ISSN 0853 - 7240 Biologi, Vol. 2, No. 8, Desember 1999

EFFECTS OF SUPPLEMENTARY UV-B RADIATION ON PEA (*Pisum sativum* L. cv. Massey Gem) LEAVES PHOTOSYNTHESIS

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ABSTRACT

Maryani and J.T. Wiskich. 1999. Effects of supplementary UV-B radiation on pea (*Pisum sativum* L. cv. Massey Gem) leaves photosynthesis. *Biologi* 2(8): 397-410.

Pea plants subjected to UV-B radiation decreased their chlorophyll content. The rates of photosynthesis measured in intact leaves and leaf slices also changed under UV-B treatment. The intact leaves taken from high UV-B plants showed a rapid decrease in the net photosynthesis to about 69%, while in natural and low UV-B treatment was about 35%. These results may be related to their decrease of stomatal conductivity and chlorophyll content.

The rates of photosynthesis in leaf slices also decreased under UV-B treatment. When expressed on both leaf weight and chlorophyll basis, the activity of CO_2-dependent O_2 evolution. Rates of O_2 evolution in chloroplasts from UV-B treated leaves were lower than controls. As UV-B has damaged the structure of chloroplasts, the reduction of photosynthesis rates could be associated to the damage thylakoid and envelope membrane. It was found that UV-B treatment also inhibited electron transport rates when artificial acceptors were applied with grana solution (broken chloroplasts).

Key words: *UV-B radiation, peas, photosynthesis*

INTISARI

Maryani and J.T. Wiskich. 1999. Pengaruh sinar UV-B terhadap fotosintesis pada daun kacang ercis (*Pisum sativum* L. cv. Massey Gem). *Biologi* 2 (8): 397-410.

Radiasi ultraviolet-B menurunkan kandungan klorofil pada daun kacang ercis. Laju fotosintesis yang diukur menggunakan daun utuh dan irisan daun juga mengalami perubahan. Daun yang diambil dari perlakuanUV-B dosis tinggi memperlihatkan penurunan laju fotosintesisnya sampai 69%. Sementara pada perlakuan dengan UV-B alami dan UV-B dosis rendah, penurunan ini berkisar 35%. Penurunan aktivitas ini

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and irreversible damage to the reaction center subunits. In particular, the D1 protein becomes degraded with the formation of photochemically inactive PS II center which convert excitation energy to heat (Schnettger *et al.*, 1994). UV-B light damaged chloroplast structure and this could result in electron transport inhibition and structural components of PS II destruction (Maryani & Wiskich, 1995).

A number of studies have also investigated the role of UV-B light in reducing the photosynthetic activity, however, only a few experiments used leaf slices and/or isolated chloroplasts. Therefore, oxygen evolution and electron transport activity was investigated in leaf slices and isolated chloroplast from UV-B treated plants.

MATERIAL AND METHODS

Plant material, cultural conditions, and UV-B treatment

Plant material, cultural conditions, and UV-B treatment were carried out exactly as described in Maryani and Wiskich (1995).

Chlorophyll determination

The chlorophyll content was determined using method as described by Porra (1989).

Net photosynthesis of intact leaf

The net photosynthesis and stomatal aperture in leaves was estimated using a Li-6200 IRGA (Infra Red Gas Analyzer) consisting of a Portable Photosynthesis system. Measurements were performed at light intensity around 1850 μ mol photons m^{-2} s^{-1}, CO_2 concentration inside the chamber was in the range of approximately 350 – 400 ppm and air temperature was 30–34°C. Third leaf pairs were used in these measurements.

Determination of O_2 evolution in leaf slices

The third leaf pairs were washed with dd-H_2O and their midribs were removed. The halves of the leaflets were laid on top of each other in a Petri dish containing 0.5 mM $CaSO_4$ and transversely sliced into 1 mm wide strips with a brand-new razor blade. The rate of O_2 evolution was measured polarographycally at 25°C in 4 ml of 10 mM phosphate buffer solution (pH 6.5). Before adding the slices, the buffer solution was bubbled with N_2 to reduce O_2 concentration to 20% saturation. $NaHCO_3$ (5 mM) was added to the reaction medium and followed by the leaf slices. The leaf slices were illuminated using a

ISSN 0853 - 7240

150 W projector lamp (Rondette, 1500 RF, Hanimex, Ireland). The intensity of light reaching the reaction vessel was about 200 $\mu\varepsilon m^{-2}s^{-1}$ PAR as measured with a light meter (Li-COR, Li-1000, Q 11648). Oxygen evolution was monitored until the O_2 concentration reached approximately 200 mM. The rate of O_2 evolution was expressed both on a fresh leaf weight basis (nmol O_2 evolved g^{-1} fwt $s.^{-1}$) and on chlorophyll content (nmol O_2 evolved mg^{-1} chl. $s.^{-1}$).

Preparation of chloroplasts

The procedure was similar to that described by Robinson and Wiskich (1977). Pea leaves (60-80 g) were ground in a Polytron blender (Kinematica, GmbH, Model K, Krie-Luzen, Switzerland) with a probe PTA-35/2 (setting # 3-4) for 2 to 3 sec. in 200 mL of ice-cold medium containing 400 mM sorbitol, 2 mM EDTA, 1 mM $MgCl_2$, 1 mM $MnCl_2$, 20 mM NaCl, 0.5 mM NaH_2PO_4, 2 mM isoascorbate, 50 mM 4-morpholineethanesulfonic acid (MES), and 0.4 % bovin serum albumin (BSA) adjusted to pH 6.2. The brei was squeezed through a double layer of miracloth containing a layer of cotton wool, and the filtrate was centrifuged at 2000 g for 30 sec in an M.S.E. Super Minor centrifuge. The crude chloroplasts pellet was resuspended in 6-8 mL of was medium containing 400 mM sorbitol, 2 mM EDTA, 1 mM $MgCl_2$, 1 mM $MnCl_2$, 20 mM NaCl, 0.5 mM NaH_2PO_4, 50 mM 4-(2-hydroxyethyl)-1-piperazine-ethanesulphonic acid (HEPES), and 0.4 % BSA adjusted to pH 6.4.

For intact cloroplasts, this resuspended pellet was loaded onto a 4 mL resuspension medium consisting of 40% Percoll and recentrifuged at 2500 g for 1 min. The pellet was resuspended in 1 mL of wash medium using a smooth brush. All procedures were carried out at 2°C using chilled solutions and apparatus.

For grana preparation, the pellet of intact chloroplasts above was resuspended in 50 mL of a medium containing 100 mM sorbitol and 5 mM $MgCl_2$ and centrifuged at 4000 g for 5 min. The final pellet was resuspended in 2-3 mL resuspending medium consisting of 100 mM sorbitol, 5 mM $MgCl_2$, and 0.5% BSA.

CO2-dependent O2 evolution measurement

Non-cyclic electron flow was measured in an O_2 electrode. The vessel was illuminated with a 150 W light projector giving a light intensity of 200 $\mu\varepsilon$ m^{-2} s^{-1} at the center of the vessel. The vessel was maintained at 25°C. A volume of grana contained 30-50 mg chlorophyll was added to 3 mL reaction medium consisting of 100 mM sorbitol, 10 mM HEPES, 5 mM $MgCl_2$, 10 mM NaH_2PO_4, 1.3 mM FeCN all at pH 7.6. Before adding the grana, the assay medium was bubbled with nitrogen to reduce the CO_2 concentration to about 20% saturation. The effects of 5 mM NH_4Cl and 1.7 mM nigericin were studied. The rate of electron flow was expressed in units of nmol O_2 evolved mg^{-1} chl. min^{-1}.

Pseudocyclic electron flow

Pseudocyclic electron flow was measured in an electrode at 25°C and illuminated with a 150 W light projector giving a light intensity of 200 $\mu\varepsilon m^{-2}$ s^{-1} at the center of the vessel. A volume of grana (equivalent to 30-50 mg chlorophyll was added to 3 mL reaction medium consisting of 100 mM sorbitol, 10 mM HEPES, 5 mM $MgCl_2$, 10 mM NaH_2PO_4, 0.3 mM methylviologen, 3.3 mM FeCN at pH 7.6. The effect of 5 mM NH_4Cl was studied.

RESULTS

Chlorophyll content

There was a tendency to partial reduction under UV-B treatment (low and high UV-B light on total chlorophyll content (Table 1).

The total chlorophyll content per unit area in low UV-B was decreased almost 10% and 25%, while in high UV-B, reductions were 12% and 32% at 8 and 12 days after

Table 1. Chlorophyll content in leaves as a function of the duration of the UV-B treatment. Each value is the mean from replications. Standard errors of the mean ranged from 0.0001-0.03 (for Chl. *a*) and 0.001-0.02 (for Chl. *b*).

Treatment	Chloropyll content ($\mu g\ mm^{-2}$)								
	Chl. *a*			Chl. *b*			Chl *a* dan *b*		
	Days after treatment								
	4	8	12	4	8	12	4	8	12
Control (Zero UV-B)	0.40	0.39	0.32	0.11	0.12	0.13	0.51	0.51	0.45
Natural UV-B	0.41	0.38	0.32	0.12	0.12	0.11	0.53	0.49	0.40
Low UV-B	0.39	0.35	0.24	0.12	0.11	0.10	0.51	0.46	0.34
High UV-B	0.37	0.33	0.23	0.10	0.12	0.10	0.47	0.45	0.31

treatment respectively. Chlorophyll a (Chl. *a*) declined to a greater extent than chlorophyll b (Chl. *b*), the later seems to be constant under UV-B treatment.

Net photosynthesis of intact leaf

Table 2 shows that UV-B radiation tended to reduce the rate of net photosynthesis of intact leaves. The magnitude of photosynthetic inhibition was considerably greater in high UV-B treated leaves (70%) with smaller inhibition (35%) being observed under either natural or low UV-B treatment.

The changes in stomatal conductivity of intact leaves are also shown. In all UV-B treated leaves, there were rapid and similar reduction in stomatal conductivity by 30%. The internal CO_2 concentration, however, was found to be slightly enhanced under high UV-B (11% increase), but was unchanged in the other treatments.

Oxygen evolution of leaf slices

In general, it was found that oxygen evolution tended to decrease with age (Table 3). Control leaf slices showed a higher rate of oxygen evolution than did treated leaves. Natural and low UV-B plants displayed a similar photosynthetic activity, but lower than control, and with no apparent change in the degree of inhibition relative to control over the period of irradiation. In contrast, high UV-b treatment caused a rapid decrease (40%) in oxygen evolution, which was reduced further as the period of radiation increased.

Table 2. Effect of UV-B radiation on the net photosynthesis, CO_2 concentration and stomatal conductivity of intact pea leaves after 4 days of exposure. Values are means of 6 replicates from at least 3 individual plant leaves.

Treatment	Net photosynthesis (μmol CO_2 $m^{-2}sec^{-1}$)	Stomatal conductivity (mol $H2O$ $m^{-2}sec^{-1}$)	Internal CO_2 concentration (ppm)
Control (Zero UV-B)	0.75 ± 0.11 (100)	0.013 ± 0.003 (100)	272 ± 2.5 (100)
Natural UV-B	0.49 ± 0.16 (65)	0.01 ± 0.002 (77)	277 ± 16 (102)
Low UV-B	0.47 ± 0.06 (63)	0.009 ± 0.001 (70)	266 ± 23 (98)
High UV-B	0.23 ± 0.08 (31)	0.009 ± 0.002 (70)	303 ± 23 (111)

Note : Numbers in brackets indicate the percentage (%) rates of the control (Zero UV-B)

ISSN 0853 - 7240

Table 3. The rate of oxygen evolution from leaf slices on fresh weight basis as a function of days of treatment. Values are means of 8 replications from at least 2 independent experiments.

Treatment	Oxygen evolution (nmol O_2 $g^{-1}fwt^{-1}$)		
	4 days	8 days	16 days
Control (Zero UV-B)	3.9 ± 0.2 (100)	3.5 ± 0.0 (100)	3.1 ± 0.3 (100)
Natural UV-B	2.7 ± 0.6 (71)	2.4 ± 0.1 (69)	2.6 ± 0.4 (83)
Low UV-B	2.8 ± 0.4 (73)	2.4 ± 0.9 (70)	2.3 ± 0.1 (73)
High UV-B	2.4 ± 0.5 (62)	2.3 ± 0.4 (67)	1.6 ± 0.1 (53)

Note: Numbers in brackets indicate the percentage (%) rates of the control (Zero UV-B)

Table 4 shows the effect of UV-B radiation on the rates of oxygen evolution as expressed on chlorophyll weight basis. Pea leaves showed a decline in oxygen evolution both with increasing time of UV-B radiation and with age. It appeared that a decrease in photosynphotosynthesis was greater when plants received a longer period of radiation. This pattern was found under natural, low and high UV-B treatments. However, high UV-B treatment still gave the greatest inhibition compared to other treatments.

Table 4. The rate of O_2 evolution from leaf slices on chlorophyll weight basis as a function of days treatment. Values are means of 8 replications from at least 2 independent experiments.

Treatment	O_2 evolution (nmol O_2 $mg^{-1}chl$ sec^{-1})		
	4 days	8 days	16 days
Control (Zero UV-B)	30.5 ± 0.8 (100)	29.1 ± 0.6 (100)	27.6 ± 2.5 (100)
Natural UV-B	24.0 ± 2.9 (83)	23.7 ± 1.2 (86)	18.9 ± 1.1 (62)
Low UV-B	22.8 ± 0.9 (78)	20.9 ± 3.9 (68)	14.8 ± 1.1 (54)
High UV-B	21.9 ± 1.7 (72)	17.1 ± 3.5 (59)	12.2 ± 1.5 (44)

Note: Numbers in brackets indicate the percentage (%) rates of the control (Zero UV-B)

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Oxygen evolution in chloroplasts

Figure 1 shows the plot of CO_2 fixation-dependent O_2 evolution as estimated in leaf chloroplasts versus time of radiation. Obviously, oxygen evolution rates declined with increasing leaf age or time of exposure. A reduction of the oxygen evolution was also observed under low, natural and high UV-B treatment, even though there was no difference between natural and low UV-B treatments. The pattern of reduction of phtosynthesis during treatment was identical between natural UV-B and low UV-B treatments. In contrast, high UV-B showed a greater reduction in oxygen evolution than the other treatments.

Non-cyclic electron transport flow

It was found that high UV-B treatment gave the lowest rate of electron flow from water to NADP under state 3 conditions (Table 5). Oxygen evolution under low UV-B radiation was not affected, while natural UV-B treatment appeared to stimulate the rate of electron flow. Electron transport-dependent O_2 evolution under state 4 was significantly affected by UV-B radiation.

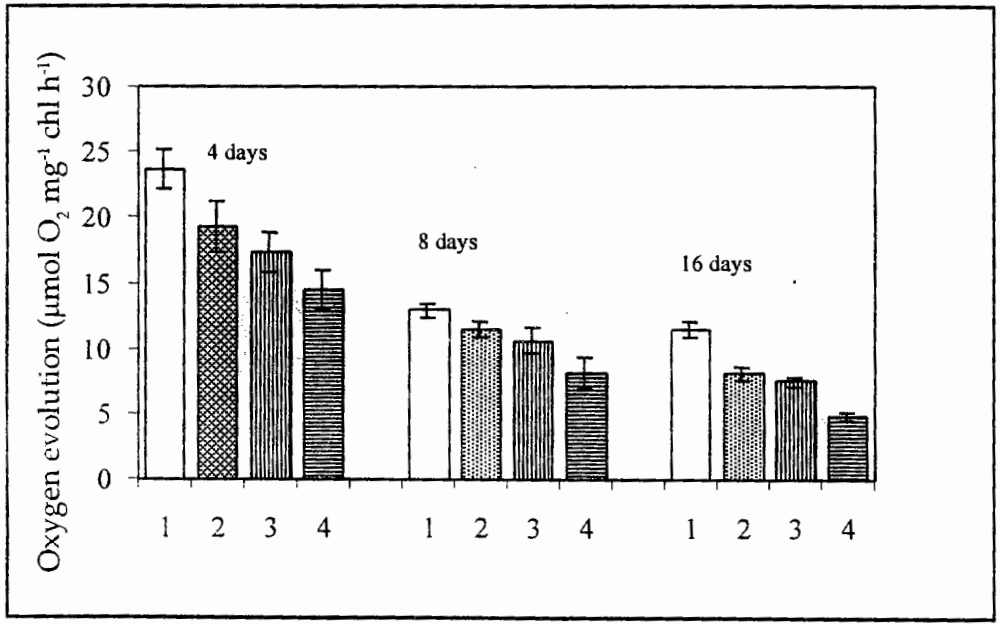

Figure 1. The rate of CO_2-dependent O_2 evolution from leaf chloroplasts. Each value is a mean of 4-6 replications from at least 2 independent experiments. 1 (Zero UV-B); 2 (Natural UV-B); 3 (Low UV-B); 4 (High UV-B).

Table 5. The rate of non-cyclic electron transport from broken chloroplasts (grana solution) expressed as nm o1O_2 mg^{-1}chl min^{-1}.

Treatment	O_2 uptake (nmol O_2 mg^{-1}chl min^{-1})			
	4 days after treatment		8 days after treatment	
	State 3	State 4	State 3	State 4
Control (Zero UV-B)	235 ± 5 (100)	66 ± 1 (100)	225 ± 22 (100)	68 ± 4 (100)
Natural UV-B	259 ± 2 (110)	61 ± 2 (92)	273 ± 25 (121)	85 ± 0 (126)
Low UV-B	213 ± 4 (91)	58 ± 4 (88)	226 ± 0 (100)	62 ± 1 (92)
High UV-B	191 ± 8 (81)	64 ± 0 (98)	183 ± 16 (81)	66 ± 2 (97)

Note: Numbers in brackets indicate the percentage (%) rates of the control (Zero UV-B)

Pseudocyclic electron transport flow

Methylviologen and azide were initially included in the reaction mixture, while ADP and uncoupler

Table 6. The rate of pseudocyclic electron flow of broken chloroplasts from pea leaves. Values are the mean of 4-8 replications from at least 4 independent experiments.

Treatment	O_2 uptake (nmol O_2 mg^{-1}chl min^{-1})			
	4 days after treatment		8 days after treatment	
	State 3	State 4	State 3	State 4
Control (Zero UV-B)	276 ± 41(100)	95 ± 8 (100)	251 ± 12 (100)	72 ± 12 (100)
Natural UV-B	243 ± 32 (88)	77 ± 7 (81)	206 ± 13 (82)	78 ± 20 (108)
Low UV-B	213 ± 27 (74)	59 ± 3 (62)	179 ± 8 (71)	53 ± 10 (74)
High UV-B	192 ± 23 (67)	57 ± 6 (60)	166 ± 8 (66)	57 ± 5 (79)

Note: Numbers in brackets indicate the percentage (%) rates of the control (Zero UV-B)

ISSN 0853 - 7240

were added after a steady rate of O_2 consumption decreased with leaf age and time of radiation. However, it appeared that the percentage of reduction by UV-B was relatively constant after 4 days of treatment (Table 6). Oxygen uptake under state 4 conditions, when ADP has run out, displayed a similar pattern to that found under state 3 condition. Compared to the control, the percentage of O_2 uptake tended to be lowered by supplementary UV-B radiation.

DISCUSSION

The rates of photosynthesis of attached leaves and detached leaf slices were lowered by UV-B treatment. This reduction was more pronounced under high UV-B radiation. With attached leaves, these reductions were primarily due to decrease in stomatal conductivity which was found to be lower under UV-B treatment. However, CO_2 concentration inside these leaves was not reduced, suggesting that the alterations of the photosynthetic activity was not due to a lowered of CO_2 availability. When measurements on leaf slices were performed with saturating CO_2 and high intensity, leaves harvested from UV-B treated plants showed a reduction in O_2 evolution both on leaf area and chlorophyll weight basis. Thus, this reduction could be due to either a decrease in chloroplast number within palisade cells (Maryani and Wickich, 1995) or reduction of chlorophyll content as photosynthetic pigments. In this study, there was a slight reduction of total chlorophyll content. It was found that UV-B radiation decreased the amount of chlorophyll pigments (Strid *et al.*, 1990; He *et al.*, 1993; He *et al.*, 1994). The total chlorophyll content decreased by 40% over 8 days of UV-B treatment compared to control plants (Strid *et al.*, 1990). This reduction could be related to a decline in pigment synthesis, mRNA transcription for chlorophyll, increase in pigment degradation or all of them. Jordan *et al.* (1991) found that there was an inhibition in the gene expression for chlorophyll *a/b* binding protein. The decrease in chlorophyll was due to an increase in its degradation, but not a decrease in their synthesis (Strid and Porra, 1992).

UV-B exposure for 8 days caused CO_2-dependent O_2 evolution, non cyclic and pseudocyclic electron transport by isolated chloroplasts to decline. These changes increased progressively and appear to be a response to the cumulative UV-b dosage. The reduction of CO_2-dependent O_2 evolution observed in isolated chloroplasts of UV-B treated plants could have been caused by damage to the chloroplast structure (Maryani & Wiskich, 1995). Damaged chloroplasts would have a reduced capacity for photosynthetic activity, and may also have a decrease in Rubisco content and activity. Although the content and activity of Rubisco has not been assayed in this study, it has been found to decline in pea leaves exposed to supplementary UV-B radiation (Strid *et al.*, 1990; Jordan *et al.*, 1992). The activity of Rubisco declined more rapidly than did the amount of Rubisco protein at any time during exposure. The reduction of Rubisco protein and activity may be associated with the cessation of gene transcription, such as the slow degradation of protein and decreases in the level of mRNA transcripts for both rbc L and rbc S as previously observed (Jordan *et al.*, 1992). Whatever the mechanism of damage, supplementary UV-B radiation appeared to have a strong impact in enzymes associated with carboxylation, light absorption and light transduction.

It was previously found that UV-B light was more effective than visible light inhibiting the electron transport capacity of isolated thylakoids. In the present study, chloroplasts from high UV-B treated plants showed a marked decrease in the activity on non-cyclic electron transport from PS II to PS I at 4 and 8 days after treatment. This result indicates that the loss of electron transport-dependent O_2 evolution reflected an inhibition in the PS complex site and reflects alteration in the chloroplast membrane organization. Previous studies showed that supplementary UV-B decreased the PS I and PS II content of pea leave on leaf-area basis (Strid *et al.*, 1990). The PS II complex was found to be more vulnerable to many environmental stresses, including UV-B (Renger *et al.*, 1989; Strid *et al.*, 1990). It has also been shown that UV-B light may reflect both donor (such as diphenylcarbazide, DPC) and acceptor (such as 2,6-dichlorophenol indophenol, DCIP) sites as well as the degradation of D1 polypeptide (Ranger *et al.*, 1989). Greenburg *et al.* (1989) reported that the quantum efficiency of degradation of the D1 polypeptide was greatest in the UV-B region and that plastoquinone was the photoreception responsible for the degradation. All these studies indicate the clear sensitivity of PS II to UV-B radiation and that

ISSN 0853 - 7240 Biologi, Vol. 2, No. 8, Desember 1999

multiple sites within the complex may be inhibited. The loss of D2 protein after UV-B irradiation of isolated thylakoids has also been reported (Friso *et al.*, 1994). Furthermore, chloroplasts isolated from leaves treated with UV-B for 30 min showed a 50% loss of PS II activity (Nedunchezhian & Kulandaivelu, 1991). The decrease was primarily due to a loss of 23 and 33 kDa extrinsic polypeptides. It is assumed that the structural changes of polypeptides are responsible for the inhibition of the oxidation of water.

Pseudocyclic electron transport activity was inhibited by UV-B radiation, but this reduction did not appear to increase with time of radiation. It was previously found that UV-B inhibited photophosphorylation and CF_0CF_1-ATPase activity in pea leaves (Strid *et al.*, 1990); Zhang *et al.*, 1994). Almost half of the photophosphorylation was lost after 8 days of exposure (Strid *et al.*, 1990). It was also found that the content of CF_0CF_1-ATPase protein decreased after 4 days of UV-B irradiance (Zhang *et al.*, 1994).

ACKNOWLEDGMENT

I sincerely thank the AusAID (Australian Agency for International Development) which granted this research via Master Degree Scholarship. I also would like to thank Joseph T. Wiskich (Botany Department, Adelaide University, South Australia) for his guidance and advises.

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Kualitas Profesi

- Dalam pemakaian modern, istilah profesi cenderung memiliki kualitas tertentu yang memiliki kesamaan
- Profesi dijalankan orang dan mendapat imbalan.
- Keanggotaan profesi biasanya dibatasi dan diatur oleh asosiasi profesi.

Profesionalisme

- To provide a foundation for effective communications and efficient performance
- Ada banyak level dan ditangani dengan berbagai cara
- Satu orang mengatakan profesional, orang lain mengatakan tidak profesional

- Makan siang dengan kawan, bermain badminton bersama tidak terkait dengan profesionalisme tapi ada nilainya