaves. Chlorophyll a content was always higher in leaves inside the canopy of all treatments.

Shade-acclimated leaves are known to contain more chlorophyll per unit mass than sun leaves (Pearcy, 1998). This occurs due to increased allocation of resources to light harvesting functions as compared to those involved in electron transport and CO_2 fixation capacity. Mohotti (1998) has reported increased chlorophyll a, b contents and unchanged Chlorophyll a: Chlorophyll b ratio in young tea with increased shading. However, in this study, such results were not evident: There was a general tendency for the chlorophyll contents to increase with shade, but the differences were not statistically significant. The total carotenoids also tended to increase, but changes in total carotenoids did not show a clear pattern.

CONCLUSIONS

The present study generated a considerable amount of important information on the effect of shade on the photosynthetic rates, anatomy and pigment concentration in tea leaves.

Overall results clearly showed that medium shade favors leaf photosynthesis compared to NS and HS. Light saturation of leaves on top of the canopies of MS were approximately 34% lower than HS while having even 11% more rate of photosynthesis in MS. These results clearly indicate the importance of maintaining medium shade levels for tea, in terms of physiological responses governing the economic performances of the crop.

Table 4. Photosynthetic pigment analysis in leaves under different shade treatments and canopy depths. Chlorophyll a (Ca) and Chlorophyll b (Cb) are expressed as µg pigments per unit fresh weight of leaves.

Shade level	Leaf position	Chlorophyll a (µg/ g)	Chlorophyll b (µg/ g)	Total chlorophyll (µg/ g)	Chlorophyll a: chlorophyll b Ratio	Total Carotenoids (µg/ cm^2 LA)
No Shade	Top	1309	511.7	1820.6	2.56	317.03
	Inside	1668	535.2	2202.8	2.66	335.34
Medium Shade	Top	1354	470.1	1824.5	2.55	261.25
	Inside	2112	899.6	3011.7	2.35	432.06
High Shade	Top	1898	839.8	2738.1	2.36	345.38
	Inside	1676	608.2	2284.5	2.76	368.79
CV		20.36	28.26	25.07	8.79	16.50
p (TRT)		0.239	0.235	0.7045	0.4342	0.5779
p (HT)		0.064	0.381	0.5145	0.5044	0.0415

LA = Leaf Area, TRT = Shade treatment, HT = Leaf position in the canopy

Maintaining regulated shade is beneficial in terms of reducing leaf temperatures and minimizing the effects of photoinhibition and thereby maximizing bush health of tea plants grown in warm tropical environments found in Sri Lanka. Even the very bottom maintenance foliage in tea canopy is not parasitic and it also contributes in terms of net photosynthesis to the productivity of tea plants. In the vertical profile of a tea canopy, the top leaves behave as sun leaves and the leaves below behave as shade leaves by acclimatization to the prevailing light environment, by means of physiological, anatomical and biochemical changes.

ACKNOWLEDGEMENTS

The authors wish to acknowledge the staff of Plant Physiology Division of the Tea Research Institute of Sri Lanka, for help in numerous ways.

REFERENCES

Barman, T.S., Baruah, U. and Sarma, A.K. (1993). Effect of light and shade on diurnal variation of photosynthesis, stomatal conductance and transpiration rate in tea. Proc. Int. Sym. Tea Tech., India. Tea Res. Asso.: 208-218.

Bauer, H. and Bauer, U. (1980). Photosynthesis in leaves of juvenile and adult phase of ivy (*Hedera helix*). Physiologia Plantarum 49: 366-372.

Barua, D.N. (1969). Light as a factor in metabolism of the tea plant. pp. 306-322. In: Luckwill, L.C. and C.V. Cutting (Eds). Physiology of Tree crops. Academic press, NewYork.

Barua, D.N. and Gogoi, B.N. (1979). Effects of Shade Removal. Two and a Bud 26(1): 40-42.

Boardman, N.K. (1977). Comparative photosynthesis of sun and shade plants. Ann. Rev. Plant Physiol. 28: 355-377.

De Costa, W.A.J.M., Mohotti, A.J. and Wijeratne, M.A. (2007). Ecophysiology of tea. Braz. J. Plant Physiol. 19(4): 299-332.

Hadfield, W. (1975a). The effect of high temperatures on some aspects of the physiology and cultivation of the tea bush, in North India. pp. 477-495. In: Evans, G. C., Bainbridge, R. and Rackham, O. (Eds). Light as an ecological factor, II, The 16th Sym. Br. Ecol. Soc., Blackwell Scientific Publications, Oxford.

Hadfield, W. (1975b). Shade in North–East India Tea Plantations, II Foliar Illumination and canopy characteristics. Two and a Bud 11(1): 102-122.

Karunaratne, P.M.A.S., Mohotti, A.J., Nissanka, S.P., and Gunasinghe, W.A.D.S.K. (2003). Effect of shade in Minimizing Photoinhibition of Photosynthesis of High Grown Tea (*Camellia sinensis* (L.) O. Kuntz) in Sri Lanka. Trop. Agric. Res. 15: 133-143.

Lichtenthaler, H.K. and Welburn, A.R. (1983). Measuring Chlorophyll and Anthocyanin Concentration. In: http://employees.csbsju.edu/SSAUPE/biol327/Lab/photosyn/chlorophyll_quant.htm (accessed on 20.09.2007).

Mohotti, A.J. (1998). Effect of irradiance and N nutrition on photosynthesis of tea (*Camellia sinensis* (L.) O. Kuntz) in comparison with sunflower (*Helianthus annus* L.). Ph.D. thesis, University of Reading, Reading.

Mohotti, A.J., Dennett, M.D. and Lawlor, D.W. (2000). Electron Transport as a Limitation to Photosynthesis of Tea (*Camellia sinensis* (L.) O. Kuntz) Trop. Agric. Res. 12: 1-10.

Mohotti, A.J. and Lawlor, D.W. (2002). Diurnal variation of photosynthesis and photoinhibition in tea: Effects of iradiance and nitrogen supply during growth in the field. J. Exp. Bot. 53(367): 313-322.

Mohotti, A.J. (2004). Shade in tea: Is it beneficial? S. L. J. Tea Sci. 69: 27-39.

Miyaji, K.I., Silva, W.S. and Alvim, P.T. (1997). Productivity of leaves of a tropical tree, *Thebroma cacao*, grown under shading, in relation to leaf age and light conditions within the canopy. Tree Phytol. 137: 463-472.

Pearcy, R.W. (1998). Acclimation to sun and shade. pp. 251-263. In: Raghavendra, A.S. (Ed.). Photosynthesis: A Comprehensive Treatise, Cambridge University Press, UK.

Rahman, F. (1988). Physiology of the Tea Bush. Two and a Bud 35: 1-14.

Rajkumar, R., Marimuthu, S. and Muraleedharan, N. (1999). Tea leaf photosynthesis in relation to light. J. plant. crops 27(2): 93-98.

Rajkumar, R., Marimuthu, S. and Muraleedharan, N. (2002). Photosynthetic Efficiency of Sun and Shade Grown Tea Plants. S. L. J. Tea Sci. 67(1/2): 67-75.

Richardson, A.D., Berlyn, G.P., Ashton, P.M.S., Thadani, R. and Cameron, I.R. (2000). Foliar plasticity of hybrid spruce in relation to crown position and stand age. Can. J. Bot. 78: 305-317.

Sakai, S. (1975). Recent studies and problems of photosynthesis of tea plant. Jap. Agric. Res. Q. 9(2): 101-106.

Smith, B.G., Stephens, W., Burgess, P.J. and Carr, M.K.V. (1993) Effect of light, temperature, irrigation and fertilizer on photosynthetic rate in tea (*Camellia Sinensis* L.). Exp. Agric. 29: 291-306.

Wen-jin, Z., Yue-rong, L., Fang-zhou, Z., Chang-song, C., Yin-gen, Z., Rong-Bing, C. and Bo-qi, W. (2004). Effects on the yield and quality of Oolong tea by covering with shading net. J. Tea Sci. 24(4): 276-282.

Wijeratne, M.A., Anandacoomaraswamy, A., Amarathunga, M.K.S.L.D., Ratnasiri, J., Basnayake, B.R.S.B. and Kalra, N. (2007). Assessment of impact of climate change on productivity of tea (*Camellia sinensis* L.) plantations in Sri Lanka. J. Natl. Sci. Found. S. L. 35(2): 119-126.

Xie, S. and Luo, X. (2003). Effect of leaf position and age on anatomical structure, photosynthesis, stomatal conductance and transpiration of Asian pear. Bot. Bull. Academia Sinica 44: 297-303.