

rubisco oxygenase and control of direct photoreduction (Mehler reaction) and Electron flow to oxygen in higher plants and algae: rates

Murray R. Badger, Susanne von Caemmerer, Sari Ruuska and Hiromi Nakano

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Electron flow to oxygen in higher plants **and algae: rates and control of direct**
and algae: rates and control of direct **photoration flow to oxygen in higher plantically algae: rates and control of direction)**
photoreduction (Mehler reaction) photoreduction (Mehler reaction)
and rubisco oxygenase

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Linear electron transport in chloroplasts produces a number of reduced components associated with Linear electron transport in chloroplasts produces a number of reduced components associated with photosystem I (PS I) that may subsequently participate in reactions that reduce O_2 . The two primary reactions that have Linear electron transport in chloroplasts produces a number of reduced comp
photosystem I (PS I) that may subsequently participate in reactions that reduce
reactions that have been extensively studied are: first, the dire ponents associated with
ce O_2 . The two primary
to superoxide by reduced
sco, oxygenase (ribulose photosystem I (PS I) that may subsequently participate in reactions that reduce O_2 . The two primary reactions that have been extensively studied are: first, the direct reduction of O_2 to superoxide by reduced donors reactions that have been extensively studied are: first, the direct reduction of O_2 to superoxide by reduced
donors associated with PS I (the Mehler reaction), and second, the rubisco oxygenase (ribulose
1,5-bisphospha donors associated with PS I (the Mehler reaction), and second, the rubisco oxygenase (ribulose 1,5-bisphosphate carboxylase oxygenase EC 4.1.1.39) reaction and associated peroxisomal and mitochondrial reactions of the pho 1,5-bisphosphate carboxylase oxygenase EC 4.1.1.39) reaction and associated peroxisomal and mitochondrial reactions of the photorespiratory pathway. This paper reviews a number of recent and past studies with higher plant drial reactions of the photorespiratory pathway. This paper reviews a number of recent and past studies
with higher plants, algae and cyanobacteria that have attempted to quantify O_2 fluxes under various
conditions and with higher plants, algae and cyanobacteria that have attempted to quantify O_2 fluxes under various
conditions and their contributions to a number of roles, including photon energy dissipation. In C_3 and
Crassulacea conditions and their contributions to a number of roles, including photon energy dissipation. In C_3 and
Crassulacean acid metabolism (CAM) plants, a Mehler O_2 uptake reaction is unlikely to support a
significant flo Crassulacean acid metabolism (CAM) plants, a Mehler O_2 uptake reaction is unlikely to support a significant flow of electron transport (probably less than 10%). In addition, if it were present it would appear to sca significant flow of electron transport (probably less than 10%). In addition, if it were present it would
appear to scale with photosynthetic carbon oxidation cycle (PCO) and photosynthetic carbon reduction
cycle (PCR) act appear to scale with photosynthetic carbon oxidation cycle (PCO) and photosynthetic carbon reduction
cycle (PCR) activity. This is supported by studies with antisense tobacco plants with reduced rubisco at
low and high tem cycle (PCR) activity. This is supported by studies with antisense tobacco plants with reduced rubisco at
low and high temperatures and high light, as well as studies with potatoes, grapes and madrone during
water stress. T low and high temperatures and high light, as well as studies with potatoes, grapes and madrone during
water stress. The lack of significant Mehler in these plants directly argues for a strong control of Mehler
reaction in and C_4 plants is primarily that the level of light-dependent O_2 uptake is generally much lower in C_4 plants and is relatively insensitive to the external CO_2 concentration. Such a major difference is readily at plants and is relatively insensitive to the external CO_2 concentration. Such a major difference is readily attributed to the operation of the C_4 CO_2 concentrating mechanism. Algae show a range of light-
dependent attributed to the operation of the C_4 CO₂ concentrating mechanism. Algae show a range of light-
dependent O_2 uptake rates, similar to C_4 plants. As in C_4 plants, the O_2 uptake appears to be largely
insens dependent O_2 uptake rates, similar to C_4 plants. As in C_4 plants, the O_2 uptake appears to be largely insensitive to CO_2 , even in species that lack a CO_2 concentrating mechanism and under conditions that a insensitive to CO_2 , even in species that lack a CO_2 concentrating mechanism and under conditions that are clearly limiting with respect to inorganic carbon supply. A part explanation for this could be that many algal are clearly limiting with respect to inorganic carbon supply. A part explanation for this could be that observed O_2 uptake may be due to a Mehler reaction and less to rubisco, compared with C_3 plants. In oxygenase activity in air. This would lead to the conclusion that perhaps a greater proportion of the observed O_2 uptake may be due to a Mehler reaction and less to rubisco, compared with C_3 plants. In contrast to a observed O_2 uptake may be due to a Mehler reaction and less to rubisco, compared with C_3 plants. In contrast to algae and higher plants, cyanobacteria appear to have a high capacity for Mehler O_2 uptake, which ap contrast to algae and higher plants, cyanobacteria appear to have a high capacity for Mehler O_2 uptake, which appears to be not well coupled or limited by ATP consumption. It is likely that in all higher plants and alg which appears to be not well coupled or limited by ATP consumption. It is likely that in all higher plants
and algae, which have a well-developed non-photochemical quenching mechanism, non-radiative energy
dissipation is t and algae, which have a well-developed non-photochemical quenching mechanism, non-radiative energy
dissipation is the major mechanism for dissipating excess photons absorbed by the light-harvesting
complexes under stressfu dissipation is the major mechanism for dissipating excess pl
complexes under stressful conditions. However, for cyanoba
photochemical quenching, the situation may well be different. reaction; The external conditions. The extended of the extended of the situation may well be different.
 Keywords: Mehler reaction; oxygen photoreduction; photon energy dissipation;

photorespiration; photon energy dissi

may wen be unterent.
n; oxygen photoreduction; p
photorespiration; rubisco

1. INTRODUCTION

COLLET EXECUTE:
Cyanobacteria some 2.5 billion years ago, photosynthetic
cyanobacteria some 2.5 billion years ago, photosynthetic
cyanomisms initiated a catastrophic change in the Earth's With the evolution of oxygenic photosynthesis by
cyanobacteria some 2.5 billion years ago, photosynthetic
organisms initiated a catastrophic change in the Earth's
atmosphere and their ancestors have been coping with the cyanobacteria some 2.5 billion years ago, photosynthetic
organisms initiated a catastrophic change in the Earth's
atmosphere and their ancestors have been coping with the
developing consequences since that time. Rubisco

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With the evolution of oxygenic photosynthesis by similarly the reduced acceptors of photosystem I (PS I) organisms initiated a catastrophic change in the Earth's electrons to their intended targets without the potential
atmosphere and their ancestors have been coping with the intervention of O_2 . A major focus of the evolu (ribulose 1,5-bisphosphate carboxylase oxygenase EC (ribulose 1,5-bisphosphate carboxylase oxygenase EC
4.1.1.39) initially fixed CO_2 in the absence of O_2 , and
similarly the reduced accentors of photosystem I (PS I) (ribulose 1,5-bisphosphate carboxylase oxygenase EC
4.1.1.39) initially fixed CO_2 in the absence of O_2 , and
similarly the reduced acceptors of photosystem I (PS I)
and II (PS II) reaction centres were able to transfe 4.1.1.39) initially fixed CO_2 in the absence of O_2 , and similarly the reduced acceptors of photosystem I (PS I) and II (PS II) reaction centres were able to transfer
electrons to their intended targets without the potential
intervention of O_1 . A major focus of the evolution and II (PS II) reaccelectrons to their intervention of O_2 . intervention of O_2 . A major focus of the evolution of photosynthetic organisms in a self-generated oxidative intervention of O_2 . A major focus of the evolution of
photosynthetic organisms in a self-generated oxidative
environment has been to manage the potentially
damaging consequences of both these unforces photosynthetic organisms in a self-generated oxidative
environment has been to manage the potentially
damaging consequences of both these unforseen
consequences and even capitalize on them where possible environment has been to manage the potentially
damaging consequences of both these unforseen
consequences and even capitalize on them where possible. *Phil. Trans. R. Soc. Lond.* B (2000) **355**, 1433–1446 **1433** © 2000 The Royal Society

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ase and carboxylase have been well documented (Cleland The competitive interactions between rubisco oxygenase and carboxylase have been well documented (Cleland *et al.* 1998; Roy & Andrews 2000) and it is clear that a number of strategies have been employed by various ase and carboxylase have been well documented (Cleland *et al.* 1998; Roy & Andrews 2000) and it is clear that a number of strategies have been employed by various photosynthetic organisms to reduce the impact of the *et al.* 1998; Roy & Andrews 2000) and it is clear that a
number of strategies have been employed by various
photosynthetic organisms to reduce the impact of the
oxygenese reaction (Badger *et al.* 1998) Chief among number of strategies have been employed by various
photosynthetic organisms to reduce the impact of the
oxygenase reaction (Badger *et al.* 1998). Chief among
these have been (i) the considerable evolutionary photosynthetic organisms to reduce the impact of the oxygenase reaction (Badger *et al.* 1998). Chief among these have been (i) the considerable evolutionary improvement of the kinetic properties of rubisco (Badger oxygenase reaction (Badger *et al.* 1998). Chief among
these have been (i) the considerable evolutionary
improvement of the kinetic properties of rubisco (Badger
et al. 1998: Tabita 1999): (ii) the development of numero these have been (i) the considerable evolutionary
improvement of the kinetic properties of rubisco (Badger
et al. 1998; Tabita 1999); (ii) the development of numerous improvement of the kinetic properties of rubisco (Badger *et al.* 1998; Tabita 1999); (ii) the development of numerous CO_2 concentrating mechanisms (Badger *et al.* 1998; Badger & Spalding 2000); and (iii) the developmen *et al.* 1998; Tabita 1999); (ii) the development of numerous CO_2 concentrating mechanisms (Badger *et al.* 1998; Badger & Spalding 2000); and (iii) the development of biochemical machinery to some with phosphoraly cola $CO₂$ concentrating mechanisms (Badger *et al.* 1998;
Badger & Spalding 2000); and (iii) the development of
biochemical machinery to cope with phosphoglycolate,
the initial product of the oxygense reaction (Douce & Badger & Spalding 2000); and (iii) the development of biochemical machinery to cope with phosphoglycolate, the initial product of the oxygenase reaction (Douce $\&$ Heldt 2000; Husic *et al*. 1987). Exercition initial product of the oxygenase reaction (Douce & Eldt 2000; Husic *et al.* 1987).
The direct photoreduction of O₂ by thylakoids has also
en extensively studied. Oxygen can interact with a

Heldt 2000; Husic *et al.* 1987).
The direct photoreduction of O_2 by thylakoids has also
been extensively studied. Oxygen can interact with a
number of components of the photosynthetic electron been extensively studied. Oxygen can interact with a
number of components of the photosynthetic electron
transport chain, including the PS II reaction centre in its
triplet ${}^{3}P_{\text{max}}^{*}$, state (Asada 1996), the reduce been extensively studied. Oxygen can interact with a number of components of the photosynthetic electron mponents of the photosynthetic electron,
including the PS II reaction centre in its
state (Asada 1996), the reduced plasto-
Cleland & Grace 1999: Osmond & Grace transport chain, including the PS II reaction centre in its
triplet ${}^{3}P_{680}^{*}$ state (Asada 1996), the reduced plasto-
quinone pool (Cleland & Grace 1999; Osmond & Grace
1995) the reduced iron sulphur (FeS) centres a triplet ${}^{3}P_{680}^{*}$ state (Asada 1996), the reduced plasto-
quinone pool (Cleland & Grace 1999; Osmond & Grace
1995), the reduced iron sulphur (FeS) centres associated
with PS I (Asada 1994) and reduced stromal accent quinone pool (Cleland & Grace 1999; Osmond & Grace 1995), the reduced iron sulphur (FeS) centres associated with PS I (Asada 1994) and reduced stromal acceptors such as ferredoxin (Fd) and monodehydroascorbate with PS I (Asada 1994) and reduced stromal acceptors with PS I (Asada 1994) and reduced stromal acceptors
such as ferredoxin (Fd) and monodehydroascorbate
reductase (MDAR) (Asada 1999; Badger 1985). However,
it is clear that in general the latter interactions of O with such as ferredoxin (Fd) and monodehydroascorbate
reductase (MDAR) (Asada 1999; Badger 1985). However,
it is clear that in general the latter interactions of O₂ with
PS I are the most quantitatively important in producin reductase (MDAR) (Asada 1999; Badger 1985). However,
it is clear that in general the latter interactions of O_2 with
PS I are the most quantitatively important in producing
reactive O_2 , radicals and are predominantly it is clear that in general the latter interactions of O_2 with
PS I are the most quantitatively important in producing
reactive O_2 radicals and are predominantly responsible **PS I** are the most quantitatively important in producing
reactive O_2 radicals and are predominantly responsible
for the direct photoreduction of O_2 by thylakoids, known
as the Mehler reaction (Asada 1999; Badger 19 reactive O_2 radicals and are predominantly responsible
for the direct photoreduction of O_2 by thylakoids, known
as the Mehler reaction (Asada 1999; Badger 1985). Evolu-
tionary changes associated with either suppres for the direct photoreduction of O_2 by thylakoids, known
as the Mehler reaction (Asada 1999; Badger 1985). Evolu-
tionary changes associated with either suppressing the
potential for direct O , photoreduction or copin as the Mehler reaction (Asada 1999; Badger 1985). Evolutionary changes associated with either suppressing the potential for direct O_2 photoreduction or coping with the tionary changes associated with either suppressing the
potential for direct O_2 photoreduction or coping with the
reactive O_2 species produced have been only briefly dealt
with by a small number of studies (Asada 199 potential for direct O_2 photoreduction or coping with the
reactive O_2 species produced have been only briefly dealt
with by a small number of studies (Asada 1996). Most
evidence points to changes in the strategies o reactive O_2 species produced have been only briefly dealt
with by a small number of studies (Asada 1996). Most
evidence points to changes in the strategies of inactivating
reactive O_1 , molecules, i.e. dealing with t with by a small number of studies (Asada 1996). Most
evidence points to changes in the strategies of inactivating
reactive O_2 molecules, i.e. dealing with the products,
while there is a scarcity of any information abou evidence points to changes in the strategies of inactivating
reactive O_2 molecules, i.e. dealing with the products,
while there is a scarcity of any information about changes
directed at suppressing the primary photore reactive O_2 molecules, i.e. dealing with the products, while there is a scarcity of any information about changes directed at suppressing the primary photoreduction steps. Figure is a scarcity of any information about changes
rected at suppressing the primary photoreduction steps.
The functional activities of O_2 uptake reactions
ediated by both rubisco and Mebler have been of **IENCES** directed at suppressing the primary photoreduction steps.
The functional activities of O_2 uptake reactions
mediated by both rubisco and Mehler have been of
considerable interest in interpreting various aspects of The functional activities of O_2 uptake reactions
mediated by both rubisco and Mehler have been of
considerable interest in interpreting various aspects of
photosynthetic physiology For rubisco, the potentially mediated by both rubisco and Mehler have been of
considerable interest in interpreting various aspects of
photosynthetic physiology. For rubisco, the potentially
inhibitory effects of O, on decreasing the rates of CO. considerable interest in interpreting various aspects of
photosynthetic physiology. For rubisco, the potentially
inhibitory effects of O_2 on decreasing the rates of CO_2
fixation and producing photogenizatory substrat photosynthetic physiology. For rubisco, the potentially
inhibitory effects of O_2 on decreasing the rates of CO_2
fixation and producing photorespiratory substrates have
been uppermost (Ogren 1984) However consideratio inhibitory effects of O_2 on decreasing the rates of CO_2
fixation and producing photorespiratory substrates have
been uppermost (Ogren 1984). However, consideration of
how electron flow supported by rubisco oxygenase fixation and producing photorespiratory substrates have
been uppermost (Ogren 1984). However, consideration of
how electron flow supported by rubisco oxygenase at
limiting CO may play a role in minimizing photoiphibibeen uppermost (Ogren 1984). However, consideration of
how electron flow supported by rubisco oxygenase at
 \Box limiting CO₂ may play a role in minimizing photoinhibi-
tory damage by excess light has also been of signifi how electron flow supported by rubisco oxygenase at
limiting CO_2 may play a role in minimizing photoinhibi-
tory damage by excess light has also been of significant
interest (Kozaki & Takeba 1996; Osmond & Biörkman limiting CO_2 may play a role in minimizing photoinhibitory damage by excess light has also been of significant
interest (Kozaki & Takeba 1996; Osmond & Björkman
1972: Osmond & Grace 1995), For Mebler Q., phototory damage by excess light has also been of significant
interest (Kozaki & Takeba 1996; Osmond & Björkman
1972; Osmond & Grace 1995). For Mehler O₂ photo-
reduction the emphasis has been on trying to determine interest (Kozaki & Takeba 1996; Osmond & Björkman
1972; Osmond & Grace 1995). For Mehler O_2 photo-
reduction, the emphasis has been on trying to determine
what rates of electron transfer to O_2 are achieved under 1972; Osmond & Grace 1995). For Mehler O_2 photo-
reduction, the emphasis has been on trying to determine
what rates of electron transfer to O_2 are achieved under
various environmental conditions and what reduced reduction, the emphasis has been on trying to determine
what rates of electron transfer to O_2 are achieved under
various environmental conditions, and what reduced
the electron transwhat rates of electron transfer to O_2 are achieved under
various environmental conditions, and what reduced
thylakoid and stromal components of the electron trans-
port chain are primarily responsible for reduction of port chain are primarily responsible for reduction of O₂ exponsible for reduction of O₂ thylakoid and stromal components of the electron transport chain are primarily responsible for reduction of O_2 (Asada 1999; Badger 1985; Polle 1996). There has also been interest in Mehler reaction as a means of mediat port chain are primarily responsible for reduction of O_2
(Asada 1999; Badger 1985; Polle 1996). There has also
been interest in Mehler reaction as a means of mediating
additional ATP generation to meet the needs of bot (Asada 1999; Badger 1985; Polle 1996). There has also
been interest in Mehler reaction as a means of mediating
additional ATP generation to meet the needs of both C_3
and C_4 photosynthesis (for a review, see Badger 1 \overline{O} and C₄ photosynthesis (for a review, see Badger 1985). As
for rubisco, however, considerable argument has also
been expended on estimating to what extent direct photoand C_4 photosynthesis (for a review, see Badger 1985). As been expended on estimating to what extent direct photo-
reduction of O_2 could also lead to photon energy dissipa-
tion and protecting from photoinhibition (Osmond & reduction of O_2 could also lead to photon energy dissipareduction of C
tion and prot
Grace 1995).

This paper presents a review of recent and past data and experiments examining the quantitative roles of both This paper presents a review of recent and past data
and experiments examining the quantitative roles of both
the rubisco oxygenase reaction and thylakoid O_2 photo-
reduction (Mebler reaction) in higher plants, algae a and experiments examining the quantitative roles of both
the rubisco oxygenase reaction and thylakoid O_2 photo-
reduction (Mehler reaction) in higher plants, algae and
cyanobacteria. Resulting from this analysis, quest the rubisco oxygenase reaction and thylakoid O_2 photo-
reduction (Mehler reaction) in higher plants, algae and
cyanobacteria. Resulting from this analysis, questions of
the potential roles of photosynthetic electron tr reduction (Mehler reaction) in higher plants, algae and
cyanobacteria. Resulting from this analysis, questions of
the potential roles of photosynthetic electron transport
supported by both rubisco oxygenase (and the associ cyanobacteria. Resulting from this analysis, questions of the potential roles of photosynthetic electron transport
supported by both rubisco oxygenase (and the associated
photorespiration) and Mehler reactions in dissipating
photochemical energy in these various phototrophs is supported by both rubisco oxygenase (and the associated photorespiration) and Mehler reactions in dissipating photochemical energy in these various phototrophs is reassessed reassessed.

2. MECHANISMS OF PHOTOSYNTHETIC O² UPTAKE

The two primary processes involved in photosynthetic 2. MECHANISMS OF PHOTOSTNTHETIC O_2 OPTAKE
The two primary processes involved in photosynthetic
 O_2 exchange have been previously reviewed (Badger
1985) and are dominated by The two primary processes is O_2 exchange have been previ
1985), and are dominated by

- (985) , and are dominated by
(i) those reactions associated with the direct photo-
reduction of O (Mehler reaction) to the superoxide those reactions associated with the direct photo-
reduction of O_2 (Mehler reaction) to the superoxide
radical by reduced electron transport components those reactions associated with the direct photo-
reduction of O_2 (Mehler reaction) to the superoxide
radical, by reduced electron transport components
associated with PS I: and reduction of O_2 (Mehler reader)
radical, by reduced electron
associated with PS I; and
those reactions linked to the radical, by reduced electron transport components
associated with PS I; and
(ii) those reactions linked to the photorespiratory cycle,
including rubisco oxygenase in the chloroplast and
- associated with PS I; and
those reactions linked to the photorespiratory cycle,
including rubisco oxygenase in the chloroplast and
glycolate oxidase and catalase-peroxidase reactions those reactions linked to the photorespiratory cycle,
including rubisco oxygenase in the chloroplast and
glycolate oxidase and catalase–peroxidase reactions
in the peroxisome including rubisco oxygenase in the chloroplast and glycolate oxidase and catalase-peroxidase reactions in the peroxisome.

(a) *Mehler oxygen photoreduction*

(a) *Mehler oxygen photoreduction*
The reactions that are responsible for the direct photo-
duction of Ω , can be separated into two major classes (a) *Mehler oxygen photoreduction*
The reactions that are responsible for the direct photo-
reduction of O_2 can be separated into two major classes.

- reduction of O_2 can be separated into two major classes.
(i) First is the interaction of O_2 with reduced FeS-X cuon of O_2 can be separated mto two major classes.
First is the interaction of O_2 with reduced FeS-X
centres associated with psaA and psaB core polypep-
tides of PS I (for a review see Asada 1999) to form First is the interaction of O_2 with reduced FeS-X
centres associated with psaA and psaB core polypep-
tides of PS I (for a review, see Asada 1999) to form
superoxide. Although it is possible for O_2 , to be centres associated with psaA and psaB core polypeptides of PS I (for a review, see Asada 1999) to form
superoxide. Although it is possible for O_2 to be
reduced by PS II and reduced plastoquinone tides of PS I (for a review, see Asada 1999) to form
superoxide. Although it is possible for O_2 to be
reduced by PS II and reduced plastoquinone
(Cleland & Grace 1999) this appears to be much superoxide. Although it is possible for O_2 to be reduced by PS II and reduced plastoquinone (Cleland & Grace 1999), this appears to be much less significant compared with the PS I–FeS reduced by PS II and reduced plastoquinone
(Cleland & Grace 1999), this appears to be much
less significant compared with the PS I–FeS
mediated reaction (Cleland & Grace 1999), this appears to be much
less significant compared with the PS I-FeS
mediated reaction. less significant compared with the PS I–FeS
mediated reaction.
(ii) A second potential pathway is the interaction of O_2
with stromal components that accept electrons from
- mediated reaction.
A second potential pathway is the interaction of O_2
with stromal components that accept electrons from
PS I and are associated intimately with the complex A second potential pathway is the interaction of O_2
with stromal components that accept electrons from
PS I and are associated intimately with the complex
during photosynthesis. Chief among these are with stromal components that accept electrons from
PS I and are associated intimately with the complex
during photosynthesis. Chief among these are PS I and are associated intimately with the complex
during photosynthesis. Chief among these are
reduced Fe-containing ferredoxin (Furbank &
Radger 1983) and the FAD enzyme MDAR (Miyake during photosynthesis. Chief among these are
reduced Fe-containing ferredoxin (Furbank &
Badger 1983) and the FAD enzyme MDAR (Miyake
et al. 1998) *educed* Fe-
Badger 1983)
et al. 1998). Badger 1983) and the FAD enzyme MDAR (Miyake
 et al. 1998).

In addition to the above reactions, which reduce O_2 to

peroxide there are a number of stromal and thylakoid

et al. 1998).
In addition to the above reactions, which reduce O_2 to superoxide, there are a number of stromal and thylakoid
enzymes that are involved in the decradation of super-In addition to the above reactions, which reduce O_2 to superoxide, there are a number of stromal and thylakoid enzymes that are involved in the degradation of super-
oxide to water so that the harmful effects of active superoxide, there are a number of stromal and thylakoid
enzymes that are involved in the degradation of super-
oxide to water, so that the harmful effects of active O_2
species such as superoxide and $H.O.$ can be avoide enzymes that are involved in the degradation of super-
oxide to water, so that the harmful effects of active O_2
species such as superoxide and H_2O_2 can be avoided. oxide to water, so that the harmful effects of active O_2
species such as superoxide and H_2O_2 can be avoided.
These reactions include ascorbate peroxidase and
MDAR. The integration of these stromal reactions species such as superoxide and H_2O_2 can be avoided.
These reactions include ascorbate peroxidase and MDAR. The integration of these stromal reactions that scavence active oxygen species with the various These reactions include ascorbate peroxidase and
MDAR. The integration of these stromal reactions
that scavenge active oxygen species with the various
O⁻-producing Mebler reactions has been described as the O_2^- -producing Mehler reactions has been described as the
Mehler ascorbate peroxidase (MAP) water-water cycle.
This cycle has been reviewed recently by Asada (1999)
and derives its name from the fact that electrons are IDAR. The integration of these stromal reactions
at scavenge active oxygen species with the various
 $\frac{1}{2}$ -producing Mehler reactions has been described as the
lebler ascorbate peroxidase (MAP) water-water cycle that scavenge active oxygen species with the various O_2^- -producing Mehler reactions has been described as the Mehler ascorbate peroxidase (MAP) water-water cycle.
This cycle has been reviewed recently by Asada (1999) Mehler ascorbate peroxidase (MAP) water–water cycle.
This cycle has been reviewed recently by Asada (1999)
and derives its name from the fact that electrons are
extracted from water by PS II used to reduce O and This cycle has been reviewed recently by Asada (1999)
and derives its name from the fact that electrons are
extracted from water by PS II, used to reduce O_2 , and
finally re-oxidized to water by the ascorbate peroxidase and derives its name from the fact that electrons are
extracted from water by PS II, used to reduce O_2 , and
finally re-oxidized to water by the ascorbate peroxidase
cycle cycle.

(b) *Photorespiration*

(b) **Photorespiration**
The reactions associated with photorespiration have
en extensively reviewed including consideration of the (b) *Photorespiration*
The reactions associated with photorespiration have
been extensively reviewed, including consideration of the

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catalytic properties of rubisco (see Cleland *et al*. 1998; Roy & Andrews 2000), and the integrated operation of catalytic properties of rubisco (see Cleland *et al.* 1998;
Roy & Andrews 2000), and the integrated operation of
chloroplastic, peroxisomal and mitochondrial reactions
associated with the processing phosophoglycolate and Roy & Andrews 2000), and the integrated operation of
chloroplastic, peroxisomal and mitochondrial reactions
associated with the processing phosophoglycolate and the
recycling of carbon, and nitrogen to the chloroplast chloroplastic, peroxisomal and mitochondrial reactions
associated with the processing phosophoglycolate and the
recycling of carbon and nitrogen to the chloroplast
(Douce & Heldt 2000; Husic et al. 1987). In higher plants associated with the processing phosophoglycolate and the recycling of carbon and nitrogen to the chloroplast (Douce & Heldt 2000; Husic *et al.* 1987). In higher plants, the O_2 consumption associated with these reactio recycling of carbon and nitrogen to the chloroplast (Douce & Heldt 2000; Husic *et al.* 1987). In higher plants,
the O_2 consumption associated with these reactions
results in a net consumption of 1.5 O_2 molecules for each
rubisco overaging reaction that fixes O_2 a the O_2 consumption associated with these reactions
results in a net consumption of 1.5 O_2 molecules for each
rubisco oxygenase reaction that fixes O_2 and produces
phosophoglycolate The metabolism of phosophoglyco results in a net consumption of 1.5 O_2 molecules for each
rubisco oxygenase reaction that fixes O_2 and produces
phosophoglycolate. The metabolism of phosophoglycolate,
similar to active O_2 , species, is absolutely rubisco oxygenase reaction that fixes O_2 and produces
phosophoglycolate. The metabolism of phosophoglycolate,
similar to active O_2 species, is absolutely essential for
survival of the photosynthetic cell and reduces phosophoglycolate. The metabolism of phosophoglycolate,
similar to active O_2 species, is absolutely essential for
survival of the photosynthetic cell and reduces the poten-
tially damaging effects of phosophoglycolate similar to active O_2 species, is absolutely essential for survival of the photosynthetic cell and reduces the potentially damaging effects of phosophoglycolate and the loss of carbon and nitrogen that could otherwise occur tially damaging effects of phosophoglycolate and the loss
of carbon and nitrogen that could otherwise occur
(Somerville & Ogren 1982). Photorespiratory O₂ uptake
is most significant in higher plants with C₁ photoof carbon and nitrogen that could otherwise occur
(Somerville & Ogren 1982). Photorespiratory O₂ uptake
is most significant in higher plants with C₃ photo-
synthesis where the passive kinetic properties of rubisco (Somerville & Ogren 1982). Photorespiratory O_2 uptake
is most significant in higher plants with C_3 photo-
synthesis, where the passive kinetic properties of rubisco
are displayed However it is much reduced in C plan is most significant in higher plants with C_3 photo-
synthesis, where the passive kinetic properties of rubisco
are displayed. However, it is much reduced in C_4 plants
where a C_2 concentrating mechanism is present synthesis, where the passive kinetic properties of rubisco
are displayed. However, it is much reduced in C_4 plants
where a CO_2 concentrating mechanism is present and
rubisco oxygenese is effectively suppressed (Badge are displayed. However, it is much reduced in C_4 plants
where a CO_2 concentrating mechanism is present and
rubisco oxygenase is effectively suppressed (Badger 1985). **(c)** *Algae and cyanobacteria*

(c) *Algae and cyanobacteria*

Similar O_2 consuming reactions exist in both algae and

cyanobacteria, in that they have both rubisco and reduced

PS I components that are capable of reducing O Similar O_2 consuming reactions exist in both algae and
cyanobacteria, in that they have both rubisco and reduced
PS I components that are capable of reducing O_2 .
However some differences exist that are worth noting cyanobacteria, in that they have both rubisco and reduced

PS I components that are capable of reducing O_2 .

However some differences exist that are worth noting.

For rubisco-related reactions there are three major For rubisco-related reactions that are visible of reducing O_2 .
For rubisco-related reactions there are three major
Ferences compared with higher plants. First, rubisco in

However some differences exist that are worth noting.
For rubisco-related reactions there are three major
differences compared with higher plants. First, rubisco in
many algae and cyanobacteria has different kinetic prop-For rubisco-related reactions there are three major
differences compared with higher plants. First, rubisco in
many algae and cyanobacteria has different kinetic prop-
erties to bigher plants, and the potential for oxygena differences compared with higher plants. First, rubisco in
many algae and cyanobacteria has different kinetic prop-
erties to higher plants, and the potential for oxygenase
activity at 21% O_2 is often greatly reduced (many algae and cyanobacteria has different kinetic propmany algae and cyanobacteria has different kinetic prop-
eties to higher plants, and the potential for oxygenase
activity at 21% O_2 is often greatly reduced (Badger *et al.* will cause PS I FeS centres and stromal comp activity at 21% O_2 is often greatly reduced (Badger *et al.* 1998). Second, metabolism of phosophoglycolate is often short circuited, so that glycolate is either excreted to the external medium or reduced by a glycolat 1998). Second, metabolism of phosophoglycolate is often
short circuited, so that glycolate is either excreted to the
external medium or reduced by a glycolate dehydro-
genase associated with the thylakoids (Goval & Tolber short circuited, so that glycolate is either excreted to the external medium or reduced by a glycolate dehydrogenase associated with the thylakoids (Goyal & Tolbert 1996: Husic et al. 1987). Finally many algae and cyanoexternal medium or reduced by a glycolate dehydrogenase associated with the thylakoids (Goyal & Tolbert 1996; Husic *et al.* 1987). Finally, many algae and cyano-bacteria have very effective CO_2 concentrating mechan-1996; Husic et al. 1987). Finally, many algae and cyanoisms that suppress rubisco oxygenase (Badger & Spalding bacteria have very effective CO_2 concentrating mechanisms that suppress rubisco oxygenase (Badger & Spalding 2000; Kaplan & Reinhold 1999; Moroney & Somanchi 1999). 00; Kaplan & Reinhold 1999; Moroney & Somanchi
99).
There are also differences associated with thylakoid-
ated reactions where the presence of chlororsepiration

There are also differences associated with thylakoid-
related reactions where the presence of chlororespiration
reactions of the thylakoid membranes are of significant
importance (Bennoun 1994) Here a terminal oxidate in related reactions where the presence of chlororespiration
reactions of the thylakoid membranes are of significant
importance (Bennoun 1994). Here a terminal oxidase in
the thylakoid membranes can accept electrons from the reactions of the thylakoid membranes are of significant
importance (Bennoun 1994). Here a terminal oxidase in
the thylakoid membranes can accept electrons from the
 h f complex and Ω is consumed probably with the $b_6 f$ complex and O_2 is consumed probably with the portance (Bennoun 1994). Here a terminal oxidase in
 f complex and O_2 is consumed probably with the
 f complex and O_2 is consumed probably with the

<u>oduction</u> of water as in cytochrome c oxidase. Although the thylakoid membranes can accept electrons from the $b_6 f$ complex and O_2 is consumed probably with the production of water as in cytochrome *c* oxidase. Although the activity of chlororespiration has been found in h $b_6 f$ complex and O_2 is consumed probably with the production of water as in cytochrome ϵ oxidase. Although the activity of chlororespiration has been found in higher plants (Casano *et al.* 2000; Roldan 1999) it i production of water as in cytochrome ϵ oxidase. Although
the activity of chlororespiration has been found in higher
plants (Casano *et al.* 2000; Roldan 1999) it is much more
significant in algae and cyanobacteria (Ben the activity of chlororespiration has been found in higher
plants (Casano *et al.* 2000; Roldan 1999) it is much more
significant in algae and cyanobacteria (Bennoun 1994;
Mi *et al.* 1992–1995). This reaction is supposed plants (Casano *et al.* 2000; Roldan 1999) it is much more significant in algae and cyanobacteria (Bennoun 1994; Mi *et al.* 1992, 1995). This reaction is supposedly supposed in the light when oxidized **PS I** competes for Mi et al. 1992, 1995). This reaction is supposedly suppressed in the light, when oxidized PS I competes for electrons. ppressed in the light, when oxidized PS I competes for
cetrons.
The scavenging of active O_2 species in the stromal
vironment may also be different. It is recognized that

electrons.
The scavenging of active O_2 species in the stromal
environment may also be different. It is recognized that
many algae and cyanobacteria actually excrete H O and The scavenging of active O_2 species in the stromal
environment may also be different. It is recognized that
many algae and cyanobacteria actually excrete H_2O_2 and
have stromal enzymes that seem especially resistant environment may also be different. It is recognized that many algae and cyanobacteria actually excrete H_2O_2 and have stromal enzymes that seem especially resistant to many algae and cyanobacteria actually excrete H_2O_2 and
have stromal enzymes that seem especially resistant to
oxidative inactivation by H_2O_2 (Takeda *et al.* 1995; Tamoi
et al. 1998–1999) This would suggest an a have stromal enzymes that seem especially resistant to oxidative inactivation by H_2O_2 (Takeda *et al.* 1995; Tamoi
et al. 1998, 1999). This would suggest an active O_2 meta-
holism that is different to bigher plan oxidative inactivation by H_2O_2 (Takeda *et al.* 1995; Tamoi
 et al. 1998, 1999). This would suggest an active O_2 meta-

bolism that is different to higher plants, where trace

amounts of H O have been found to dr *et al.* 1998, 1999). This would suggest an active O_2 meta-
bolism that is different to higher plants, where trace
amounts of H_2O_2 have been found to dramatically inhibit
the thiol-regulated enzymes of the chloropl bolism that is different to higher plants, where trace
amounts of H_2O_2 have been found to dramatically inhibit
the thiol-regulated enzymes of the chloroplast (Kaiser
1976–1979) amounts of H
the thiol-reg
1976, 1979). *Phil. Trans. R. Soc. Lond.* B (2000)

3. FACTORS POTENTIATING PHOTOSYNTHETIC S POTENTIATING PHOTOSYN[.]
OXYGEN CONSUMPTION

OXYGEN CONSUMPTION
In trying to understand the nature and magnitude of **PHOTOSYMPTION**
In trying to understand the nature and magnitude of
photosynthetic O_2 fluxes associated with various photo-
trophs, it is important to understand what mechanistic In trying to understand the nature and magnitude of
photosynthetic O_2 fluxes associated with various photo-
trophs, it is important to understand what mechanistic
and environmental factors may influence the occurrence photosynthetic O_2 fluxes associated with various photo-
trophs, it is important to understand what mechanistic
and environmental factors may influence the occurrence
of both Mebler reaction and rubisco oxygenase trophs, it is important to understand what mechanistic
and environmental factors may influence the occurrence
of both Mehler reaction and rubisco oxygenase.
For rubisco oxygenase-photorespiration, a number of and environmental factors may influence the occurrence

(c) *Algae and cyanobacteria* presence of a complete photorespiratory cycle in higher
Similar O_2 consuming reactions exist in both algae and plants with glycolate oxidase activity, and shuttling of
anobacteria, in that of both Mehler reaction and rubisco oxygenase.
For rubisco oxygenase-photorespiration, a number of obvious factors may influence the O_2 exchange. The levels of CO, and O, at the active site of rubisco are most For rubisco oxygenase-photorespiration, a number of
obvious factors may influence the O_2 exchange. The levels
of CO_2 and O_2 at the active site of rubisco are most
important Thus stomatal limitations in higher plan obvious factors may influence the O_2 exchange. The levels
of CO_2 and O_2 at the active site of rubisco are most
important. Thus stomatal limitations in higher plants and
the presence of a CO₋ concentrating mechan of CO_2 and O_2 at the active site of rubisco are most
important. Thus stomatal limitations in higher plants and
the presence of a CO_2 concentrating mechanism such as C_4 photosynthesis will obviously have a major effect on the presence of a CO_2 concentrating mechanism such as C_4 photosynthesis will obviously have a major effect on modifying rubisco-related O_2 uptake. Additionally, changes in the kinetic properties of rubisco that wo C_4 photosynthesis will obviously have a major effect on
modifying rubisco-related O_2 uptake. Additionally,
changes in the kinetic properties of rubisco that would
alter ovverage activity are also important. Red alga modifying rubisco-related O_2 uptake. Additionally,
changes in the kinetic properties of rubisco that would
alter oxygenase activity are also important. Red algal-
type rubiscos with improved $CO-O$ specificity are a changes in the kinetic properties of rubisco that would
alter oxygenase activity are also important. Red algal-
type rubiscos, with improved CO_2-O_2 specificity are a
good example of this (Badger *et al.* 1998: Uemura *e* alter oxygenase activity are also important. Red algal-
type rubiscos, with improved CO_2-O_2 specificity are a
good example of this (Badger *et al.* 1998; Uemura *et al.*
1997), but cyanobacterial rubisco also has much r good example of this (Badger *et al.* 1998; Uemura *et al.* 1997), but cyanobacterial rubisco also has much reduced oxygenase activity in air (Badger *et al.* 1998). Finally, the presence of a complete photorespiratory cyc 1997), but cyanobacterial rubisco also has much reduced oxygenase activity in air (Badger *et al.* 1998). Finally, the oxygenase activity in air (Badger *et al.* 1998). Finally, the presence of a complete photorespiratory cycle in higher plants with glycolate oxidase activity, and shuttling of redox equivalents between the chloroplast pero presence of a complete photorespiratory cycle in higher
plants with glycolate oxidase activity, and shuttling of
redox equivalents between the chloroplast, peroxisome
and mitochondria, means, that the potential for O. plants with glycolate oxidase activity, and shuttling of
redox equivalents between the chloroplast, peroxisome
and mitochondria, means that the potential for O_2
untake may be enhanced at least 50% compared with redox equivalents between the chloroplast, peroxisome
and mitochondria, means that the potential for O_2
uptake may be enhanced at least 50% compared with
algae and cyanobacteria and mitochondria, mean
uptake may be enhanced
algae and cyanobacteria.
For Mehler O untake take may be enhanced at least 50% compared with
gae and cyanobacteria.
For Mehler O_2 uptake, the mechanisms that may alter
a potential for O_2 reduction are less well defined.

There are also differences associated with thylakoid-system electron flow imposed by thylakoid ΔpH and the related reactions where the presence of chlororespiration cytochrome $b_6 f$ complex (Price *et al.* 1998). Thus algae and cyanobacteria.

For Mehler O_2 uptake, the mechanisms that may alter

the potential for O_2 reduction are less well defined. A

limitation of electron acceptors, such as $NADP^+$ at PS I For Mehler O_2 uptake, the mechanisms that may alter
the potential for O_2 reduction are less well defined. A
limitation of electron acceptors, such as NADP⁺ at PS I
will cause PS I E-S centres and stromal component the potential for O_2 reduction are less well defined. A
limitation of electron acceptors, such as $NADP^+$ at PS I
will cause PS I FeS centres and stromal components such
as Ed and MDAR to increase their reduction level limitation of electron acceptors, such as NADP⁺ at PS I
will cause PS I FeS centres and stromal components such
as Fd and MDAR to increase their reduction levels, thus
potentiating increased O₋ reduction However the po will cause PS I FeS centres and stromal components such as Fd and MDAR to increase their reduction levels, thus potentiating increased O_2 reduction. However, the potential of a reduced component either in the thulakoid as Fd and MDAR to increase their reduction levels, thus
potentiating increased O_2 reduction. However, the poten-
tial of a reduced component either in the thylakoid
membrane or stroma to interact with O may be influpotentiating increased O_2 reduction. However, the potential of a reduced component either in the thylakoid
membrane or stroma to interact with O_2 may be influ-
enced by structural modifications that limit the access tial of a reduced component either in the thylakoid
membrane or stroma to interact with O_2 may be influ-
enced by structural modifications that limit the access of
 O_1 to the reduced centres of those reduced molecule O_2 to the reduced centres of those reduced molecules.
Such a level of control of Mehler reaction has not been
described but is possible. On the donor side of PS I, the
state of PS I reduction is controlled by limitatio whence or stroma to interact with O_2 may be influed by structural modifications that limit the access of to the reduced centres of those reduced molecules. enced by structural modifications that limit the access of O_2 to the reduced centres of those reduced molecules.
Such a level of control of Mehler reaction has not been
described but is possible. On the donor side of Such a level of control of Mehler reaction has not been
described but is possible. On the donor side of PS I, the
state of PS I reduction is controlled by limitations of inter-
system electron flow imposed by thylakoid ApH described but is possible. On the donor side of PS I, the state of PS I reduction is controlled by limitations of inter-
system electron flow imposed by thylakoid ΔpH and the cytochrome h, f complex (Price *et al.* 199 cytochrome $b_6 f$ complex (Price *et al.* 1998). Thus when state of PS I reduction is controlled by limitations of intersystem electron flow imposed by thylakoid ΔpH and the cytochrome $b_6 f$ complex (Price *et al.* 1998). Thus when CO_2 and O_2 are limiting as PS I acceptors in higher plants. PS I becomes less rather than more reduc cytochrome $b_6 f$ complex (Price *et al.* 1998). Thus when CO_2 and O_2 are limiting as PS I acceptors in higher plants, PS I becomes less rather than more reduced due to a slowing in the rate of intersystem electron f $CO₂$ and $O₂$ are limiting as PS I acceptors in higher
plants, PS I becomes less rather than more reduced due
to a slowing in the rate of intersystem electron flow and
the quantum vield of both PS I and PS II plants, PS I becomes less rather than more reduced due
to a slowing in the rate of intersystem electron flow and
the quantum yield of both PS I and PS II remains
matched. This downregulation is due to a reduced to a slowing in the rate of intersystem electron flow and the quantum yield of both PS I and PS II remains
matched. This downregulation is due to a reduced
availability of ADP (ATP consumption) and a ΔpH
increase rather than a lack of $NADP^+$ In addition to matched. This downregulation is due to a reduced
availability of ADP (ATP consumption) and a ΔpH
increase, rather than a lack of NADP⁺. In addition to
the above the nature of the active O scavenging pathavailability of ADP (ATP consumption) and a ΔpH
increase, rather than a lack of NADP⁺. In addition to
the above, the nature of the active O₂ scavenging path-
wavs may influence the notential for O₂ exchange. The increase, rather than a lack of NADP⁺. In addition to
the above, the nature of the active O_2 scavenging path-
ways may influence the potential for O_2 exchange. The
potential of algae and cyanobacteria to excrete H the above, the nature of the active O_2 scavenging path-
ways may influence the potential for O_2 exchange. The
potential of algae and cyanobacteria to excrete H_2O_2 to
the external medium would increase the observ potential of algae and cyanobacteria to excrete H_2O_2 to ways may influence the potential for O_2 exchange. The potential of algae and cyanobacteria to excrete H_2O_2 to the external medium would increase the observed O_2 potential of algae and cyanobacteria to excrete H_2O_2 to
the external medium would increase the observed O_2
uptake due to the failure of reduced O_2 to be recycled
to water the extern
uptake due
to water.
Fination take due to the failure of reduced O_2 to be recycled
water.
Environmental factors may obviously affect the poten-
Lof rubisco and Mebler O, untake For rubisco factors

to water.
Environmental factors may obviously affect the potential of rubisco and Mehler O_2 uptake. For rubisco, factors such as water stress that close stomata and limit $CO₂$ will tial of rubisco and Mehler O_2 uptake. For rubisco, factors
such as water stress that close stomata and limit CO_2 will
increase oxygenase. In aquatic environments, where the
diffusion of CO_2 and O_2 is much reduce such as water stress that close stomata and limit CO_2 will
increase oxygenase. In aquatic environments, where the
diffusion of CO_2 and O_2 is much reduced (Badger &
Spalding 2000) increasing carbon limitation and bi increase oxygenase. In aquatic environments, where the
diffusion of CO_2 and O_2 is much reduced (Badger &
Spalding 2000), inorganic carbon limitation and high O_2
stress will also be developed. Oxygenase potential w diffusion of CO_2 and O_2 is much reduced (Badger & Spalding 2000), inorganic carbon limitation and high O_2 stress will also be developed. Oxygenase potential will increase at elevated temperatures due to its effect Spalding 2000), inorganic carbon limitation and high O_2 stress will also be developed. Oxygenase potential will increase at elevated temperatures due to its effects on the

kinetic properties of the enzyme (Badger & Collatz 1977;

Iordan & Ogren 1984) kinetic properties of the
Jordan & Ogren 1984).
For Mebler O, untake

Jordan & Ogren 1984).
For Mehler O₂ uptake, environmental factors that lead Jordan & Ogren 1984).
For Mehler O_2 uptake, environmental factors that lead
to a potential for thylakoid and stromal components to
become more reduced and the NADPH pool to be more For Mehler O_2 uptake, environmental factors that lead
to a potential for thylakoid and stromal components to
become more reduced, and the NADPH pool to be more
oxidized will increase the O_2 , photoreduction potential to a potential for thylakoid and stromal components to
become more reduced, and the NADPH pool to be more
oxidized, will increase the O_2 photoreduction potential.
This includes high light and a lack of PS I accentors a become more reduced, and the NADPH pool to be more oxidized, will increase the O_2 photoreduction potential.
This includes high light and a lack of PS I acceptors as oxidized, will increase the O_2 photoreduction potential.
This includes high light and a lack of PS I acceptors as symight occur under water stress, CO_2 limitation and low definementures temperatures.

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4. MEASURING RUBISCO OXYGENASE AND MEHLER REACTIONS *IN VIVO*

with isolated rubisco, thylakoids and even PS I particles, Although O_2 uptake reactions have been characterized
with isolated rubisco, thylakoids and even PS I particles,
it is obviously of most interest to quantify the various O_2
untake reactions in rine under relevant env with isolated rubisco, thylakoids and even PS I particles,
it is obviously of most interest to quantify the various O_2
uptake reactions *in vivo* under relevant environmental
conditions This however is not a trivial fe it is obviously of most interest to quantify the various O_2
uptake reactions *in vivo* under relevant environmental
conditions. This, however, is not a trivial feat. Measuring
the various O_2 uptake reactions that oc uptake reactions *in vivo* under relevant environmental
conditions. This, however, is not a trivial feat. Measuring
the various O_2 uptake reactions that occur simultaneously
with the evolution of O_2 at PS II is almo conditions. This, however, is not a trivial feat. Measuring
the various O_2 uptake reactions that occur simultaneously
with the evolution of O_2 at PS II is almost impossible and
annroaches can at best, be only annrox

The various O_2 uptake reactions that occur simultaneously
with the evolution of O_2 at PS II is almost impossible and
approaches can, at best, be only approximations.

The fact that O_2 evolved at PS II is derived from $\overline{\circ}$ medium, means that $^{16}O_2$ and $^{18}O_2$ and mass spectrowater, while O_2 uptake is from the O_2 pool in the medium, means that ¹⁶ O_2 and ¹⁸ O_2 and mass spectrometry can be used to resolve the gross fluxes of O_2 evolution and O_2 uptake (Hoch & Kok 1963; Mebler medium, means that ¹⁶O₂ and ¹⁸O₂ and mass spectrometry can be used to resolve the gross fluxes of O₂ evolution and O₂ uptake (Hoch & Kok 1963; Mehler & Brown 1952) While this gives a definitive answer for the metry can be used to resolve the gross fluxes of O_2 evolution and O_2 uptake (Hoch & Kok 1963; Mehler & Brown 1952). While this gives a definitive answer for the absolute rate of PS II driven O_2 evolution other le tion and O_2 uptake (Hoch & Kok 1963; Mehler & Brown
1952). While this gives a definitive answer for the absolute
rate of PS II driven O_2 evolution, other less direct
methods and inferences must resolve the component 1952). While this gives a definitive answer for the absolute
rate of PS II driven O_2 evolution, other less direct
methods and inferences must resolve the components of
gross O untake O pe potential problem with thi rate of PS II driven O_2 evolution, other less direct
methods and inferences must resolve the components of
gross O_2 uptake. One potential problem with this tech-
nique may be encountered in photosynthetic systems methods and inferences must resolve the components of gross O_2 uptake. One potential problem with this technique may be encountered in photosynthetic systems gross O_2 uptake. One potential problem with this technique may be encountered in photosynthetic systems
where either O_2 efflux from PS II or O_2 influx may be
restricted by diffusion barriers (for a review see Bad nique may be encountered in photosynthetic systems
where either O_2 efflux from PS II or O_2 influx may be
restricted by diffusion barriers (for a review, see Badger
1985) This could lead to different O isotone ratios where either O_2 efflux from PS II or O_2 influx may be
restricted by diffusion barriers (for a review, see Badger
1985). This could lead to different O_2 isotope ratios inside
the photosynthetic compartments compar restricted by diffusion barriers (for a review, see Badger 1985). This could lead to different O_2 isotope ratios inside the photosynthetic compartments compared with the isotopic ratios measured externally by mass spec 1985). This could lead to different O_2 isotope ratios inside This could happen in C_4 plants, for example, with PS II isotopic ratios measured externally by mass spectrometry.
This could happen in C_4 plants, for example, with PS II
activities operational in the bundle sheath or in other
organisms with a CO concentrating mechanism that This could happen in C_4 plants, for example, with PS II activities operational in the bundle sheath or in other organisms with a CO_2 concentrating mechanism that restricts O diffusion activities operational i
organisms with a CC
restricts O_2 diffusion.
Manipulation of CC ganisms with a CO_2 concentrating mechanism that
stricts O_2 diffusion.
Manipulation of CO_2 and O_2 levels is a common
ateav to be employed. This approach assumes that

restricts O_2 diffusion.
Manipulation of CO_2 and O_2 levels is a common
strategy to be employed. This approach assumes that
(i) rubisco oxygenase is suppressed by saturating CO. Manipulation of CO_2 and O_2 levels is a common
strategy to be employed. This approach assumes that
(i) rubisco oxygenase is suppressed by saturating CO_2
and that the remaining light-stimulated O_2 untake may strategy to be employed. This approach assumes that

(i) rubisco oxygenase is suppressed by saturating CO_2

and that the remaining light-stimulated O_2 uptake may

be ascribed to Mebler linked reactions: and (ii) that (i) rubisco oxygenase is suppressed by saturating CO_2
and that the remaining light-stimulated O_2 uptake may
be ascribed to Mehler linked reactions; and (ii) that
oxygenase has a relatively low affinity for O commar and that the remaining light-stimulated O_2 uptake may
be ascribed to Mehler linked reactions; and (ii) that
oxygenase has a relatively low affinity for O_2 compared
with Mehler reactions, thus allowing Mehler to proc be ascribed to Mehler linked reactions; and (ii) that
oxygenase has a relatively low affinity for O_2 compared
with Mehler reactions, thus allowing Mehler to proceed
more effectively at low O_2 . The problems with thes oxygenase has a relatively low affinity for O_2 compared
with Mehler reactions, thus allowing Mehler to proceed
more effectively at low O_2 . The problems with these
assumptions are that Mehler reactions may also be with Mehler reactions, thus allowing Mehler to proceed
more effectively at low O_2 . The problems with these
assumptions are that Mehler reactions may also be
decreased by elevated CO if the NADPH pool becomes more effectively at low O_2 . The problems with these
assumptions are that Mehler reactions may also be
decreased by elevated CO_2 if the NADPH pool becomes
more ovidized and that some Mehler reactions such as assumptions are that Mehler reactions may also be
decreased by elevated CO_2 if the NADPH pool becomes
more oxidized and that some Mehler reactions, such as
those in the stroma associated with Ed and MDAR decreased by elevated CO_2 if the NADPH pool becomes
more oxidized and that some Mehler reactions, such as
those in the stroma associated with Fd and MDAR,
require quite high levels of O_1 for maximum activity more oxidized and that some Mehler reactions, such as
those in the stroma associated with Fd and MDAR,
require quite high levels of O_2 for maximum activity
(Furbank & Badger 1983: Mivake et al. 1998) those in the stroma associated with Fd and
require quite high levels of O_2 for maximu
(Furbank & Badger 1983; Miyake *et al.* 1998).
Apart from the mass spectrometric approach quire quite high levels of O_2 for maximum activity
urbank & Badger 1983; Miyake *et al.* 1998). co
Apart from the mass spectrometric approach, quantum elected of PS II (ϕ PS II) measured by chlorophyll fluores

(Furbank & Badger 1983; Miyake *et al.* 1998).
Apart from the mass spectrometric approach, quantum
yield of PS II (ϕ PS II) measured by chlorophyll fluores-
cence (Genty *et al.* 1989) can be used to measure the flux Apart from the mass spectrometric approach, quantum
yield of PS II (ϕ PS II) measured by chlorophyll fluores-
cence (Genty *et al.* 1989) can be used to measure the flux
of electrons through PS II and compared with the yield of PS II (ϕ PS II) measured by chlorophyll fluorescence (Genty *et al.* 1989) can be used to measure the flux of electrons through PS II and compared with the rate of CO₋ fixation (Cornic $\&$ Briantais 1991; Gh cence (Genty *et al.* 1989) can be used to measure the flux
of electrons through PS II and compared with the rate of
 CO_2 fixation (Cornic & Briantais 1991; Ghashghaie &
Cornic 1994: Laisk & Loreto 1996) This is generall of electrons through PS II and compared with the rate of CO_2 fixation (Cornic & Briantais 1991; Ghashghaie & Cornic 1994; Laisk & Loreto 1996). This is generally most applicable at high CO_2 or low O_2 where rubisco $CO₂$ fixation (Cornic & Briantais 1991; Ghashghaie & Cornic 1994; Laisk & Loreto 1996). This is generally most applicable at high $CO₂$ or low $O₂$ where rubisco oxygen-
ase is suppressed and electron flo Cornic 1994; Laisk & Loreto 1996). This is generally most
applicable at high CO_2 or low O_2 where rubisco oxygen-
ase is suppressed, and electron flow can be assumed to be
divided between PCR cycle activity and other applicable at high CO_2 or low O_2 where rubisco oxygenase is suppressed, and electron flow can be assumed to be divided between PCR cycle activity and other electron

 $\frac{1}{\sqrt{2\pi}}$ acceptors such as O_2 . Although this gives a good measure of PS II electron flow the limitations to the manipulation acceptors such as O_2 . Although this gives a good measure
of PS II electron flow, the limitations to the manipulation
of CO, and O, remain as discussed above of $CO₂$ and $O₂$ remain as discussed above. PS II electron flow, the limitations to the manipulation CO_2 and O_2 remain as discussed above.
Finally, to investigate the potential for Mehler O_2 uptake
an in vive photosynthetic system, genetic or chemical

Although O₂ uptake reactions have been characterized
Although O₂ uptake reactions have been characterized
in of this approach is any pleiotropic compensation in with the evolution of O_2 at PS II is almost impossible and
approaches can, at best, be only approximations.
The fact that O_2 evolved at PS II is derived from
water, while O_2 uptake is from the O_2 pool in the
w of CO_2 and O_2 remain as discussed above.
Finally, to investigate the potential for Mehler O_2 uptake
in an *in vivo* photosynthetic system, genetic or chemical
means can be employed to vary the potential of both Finally, to investigate the potential for Mehler O_2 uptake
in an *in vivo* photosynthetic system, genetic or chemical
means can be employed to vary the potential of both
systems. This can be done for example, by specif in an *in vivo* photosynthetic system, genetic or chemical means can be employed to vary the potential of both systems. This can be done, for example, by specifically means can be employed to vary the potential of both
systems. This can be done, for example, by specifically
decreasing the potential of the photosynthetic carbon
oxidation (PCR) cycle activity by the use of antisense systems. This can be done, for example, by specifically
decreasing the potential of the photosynthetic carbon
oxidation (PCR) cycle activity by the use of antisense
RNA approaches aimed at rubisco or other PCR cycle decreasing the potential of the photosynthetic carbon
oxidation (PCR) cycle activity by the use of antisense
RNA approaches aimed at rubisco or other PCR cycle
enzymes without reducing the canacity of the thylakoid oxidation (PCR) cycle activity by the use of antisense RNA approaches aimed at rubisco or other PCR cycle enzymes without reducing the capacity of the thylakoid and stromal reactions associated with Mehler O_2 uptake
(Hudson *et al.* 1992). The most significant potential limita-
tion of this approach is any pleiotropic compensation in
antisense trangenics that might change the (Hudson *et al.* 1992). The most significant potential limitation of this approach is any pleiotropic compensation in antisense trangenics that might change the potential of thylakoid-related reactions. A similar approach tion of this approach is any pleiotropic compensation in
antisense trangenics that might change the potential of
thylakoid-related reactions. A similar approach may be to
target either carbon metabolism or thylakoid reacti antisense trangenics that might change the potential of thylakoid-related reactions. A similar approach may be to target either carbon metabolism or thylakoid reactions with 'specific inhibitors' that may be introduced into intact tissue. This has been done with algae and cyano target either carbon metabolism or thylakoid reactions with 'specific inhibitors' that may be introduced into intact tissue. This has been done with algae and cyano-
bacteria, with compounds such as glycolaldehyde and
PS I artificial acceptors (Li & Canvin 1998; Miller &
Canvin 1989) but has been less used in higher plants bacteria, with compounds such as glycolaldehyde a
PS I artificial acceptors (Li & Canvin 1998; Miller
Canvin 1989) but has been less used in higher plants.

5. THE ACTIVITY AND PHYSIOLOGICAL FUNCTION E ACTIVITY AND PHYSIOLOGICAL FUNCTION
OF PHOTOSYNTHETIC OXYGEN UPTAKE
IN PHOTOTROPHS OF PHOTOSYNTHETIC OXYGEN UPTAKE
IN PHOTOTROPHS

(a) *C***³** *plants*

 $\begin{array}{c} \textbf{(a)} \text{ } \textbf{C}_3 \text{ plants} \end{array}$
Although both photorespiration and the Mehler reac-(a) C_3 plants

Although both photorespiration and the Mehler reac-

tion can be seen as unwanted reactions resulting from the

presence of high Q_2 , in the atmosphere, both reactions Although both photorespiration and the Mehler reaction can be seen as unwanted reactions resulting from the presence of high O_2 in the atmosphere, both reactions have been ascribed a role in dissinating excess light tion can be seen as unwanted reactions resulting from the
presence of high O_2 in the atmosphere, both reactions
have been ascribed a role in dissipating excess light
energy and thus protecting against photodamage in presence of high O_2 in the atmosphere, both reactions
have been ascribed a role in dissipating excess light
energy and thus protecting against photodamage in
higher plants and other overgoic phototrophs (Osmond have been ascribed a role in dissipating excess light
energy and thus protecting against photodamage in
higher plants and other oxygenic phototrophs (Osmond
& Grace 1995). The metabolic functions of the photoenergy and thus protecting against photodamage in
higher plants and other oxygenic phototrophs (Osmond
& Grace 1995). The metabolic functions of the photo-
respiratory cycle are obviously essential for the recovery higher plants and other oxygenic phototrophs (Osmond & Grace 1995). The metabolic functions of the photo-
respiratory cycle are obviously essential for the recovery
of carbon and nitrogen associated with the production of respiratory cycle are obviously essential for the recovery
of carbon and nitrogen associated with the production of glycolate (Somerville & Ogren 1982) and C_3 plants are of carbon and nitrogen associated with the production of glycolate (Somerville & Ogren 1982) and C_3 plants are unable to grow without it. However, recent work with transcenic tobacco with altered levels of chloroplast glycolate (Somerville & Ogren 1982) and C_3 plants are
unable to grow without it. However, recent work with
transgenic tobacco with altered levels of chloroplast gluta-
mine synthetase (Kozaki & Takeba 1996) has clearly unable to grow without it. However, recent work with
transgenic tobacco with altered levels of chloroplast gluta-
mine synthetase (Kozaki & Takeba 1996) has clearly
emphasized its role in limiting photodamage at high transgenic tobacco with altered levels of chloroplast gluta-
mine synthetase (Kozaki & Takeba 1996) has clearly
emphasized its role in limiting photodamage at high light. phasized its role in limiting photodamage at high
ht.
The potential photoprotective role of the Mehler reac-

light.
The potential photoprotective role of the Mehler reaction has been less well documented. Various experimental
approaches have been used to infer that up to 30% of The potential photoprotective role of the Mehler reaction has been less well documented. Various experimental approaches have been used to infer that up to 30% of electron transport could proceed directly to Ω , unde tion has been less well documented. Various experimental
approaches have been used to infer that up to 30% of
electron transport could proceed directly to O_2 under
various conditions (Lovelock & Winter 1996; Oemond approaches have been used to infer that up to 30% of
electron transport could proceed directly to O_2 under
various conditions (Lovelock & Winter 1996; Osmond &
Grace 1995). However the data have been equivocal and electron transport could proceed directly to O_2 under
various conditions (Lovelock & Winter 1996; Osmond &
Grace 1995). However, the data have been equivocal and various conditions (Lovelock & Winter 1996; Osmond &
Grace 1995). However, the data have been equivocal and
some questions have remained about the quantitative
contributions of both Mehler reaction and photorespira-Grace 1995). However, the data have been equivocal and
some questions have remained about the quantitative
contributions of both Mehler reaction and photorespira-
tion to supporting extra electron transport under various some questions have remained about the quantitative
contributions of both Mehler reaction and photorespira-
tion to supporting extra electron transport under various
conditions. In an attempt to resolve the quantitative contributions of both Mehler reaction and photorespira-
tion to supporting extra electron transport under various
conditions. In an attempt to resolve the quantitative tion to supporting extra electron transport under various
conditions. In an attempt to resolve the quantitative
contribution of both O_2 consuming reactions to sustain
electron transport, the following attempts to summa conditions. In an attempt to resolve the quantitative
contribution of both O_2 consuming reactions to sustain
electron transport, the following attempts to summarize
recent and past data that may lead to a clearer pictu contribution of both O_2 consuming reactions to sustain electron transport, the following attempts to summarize recent and past data that may lead to a clearer picture. (i) *Transgenics with reduced rubisco*

With the development of antisense RNA approaches to (i) Transgenics with reduced rubisco
With the development of antisense RNA approaches to
altering aspects of plant metabolism, the opportunity has
arisen to study the potential contributions of Mebler and With the development of antisense RNA approaches to
altering aspects of plant metabolism, the opportunity has
arisen to study the potential contributions of Mehler and
photorespiratory O exchange in plants where there have altering aspects of plant metabolism, the opportunity has
arisen to study the potential contributions of Mehler and
photorespiratory O_2 exchange in plants where there have
been manipulations of the relative canceities arisen to study the potential contributions of Mehler and
photorespiratory O_2 exchange in plants where there have
been manipulations of the relative capacities of thylakoid

Figure 1. Net CO_2 and O_2 exchange, together with gross O_2 evolution and uptake of (*a*) wild-type and (*b*,*c*) anti-SSu tobacco ((*b*) 40% rubisco; (*c*) 10% rubisco), in response to external CO_2 . The data are Figure 1. Net CO_2 and O_2 exchange, together with gross O_2 evolution and uptake of (*a*) wild-type and (*b*,*c*) anti-SSu tobacc ((*b*) 40% rubisco; (*c*) 10% rubisco), in response to external CO_2 . The data are t (*b*) 40% rubisco; *(c*) 10% rubisco), in response to external CO₂. The data are taken from Ruuska *et al.* (2000) and the methods are described therein. The measurements were made at 20% O₂, 970 µmol m⁻²s⁻¹ irrad averages of data obtained from three to four plants of each genotype. The amount of rubisco in each genotype, compared with

electron transport and stromal rubisco, PCR and PCO recycle capacities. Recent studies of transcenic tobacco with tion electron transport and stromal rubisco, PCR and PCO
cycle capacities. Recent studies of transgenic tobacco with
an antisense gene directed against the mRNA of the electron transport and stromal rubisco, PCR and PCO
cycle capacities. Recent studies of transgenic tobacco with
an antisense gene directed against the mRNA of the
small subunit of rubisco have provided invaluable insights cycle capacities. Recent studies of transgenic tobacco with
an antisense gene directed against the mRNA of the
small subunit of rubisco have provided invaluable insights
into the role of Ω , as an electron accentor durin an antisense gene directed against the mRNA of the
small subunit of rubisco have provided invaluable insights
into the role of O_2 as an electron acceptor during photo-
synthesis (Ruuska *et al.* 2000) Rubisco canacity small subunit of rubisco have provided invaluable insights
into the role of O_2 as an electron acceptor during photo-
synthesis (Ruuska *et al.* 2000). Rubisco capacity was
reduced by up to 90% in the most severely affe into the role of O_2 as an electron acceptor during photo-
synthesis (Ruuska *et al.* 2000). Rubisco capacity was
reduced by up to 90% in the most severely affected plants without a similar reduction in electron transport capacity, reduced by up to 90% in the most severely affected plants
without a similar reduction in electron transport capacity,
thus providing an opportunity to quantify the contribu-
tion of Mehler reaction O, untake in plants wher without a similar reduction in electron transport capacity,
thus providing an opportunity to quantify the contribu-
tion of Mehler reaction O_2 uptake in plants where the
potential contribution of photorespiratory O_2 thus providing an opportunity to quantify the contribu-
tion of Mehler reaction O_2 uptake in plants where the
potential contribution of photorespiratory O_2 varied
greatly greatly. potential contribution of photorespiratory O₂ varied
greatly.
In the studies of Ruuska *et al.* (2000), concurrent

greatly.

In the studies of Ruuska *et al.* (2000), concurrent

measurements of chlorophyll fluorescence and CO_2

assimilation rates at different CO and O partial pres-In the studies of Ruuska *et al.* (2000), concurrent
measurements of chlorophyll fluorescence and CO_2
assimilation rates at different CO_2 and O_2 partial pres-
sures showed close linear relationships between chloromeasurements of chlorophyll fluorescence and CO_2
assimilation rates at different CO_2 and O_2 partial pres-
sures showed close linear relationships between chloro-
plast electron transport rates calculated from chlor assimilation rates at different CO_2 and O_2 partial pressures showed close linear relationships between chlorosures showed close linear relationships between chloro-
plast electron transport rates calculated from chlorophyll
fluorescence and from CO_2 fixation. Furthermore, these
relationships were similar for wild-type and tran plast electron transport rates calculated from chlorophyll
fluorescence and from CO_2 fixation. Furthermore, these
relationships were similar for wild-type and transgenic
plants, indicating that the reduced canceity for fluorescence and from $CO₂$ fixation. Furthermore, these relationships were similar for wild-type and transgenic
plants, indicating that the reduced capacity for rubisco
carboxylase and oxygenase activity in the transgenic
plants did not result in extra electron transport to som plants, indicating that the reduced capacity for rubisco carboxylase and oxygenase activity in the transgenic
plants did not result in extra electron transport to some
other alternative electron acceptor such as the Mehler carboxylase and oxygenase activity in the transgenic

reaction. More direct investigations of O_2 uptake reactions using mass spectrometry showed a number of results that supported this initial observation. There was an excellent correlation between electron transport rate that supported this initial observation. There was an excellent correlation between electron transport rates that supported this initial observation. There was an excellent correlation between electron transport rates measured from CO_2 fixation, chlorophyll fluorescence and gross O_2 evolution in wild-type and transgenics at excellent correlation between electron transport rates
measured from CO_2 fixation, chlorophyll fluorescence
and gross O_2 evolution in wild-type and transgenics at all
 O_2 concentrations. In all tobacco lines studie measured from CO_2 fixation, chlorophyll fluorescence
and gross O_2 evolution in wild-type and transgenics at all
 O_2 concentrations. In all tobacco lines studied, the dark
rates of respiratory O_2 untake were simi and gross O_2 evolution in wild-type and transgenics at all O_2 concentrations. In all tobacco lines studied, the dark rates of respiratory O_2 uptake were similar to the O_2 uptake in the light measured at very h O_2 concentrations. In all tobacco lines studied, the dark
rates of respiratory O_2 uptake were similar to the O_2
uptake in the light measured at very high CO_2 , where
photorespiratory O_2 uptake should be suppr rates of respiratory O_2 uptake were similar to the O_2
uptake in the light measured at very high CO_2 , where
photorespiratory O_2 uptake should be suppressed (figure 1).
This strongly suggested that at high CO, th uptake in the light measured at very high CO_2 , where
photorespiratory O_2 uptake should be suppressed (figure 1).
This strongly suggested that at high CO_2 there was little
evidence for a significant light-dependent photorespiratory O_2 uptake should be suppressed (figure 1).
This strongly suggested that at high CO_2 there was little This strongly suggested that at high CO_2 there was little evidence for a significant light-dependent O_2 uptake such as Mehler reaction. At the CO_2 compensation point, the rates of rubisco oxygenses activity calcula evidence for a significant light-dependent O_2 uptake such
as Mehler reaction. At the CO_2 compensation point, the
rates of rubisco oxygenase activity calculated from O_2
untake were linearly related to the rubisco c as Mehler reaction. At the CO_2 compensation point, the rates of rubisco oxygenase activity calculated from O_2 uptake were linearly related to the rubisco content of the measured leaves (figure 2). Indeed, all analyse rates of rubisco oxygenase activity calculated from O_2 uptake were linearly related to the rubisco content of the measured leaves (figure 2). Indeed, all analyses under compensation point conditions strongly suggested uptake were linearly related to the rubisco content of the measured leaves (figure 2). Indeed, all analyses under
compensation point conditions strongly suggested that in
both wild-type and transgenics light-stimulated O_2
untake could be accounted for solely by the varying compensation point conditions strongly suggested that in
both wild-type and transgenics light-stimulated O_2
uptake could be accounted for solely by the varying
rubisco expresses activity in the measured plants. Thus both wild-type and transgenics light-stimulated O_2
uptake could be accounted for solely by the varying
rubisco oxygenase activity in the measured plants. Thus
again there was little room for inferring the operation uptake could be accounted for solely by the varying
rubisco oxygenase activity in the measured plants. Thus
again there was little room for inferring the operation rubisco oxygenase activity in the measured plants. Thus of a significant Mehler reaction under $CO₂$ -limited conditions.

reaction. More direct investigations of O_2 uptake reacreaction. More direct investigations of O_2 uptake reactions using mass spectrometry showed a number of results that supported this initial observation. There was an

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% rates (for a review, see Ruuska *et al.* 2000).
(ii) *Environmental influences* Figure 2. (*a*) Gross O_2 uptake rates and (*b*) rubisco oxygenase
rates, V_o at the CO_2 compensation point, Γ . The data in (*b*)
were calculated from (*a*) as a function of rubisco site rates, V_0 at the CO₂ compensation point, Γ . The data in (*b*) were calculated from (*a*), as a function of rubisco site rates, V_o at the CO₂ compensation point, Γ . The data in (*b* were calculated from (*a*), as a function of rubisco site concentrations in wild-type and anti-SSu tobacco plants.
Measurements were made at 20% 10% and were calculated from (a) , as a function of rubisco site
concentrations in wild-type and anti-SSu tobacco plants.
Measurements were made at 20%, 10% and 2% O₂ and
25 °C. The calculation of *V*, was as previously describ concentrations in wild-type and anti-SSu tobacco plants.
Measurements were made at 20% , 10% and 2% O₂ and
 25° C. The calculation of V_0 was as previously described
(Runska *et al.* 2000). The lines are th Measurements were made at 20%, 10% and 2% O_2 and
25 °C. The calculation of V_o was as previously described
(Ruuska *et al.* 2000). The lines are the theoretical oxygenase
or O untake rates predicted from the equation 25 °C. The calculation of V_0 was as previously described
(Ruuska *et al.* 2000). The lines are the theoretical oxygenase
or O_2 uptake rates predicted from the equation for oxygenase
rates (for a rayiaw see Buuska *e* (Ruuska *et al.* 2000). The lines are the theore
or O₂ uptake rates predicted from the equati
rates (for a review, see Ruuska *et al.* 2000).

Changes in the relative contributions of both phototo occur as a result of environmental stresses that may cause limitations to carbon assimilation or excess light to occur as a result of environmental stresses that may
cause limitations to carbon assimilation or excess light
interception by the photosystems (Asada 1999; Osmond
& Grace 1995; Polle 1996) These stresses include high cause limitations to carbon assimilation or excess light
interception by the photosystems (Asada 1999; Osmond
& Grace 1995; Polle 1996). These stresses include high
light water deficit and both low and high temperature interception by the photosystems (Asada 1999; Osmond & Grace 1995; Polle 1996). These stresses include high light, water deficit and both low and high temperature D_{stresses}.

(iii) *Combined water de¢cit and high light stress*

Closure of stomata and the presence of high light intensities generally accompany water stress in leaves. Under Closure of stomata and the presence of high light intensities generally accompany water stress in leaves. Under
these conditions, plants experience their most stressful
conditions with respect to a potential limitation of sities generally accompany water stress in leaves. Under
these conditions, plants experience their most stressful
conditions with respect to a potential limitation of elec-
tron acceptors at PS I and the continued input of these conditions, plants experience their most stressful
conditions with respect to a potential limitation of elec-
tron acceptors at PS I and the continued input of light
energy into the chlorophyll antennae. It is theref conditions with respect to a potential limitation of electron acceptors at PS I and the continued input of light
energy into the chlorophyll antennae. It is therefore not
surprising that there has been considerable interes tron acceptors at PS I and the continued input of light
energy into the chlorophyll antennae. It is therefore not
surprising that there has been considerable interest in the
ability of various energy dissinating mechanisms enabling plants to minimize long-term damage under ability of various energy dissipating mechanisms in
enabling plants to minimize long-term damage under
these conditions. The role of photorespiration, Mehler
reaction and non-radiative (thermal) energy dissipation enabling plants to minimize long-term damage under
these conditions. The role of photorespiration, Mehler
reaction and non-radiative (thermal) energy dissipation
in the antennae have all been implicated and the quantithese conditions. The role of photorespiration, Mehler
reaction and non-radiative (thermal) energy dissipation
in the antennae have all been implicated and the quanti-
tative contribution of each considered reaction and non-radiative (thermal) energy dissipation
in the antennae have all been implicated and the quanti-
tative contribution of each considered.

(Flexas *et al*. 1999) and madrone (*Arbutus menziesii*) (O. Recent studies focusing on water-stressed grapes
(Flexas *et al.* 1999) and madrone *(Arbutus menziesii*) (O.
Björkman and M. R. Badger, unpublished data; Osmond
et al. 1997) have added some interesting data, pointing to (Flexas *et al.* 1999) and madrone *(Arbutus menziesii)* (O. Björkman and M. R. Badger, unpublished data; Osmond *et al.* 1997) have added some interesting data, pointing to a minimal role for the Mebler reaction under suc Björkman and M. R. Badger, unpublished data; Osmond
et al. 1997) have added some interesting data, pointing to
a minimal role for the Mehler reaction under such condi-
tions. One difficult aspect of studying water stress i *et al.* 1997) have added some interesting data, pointing to a minimal role for the Mehler reaction under such conditions. One difficult aspect of studying water stress is that a minimal role for the Mehler reaction under such condi-
tions. One difficult aspect of studying water stress is that
it is accompanied by stomatal closure that makes it
difficult to schieve saturating levels of CO, in the tions. One difficult aspect of studying water stress is that
it is accompanied by stomatal closure that makes it
difficult to achieve saturating levels of CO_2 in the chloro-
plast Under these conditions there is an over it is accompanied by stomatal closure that makes it
difficult to achieve saturating levels of CO_2 in the chloro-
plast. Under these conditions, there is an over estimation
of Mehler reaction at elevated CO, through a fa difficult to achieve saturating levels of CO_2 in the chloro-
plast. Under these conditions, there is an over estimation
of Mehler reaction at elevated CO_2 through a failure to
suppress rubisco oxygenase fully. In wate plast. Under these conditions, there is an over estimation
of Mehler reaction at elevated CO_2 through a failure to
suppress rubisco oxygenase fully. In water-stressed pota-
toes (Tourneux & Peltier 1994) grapes (Flexas of Mehler reaction at elevated CO₂ through a failure to
suppress rubisco oxygenase fully. In water-stressed pota-
toes (Tourneux & Peltier 1994), grapes (Flexas *et al.* 1999)
and madrone (O. Biörkman and M. R. Badger, u suppress rubisco oxygenase fully. In water-stressed potatoes (Tourneux & Peltier 1994), grapes (Flexas *et al.* 1999) and madrone (O. Björkman and M. R. Badger, unpubtoes (Tourneux & Peltier 1994), grapes (Flexas *et al.* 1999)
and madrone (O. Björkman and M. R. Badger, unpub-
lished data) it is obvious that the CO_2 required was
considerably increased compared with unstressed plants and madrone (O. Björkman and M. R. Badger, unpub-
lished data) it is obvious that the CO_2 required was
considerably increased compared with unstressed plants.
However, when CO_2 was elevated sufficiently sometimes lished data) it is obvious that the CO_2 required was considerably increased compared with unstressed plants.
However, when CO_2 was elevated sufficiently, sometimes considerably increased compared with unstressed plants.
However, when CO_2 was elevated sufficiently, sometimes
requiring as high as 2% CO_2 , O_2 uptake in the light was
suppressed to near dark levels of O , uptak However, when CO_2 was elevated sufficiently, sometimes
requiring as high as 2% CO_2 , O_2 uptake in the light was
suppressed to near dark levels of O_2 uptake. In madrone
at the CO, compensation point, bigh level requiring as high as 2% CO₂, O₂ uptake in the light was
suppressed to near dark levels of O₂ uptake. In madrone
at the CO₂ compensation point, high levels of O₂ uptake
were observed showing an O₂ affinity r suppressed to near dark levels of O_2 uptake. In madrone
at the CO_2 compensation point, high levels of O_2 uptake
were observed, showing an O_2 affinity requiring in excess
of 30% O_2 for half saturation. At hig at the CO_2 compensation point, high levels of O_2 uptake
were observed, showing an O_2 affinity requiring in excess
of 30% O_2 for half saturation. At high light intensities,
the O_2 uptake rates at the compensa were observed, showing an O_2 affinity requiring in excess
of 30% O_2 for half saturation. At high light intensities,
the O_2 uptake rates at the compensation point in air were
able to support about 50% of the maxim of 30% O_2 for half saturation. At high light intensities,
the O_2 uptake rates at the compensation point in air were
able to support about 50% of the maximum electron transport rate at saturating $CO₂$.

Recent studies focusing on water-stressed grapes

. An analysis of the contribution of the pathways for transport rate at saturating CO_2 .
An analysis of the contribution of the pathways for
energy dissipation in madrone under the highest irradi-
ance and most water-stressed conditions indicated that An analysis of the contribution of the pathways for
energy dissipation in madrone under the highest irradi-
ance and most water-stressed conditions indicated that
non-radiative energy dissipation (NRD) was by far the energy dissipation in madrone under the highest irradiance and most water-stressed conditions indicated that
non-radiative energy dissipation (NRD) was by far the
most important contributing in excess of 60% photon ance and most water-stressed conditions indicated that
non-radiative energy dissipation (NRD) was by far the
most important, contributing in excess of 60% photon
dissipation. Residual CO, untake was as low as 5% non-radiative energy dissipation (NRD) was by far the
most important, contributing in excess of 60% photon
dissipation. Residual CO_2 uptake was as low as 5%,
while photosynthetic O_2 uptake was responsible for the most important, contributing in excess of 60% photon
dissipation. Residual CO_2 uptake was as low as 5%,
while photosynthetic O_2 uptake was responsible for the
remainder (around 35%). From the O_2 exchange characdissipation. Residual CO_2 uptake was as low as 5%,
while photosynthetic O_2 uptake was responsible for the
remainder (around 35%). From the O_2 exchange charac-
teristics described above, the conclusion was reached while photosynthetic O_2 uptake was responsible for the
remainder (around 35%). From the O_2 exchange charac-
teristics described above, the conclusion was reached that
photorespiratory O_1 uptake, probably contribu remainder (around 35%). From the O_2 exchange characteristics described above, the conclusion was reached that photorespiratory O_2 uptake probably contributed the teristics described above, the conclusion was reached that
photorespiratory O_2 uptake probably contributed the
great majority of this O_2 uptake and the Mehler reaction
was only a minor component (O Biörkman and M R photorespiratory O_2 uptake probably contributed the great majority of this O_2 uptake and the Mehler reaction was only a minor component (O. Björkman and M. R. Radger uppublished data) great majority of this O_2 up
was only a minor compone
Badger, unpublished data).
However, the above concl was only a minor component (O. Björkman and M. R.
Badger, unpublished data).
However, the above conclusions are somewhat at odds

Changes in the relative contributions of both photo-
respirators in wheat is associated with a Mehler respiratory and Mehler O₂ uptake have been suggested
reaction. These studies attempted to measure the photo-Badger, unpublished data).
However, the above conclusions are somewhat at odds
with the findings of Biehler & Fock (1996), where it has
been suggested that a rise in Ω , untake during water-However, the above conclusions are somewhat at odds
with the findings of Biehler & Fock (1996), where it has
been suggested that a rise in O_2 uptake during water-
stress imposition in wheat is associated with a Mehler with the findings of Biehler & Fock (1996), where it has
been suggested that a rise in O_2 uptake during water-
stress imposition in wheat is associated with a Mehler
reaction. These studies attempted to measure the pho been suggested that a rise in O_2 uptake during waterstress imposition in wheat is associated with a Mehler
reaction. These studies attempted to measure the photo-
respiratory component of O_2 uptake by measuring glyco-
late synthesis rates. They found a decrease in glyco reaction. These studies attempted to measure the photo-
respiratory component of O_2 uptake by measuring glycolate
late synthesis rates. They found a decrease in glycolate
production and an increased O uptake attribut respiratory component of O_2 uptake by measuring glycolate
late synthesis rates. They found a decrease in glycolate
production and an increased O_2 uptake attributable to
Mebler reactions. However, under conditions of late synthesis rates. They found a decrease in glycolate production and an increased O_2 uptake attributable to production and an increased O_2 uptake attributable to
Mehler reactions. However, under conditions of closing
stomata, and an undefined and declining chloroplastic
CO, it is always a strong possibility that in C, plants $CO₂$, it is always a strong possibility that in $C₃$ plants rubisco oxygenase will be stimulated. ler reactions. However, under conditions of closing
ata, and an undefined and declining chloroplastic
, it is always a strong possibility that in C_3 plants
sco oxygenase will be stimulated stomata, and an undefined and declining chloroplastic

(iv) *Temperature*

energy into the chlorophyll antennae. It is therefore not
 \sim ability of various energy dissipating mechanisms in
 \sim ability of various energy dissipating mechanisms in

energy dissipation will increase at elevated t High temperatures cause a decrease in the affinity of (iv) *Temperature*
High temperatures cause a decrease in the affinity of
rubisco for CO_2 while increasing the relative affinity for
 O . However, the V of both reactions increases simi- O_2 . However, the V_{max} of both reactions increases similarly (Badger & Collatz 1977; Jordan & Ogren 1984).
Thus the potential for photorespiratory O_2 uptake and energy dissipation will increase at elevated tempe High temperatures cause a decrease in the affinity of
bisco for CO_2 while increasing the relative affinity for
. However, the V_{max} of both reactions increases simi-
. (Radger & Collatz 1977: Iordan & Ogrep 1984) rubisco for CO_2 while increasing the relative affinity for O_2 . However, the V_{max} of both reactions increases similarly (Badger & Collatz 1977; Jordan & Ogren 1984).
Thus the potential for photorespiratory O unta larly (Badger & Collatz 1977; Jordan & Ogren 1984). Thus the potential for photorespiratory O_2 uptake and energy dissipation will increase at elevated temperatures, lower temperatures, a decrease in the activity of oxygeother parts of the photosynthetic machinery. However, at
lower temperatures, a decrease in the activity of oxyge-
nase activity and a decrease in V_{max} of both rubisco reac-
tions will mean that the potential for photo lower temperatures, a decrease in the activity of oxygenase activity and a decrease in V_{max} of both rubisco reactions will mean that the potential for photorespiratory O_2 untake will decrease. When combined with b nase activity and a decrease in V_{max} of both rubisco reactions will mean that the potential for photorespiratory O_2 uptake will decrease. When combined with high light

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Figure 3. Gross O_2 evolution and uptake rates in wild-type and 40% anti-SSu tobacco plants as a function of leaf temperary Fluxes at (*a*) high (2%) CO₂ and (*b*) the compensation point (*Γ*). (*c*,*d*) A comparison ŏ Figure 3. Gross O₂ evolution and uptake rates in wild-type and 40% anti-SSu tobacco plants as a
Fluxes at (a) high (2%) CO₂ and (b) the compensation point (*Γ*). (c,*d*) A comparison of gross O₂ v
2 and 21% O₂ in is a function of leaf temper
 v_2 uptake at high CO_2 at irradiance and various
nemmerer and M-R-Bad Fluxes at (a) high (2%) CO_2 and (b) the compensation point (*Γ*). (c,d) A comparison of gross O_2 uptake at high CO_2 at 2 and 21% O_2 in the light and the dark. Measurements were made at 1.7 mmol quanta m⁻² s⁻¹ 2 and 21% O_2 in the l
temperatures, as previ
(unpublished data).

intensities, this will mean that rubisco oxygenaseintensities, this will mean that rubisco oxygenase-
supported O_2 uptake will play a greater role as an
electron accentor at elevated temperatures, and converintensities, this will mean that rubisco oxygenase-
supported O_2 uptake will play a greater role as an
electron acceptor at elevated temperatures, and conver-
selv will decline in importance at low temperatures supported O_2 uptake will play a greater role as an electron acceptor at elevated temperatures, and conversely will decline in importance at low temperatures.
Considering this light-stimulated Mebler reaction may temperatures. be expected to increase in quantitative importance at low
temperatures.
Testing this and other aspects of rubisco's response to

temperatures.
Testing this and other aspects of rubisco's response to
temperature, H. Nakano, S. von Caemmerer and M. R.
Radger (unpublished data) have investigated the response Testing this and other aspects of rubisco's response to
temperature, H. Nakano, S. von Caemmerer and M. R.
Badger (unpublished data) have investigated the response
of photosynthetic O. exchange in the rubisco antisense temperature, H. Nakano, S. von Caemmerer and M. R.
Badger (unpublished data) have investigated the response
of photosynthetic O₂ exchange in the rubisco antisense
tehacco transgenies described in $\delta 5(a)(i)$ with about Badger (unpublished data) have investigated the response
of photosynthetic O_2 exchange in the rubisco antisense
tobacco transgenics described in $\S 5(a)(i)$, with about % of photosynthetic O_2 exchange in the rubisco antisense
tobacco transgenics described in §5(a)(i), with about
40% of wild-type rubisco levels. Figure 3*a* shows that
over a temperature range from 7–40 °C electron tran tobacco transgenics described in §5(a)(i), with about 40% of wild-type rubisco levels. Figure 3*a* shows that over a temperature range from 7-40 °C electron transport at very high CO and 21% O measured by gross O 40% of wild-type rubisco levels. Figure 3*a* shows that
over a temperature range from 7–40°C electron transport
at very high CO_2 and 21% O_2 , measured by gross O_2
evolution was similar in magnitude and response in over a temperature range from 7–40°C electron transport
at very high CO_2 and 21% O_2 , measured by gross O_2
evolution, was similar in magnitude and response in the
wild-type and transgenics. At the CO_2 compensatio at very high CO_2 and 21% O_2 , measured by gross O_2 carboxykinase (PCK) type C_4 plants have O_2 uptakes evolution, was similar in magnitude and response in the that approach the lower end of $C_3 O_2$ uptake evolution, was similar in magnitude and response in the
wild-type and transgenics. At the CO_2 compensation
point, the gross O_2 evolution scaled with the rubisco
content of the leaves (figure 3b) Considering O, untake wild-type and transgenics. At the CO_2 compensation
point, the gross O_2 evolution scaled with the rubisco
content of the leaves (figure 3*c*). Considering O_2 uptake
at very high CO_2 (figure 3*c*) at 2% O_2 O up point, the gross O_2 evolution scaled with the rubisco
content of the leaves (figure 3*b*). Considering O_2 uptake
at very high CO_2 (figure 3*c*), at 2% O_2 , O_2 uptake was
similar in the light and in the dark i content of the leaves (figure 3*b*). Considering O_2 uptake
at very high CO_2 (figure 3*c*), at 2% O_2 , O_2 uptake was
similar in the light and in the dark in both wild-type and
transcenies at all temperatures (fig at very high CO_2 (figure 3*c*), at 2% O_2 , O_2 uptake was similar in the light and in the dark in both wild-type and transgenics at all temperatures (figure 3*c*,*d*). At 21% O_2 , O_2 uptake was similar between transgenics at all temperatures (figure $3c,d$). At 21% O₂, similar in the light and in the dark in both wild-type and transgenics at all temperatures (figure 3c,d). At 21% O_2 ,
 O_2 uptake was similar between wild-type and transgenics

at temperatures below 25 °C, but appeared to show a

greater increase in wild-type up to 40 °C (fig O_2 uptake was similar between wild-type and transgenics
at temperatures below 25 °C, but appeared to show a
greater increase in wild-type up to 40 °C (figure 3*c*),
probably indicating a inability to entirely suppress at temperatures below 25 °C, but appeared to show a greater increase in wild-type up to 40 °C (figure 3c), probably indicating a inability to entirely suppress rubisco oxygense at these bigher temperatures greater increase in wild-type up to 40° C (figure $3c$), probably indicating a inability to entirely suppress rubisco oxygenase at these higher temperatures.
The results over a wide temperature range show no probably indicating a inability to entirely suppress rubisco

evidence for any increased photosynthetic O_2 uptake at The results over a wide temperature range show no
evidence for any increased photosynthetic O_2 uptake at
low temperatures that could be ascribed to a greater
activity of Mehler reaction or any O uptake at high evidence for any increased photosynthetic O_2 uptake at how temperatures that could be ascribed to a greater activity of Mehler reaction or any O_2 uptake at high temperatures that cannot be explained adequately by low temperatures that could be ascribed to a greater
activity of Mehler reaction or any O_2 uptake at high
temperatures that cannot be explained adequately by
increasing rubisco oxygenase activity. activity of Mehler reaction or any O_2 uptake at high
temperatures that cannot be explained adequately by
increasing rubisco oxygenase activity.

(b) *C***⁴** *plants*

electron acceptor at elevated temperatures, and conver-
sely will decline in importance at low temperatures. experimental evidence has been produced to change our Considering this, light-stimulated Mehler reaction may views. The difference between C_3 and C_4 plants is
be expected to increase in quantitative importance at low primarily that the level of light-dependent O_2 up (b) C_4 plants

Photosynthetic O_2 uptake in C_4 plants has been

eviously reviewed (Badger 1985) and little new (b) C_4 plants

Photosynthetic O_2 uptake in C_4 plants has been

previously reviewed (Badger 1985) and little new

experimental evidence has been produced to change our Photosynthetic O_2 uptake in C_4 plants has been
previously reviewed (Badger 1985) and little new
experimental evidence has been produced to change our
views. The difference between C_4 and C_5 plants is previously reviewed (Badger 1985) and little new experimental evidence has been produced to change our
views. The difference between C_3 and C_4 plants is
primarily that the level of light-dependent O_2 uptake is
generally much lower in C_1 plants and is relativ views. The difference between C_3 and C_4 plants is
primarily that the level of light-dependent O_2 uptake is
generally much lower in C_4 plants and is relatively insen-
sitive to the external CO₋ concentration. primarily that the level of light-dependent O_2 uptake is generally much lower in C_4 plants and is relatively insensitive to the external CO_2 concentration. Such a major generally much lower in C_4 plants and is relatively insensitive to the external CO_2 concentration. Such a major difference is readily attributed to the operation of the C_4 CO_2 concentrating mechanism that suppre difference is readily attributed to the operation of the C_4
 CO_2 concentrating mechanism that suppresses rubisco
oxygenase activity in the bundle sheath. This difference,
in fact, points to the conclusion that PCO cyc $CO₂$ concentrating mechanism that suppresses rubisco
oxygenase activity in the bundle sheath. This difference,
in fact, points to the conclusion that PCO cycle $O₂$ uptake is the major light-dependent O_2 uptake process at in fact, points to the conclusion that PCO cycle O_2
uptake is the major light-dependent O_2 uptake process at
limiting CO_2 in C_3 plants. The phosphoenolpyruvate
carboxykinase (PCK) type C_1 plants have O_2 u uptake is the major light-dependent O_2 uptake process at
limiting CO_2 in C_3 plants. The phosphoenolpyruvate
carboxykinase (PCK) type C_4 plants have O_2 uptakes
that approach the lower end of C_1 . O, uptake limiting CO_2 in C_3 plants. The phosphoenolpyruvate
carboxykinase (PCK) type C_4 plants have O_2 uptakes
that approach the lower end of $C_3 O_2$ uptake (Furbank &
Radger 1982). However, this extra O_2 uptake app that approach the lower end of $C_3 O_2$ uptake (Furbank & that approach the lower end of $C_3 O_2$ uptake (Furbank & Badger 1982). However, this extra O_2 uptake appears to be associated with bundle sheath mitochondrial O_2 uptake associated with NAD-malic enzume activity Badger 1982). However, this extra O_2 uptake appears to
be associated with bundle sheath mitochondrial O_2
uptake, associated with NAD-malic enzyme activity
involved in malate decarboxylation (Hatch 1997) be associated with bundle sheath mitochondri
uptake, associated with NAD-malic enzyme a
involved in malate decarboxylation (Hatch 1997).
Despite the low O, uptake rates particular take, associated with NAD-malic enzyme activity
volved in malate decarboxylation (Hatch 1997).
Despite the low O_2 uptake rates, particularly in
ADP-malic enzyme C types photosynthetic Q uptake

involved in malate decarboxylation (Hatch 1997).
Despite the low O_2 uptake rates, particularly in NADP-malic enzyme C_4 types, photosynthetic O_2 uptake % isomorphic (Hatch 1997).

uptake rates, particularly in

types, photosynthetic O₂ uptake

to occur at quite high rates in Despite the low O_2 uptake rates, particularly in
NADP-malic enzyme C_4 types, photosynthetic O_2 uptake
clearly has the potential to occur at quite high rates in
isolated mesonbull chloroplasts of a range of C spec NADP-malic enzyme C_4 types, photosynthetic O_2 v
clearly has the potential to occur at quite high ra
isolated mesophyll chloroplasts of a range of C_4 sp
Furthermore, the rates observed can be related isolated mesophyll chloroplasts of a range of C_4 species.
Furthermore, the rates observed can be related to the
ATP energy requirements of the substrates being metabo-
lized (Eurhank et al. 1983). These observations we clearly has the potential to occur at quite high rates in isolated mesophyll chloroplasts of a range of C_4 species.
Furthermore, the rates observed can be related to the ATP energy requirements of the substrates being Furthermore, the rates observed can be related to the ATP energy requirements of the substrates being metabolized (Furbank *et al.* 1983). These observations were used ATP energy requirements of the substrates being metabo-
lized (Furbank *et al.* 1983). These observations were used
to infer a potential role of a Mehler reaction in C_4
mesophyll chloroplasts for the production of extr to infer a potential role of a Mehler reaction in C_4
mesophyll chloroplasts for the production of extra ATP
via pseudocyclic photophosphorylation. Thus while the
potential exists for a Mehler reaction to run in isolate mesophyll chloroplasts for the production of extra ATP via pseudocyclic photophosphorylation. Thus while the potential exists for a Mehler reaction to run in isolated chloroplasts, evidence for significant rates from intac via pseudocyclic photophosphorylation. Thus while the
potential exists for a Mehler reaction to run in isolated
chloroplasts, evidence for significant rates from intact
leaf tissue is lacking Laisk & Edwards (1998) using potential exists for a Mehler reaction to run in isolated
chloroplasts, evidence for significant rates from intact
leaf tissue is lacking. Laisk & Edwards (1998), using

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chlorophyll fluorescence estimates of electron transport under various conditions in C_4 plants, have suggested chlorophyll fluorescence estimates of electron transport
under various conditions in C_4 plants, have suggested
that the Mehler reaction is a more important sink for
electrons in C_1 plants than photorespiration: howe under various conditions in C_4 plants, have suggested
that the Mehler reaction is a more important sink for
electrons in C_4 plants than photorespiration; however the
rates of estimated O_2 untake were low compared that the Mehler reaction is a more important sink for
electrons in C_4 plants than photorespiration; however the
rates of estimated O_2 uptake were low compared with
potential rates measured in isolated chloroplasts a electrons in C_4 plants than photorespiration; however the
rates of estimated O_2 uptake were low compared with
potential rates measured in isolated chloroplasts and
insufficient to meet the extra ATP demands rates of estimated O_2 uptake were low con
potential rates measured in isolated chlor
insufficient to meet the extra ATP demands. insufficient to meet the extra ATP demands.
(c) *CAM plants*

Photosynthetic $CO₂$ fixation in the light in Crassula-(c) CAM plants

Photosynthetic CO_2 fixation in the light in Crassula-

cean acid metabolism (CAM) plants can occur under

two separate conditions During the early part of the day Photosynthetic CO_2 fixation in the light in Crassula-
cean acid metabolism (CAM) plants can occur under
two separate conditions. During the early part of the day,
during phase III photosynthesis occurs behind closed cean acid metabolism (CAM) plants can occur under
two separate conditions. During the early part of the day,
during phase III, photosynthesis occurs behind closed
stomata while malate is being decarboxylated to release two separate conditions. During the early part of the day,
during phase III, photosynthesis occurs behind closed
stomata while malate is being decarboxylated to release
CO. This may be followed (phase IV) by a period when during phase III, photosynthesis occurs behind closed
stomata while malate is being decarboxylated to release
CO₂. This may be followed (phase IV) by a period when
stomata open and rubisco fixes CO₂ directly from the stomata while malate is being decarboxylated to release CO_2 . This may be followed (phase IV) by a period when
stomata open and rubisco fixes CO_2 directly from the
atmosphere. Osmond & Grace (1995) poted that during $CO₂$. This may be followed (phase IV) by a period when
stomata open and rubisco fixes $CO₂$ directly from the
atmosphere. Osmond & Grace (1995) noted that during
phase III. Mebler O, untake may represent up to stomata open and rubisco fixes CO_2 directly from the is probably by far the most important energy dissipative
atmosphere. Osmond & Grace (1995) noted that during electron flow. However, it is still much less than the no atmosphere. Osmond & Grace (1995) noted that during
phase III, Mehler O_2 uptake may represent up to 50%
maximal whole-chain electron transport. This analysis
would assume that rubisco was CO, saturated during this phase III, Mehler O_2 uptake may represent up to 50% maximal whole-chain electron transport. This analysis would assume that rubisco was CO_2 saturated during this period, and the observed uptake may be ascribed to the maximal whole-chain electron transport. This analysis
would assume that rubisco was CO_2 saturated during this
period, and the observed uptake may be ascribed to the
Mebler reaction Subsequent to this Maxwell et al. (199 would assume that rubisco was CO_2 saturated during this
period, and the observed uptake may be ascribed to the
Mehler reaction. Subsequent to this, Maxwell *et al.* (1998)
have shown that O , untake during both phase I period, and the observed uptake may be ascribed to the
Mehler reaction. Subsequent to this, Maxwell *et al.* (1998)
have shown that O_2 uptake during both phase III and
phase IV in Kalenchae diagreementiana and Hava car Mehler reaction. Subsequent to this, Maxwell *et al.* (1998)
have shown that O_2 uptake during both phase III and
phase IV in *Kalenchoe diagremontiana* and *Hoya carnosa* is
CO sensitive and if care is taken to ensure CO_2 sensitive and, if care is taken to ensure CO_2 saturashown that O_2 uptake during both phase III: IV in Kalenchoe diagremontiana and Hoya carn
sensitive and, if care is taken to ensure CO_2 sat
there is probably little evidence for a signiphase IV in Kalenchoe diagremontiana and Hoya carnosa is CO_2 sensitive and, if care is taken to ensure CO_2 saturation, there is probably little evidence for a significant light-stimulated Mehler O_2 untake in either tion, there is probably little evidence for a significant light-stimulated Mehler O_2 uptake in either phase. Due tion, there is probably little evidence for a significant
light-stimulated Mehler O_2 uptake in either phase. Due
to diffusional limitations imposed by both stomata and
the internal leaf structure in $C^{\text{A}}M$ plants (light-stimulated Mehler O_2 uptake in either phase. Due
to diffusional limitations imposed by both stomata and
the internal leaf structure in CAM plants (Maxwell *et al.*
1997), special care needs to be taken to ensure the internal leaf structure in CAM plants (Maxwell *et al.* 1997), special care needs to be taken to ensure that rubisco is CO_2 saturated and the observed light-
denendent O_2 untake cannot be due by and large to rubi 1997), special care needs to be taken to ensure that rubisco is CO_2 saturated and the observed light-dependent O_2 uptake cannot be due by and large to rubisco.

dependent O_2 uptake cannot be due by and large to rubisco.
(i) *The role of the Mehler reaction in balancing ATP-NADPH*
consumption demands *(i)* The role of the Mehler reaction in balancing ATP-NADPH

consumption demands
The different rates of ATP and NADPH consumption
by the PCR and PCO cycles in C_3 plants and the C_4 CO₂
concentrating mechanism have led to the notion that elec-The different rates of ATP and NADPH consumption
by the PCR and PCO cycles in C_3 plants and the C_4 CO₂
concentrating mechanism have led to the notion that elec-
tron transport to Ω untake in a Mebler reaction m by the PCR and PCO cycles in C_3 plants and the C_4 CO₂ concentrating mechanism have led to the notion that electron transport to O_2 uptake in a Mehler reaction may serve to balance requirements and allow balance concentrating mechanism have led to the notion that electron transport to O_2 uptake in a Mehler reaction may
serve to balance requirements and allow balanced elec-
tron transport. However, the required rate depends ver tron transport to O_2 uptake in a Mehler reaction may
serve to balance requirements and allow balanced elec-
tron transport. However, the required rate depends very
much on the assumed stochlometries. Bunska et al. serve to balance requirements and allow balanced electron transport. However, the required rate depends very much on the assumed stoichiometries. Ruuska *et al.* tron transport. However, the required rate depends very
much on the assumed stoichiometries. Ruuska *et al.*
(2000), working with the antisense rubisco transgenic
tobacco showed that with an assumption of an H^+ / ATP much on the assumed stoichiometries. Ruuska *et al.*
(2000), working with the antisense rubisco transgenic lobacco, showed that with an assumption of an H^+/ATP ratio of 3 and no O-cycle activity 13% of total electron (2000), working with the antisense rubisco transgenic
tobacco, showed that with an assumption of an H^+/ATP
ratio of 3 and no Q-cycle activity, 13% of total electron
flow would need to so to Ω or other electron accepto tobacco, showed that with an assumption of an H⁺/ATP ratio of 3 and no Q-cycle activity, 13% of total electron flow would need to go to O_2 or other electron acceptor at high CO, concentrations. On the other hand an H ratio of 3 and no Q-cycle activity, 13% of total electron
flow would need to go to O_2 or other electron acceptor at
high CO_2 concentrations. On the other hand an H⁺/ATP
ratio of 4 together with O-cycle activity are flow would need to go to O_2 or other electron acceptor at
high CO_2 concentrations. On the other hand an H^+/ATP
ratio of 4 together with Q-cycle activity are now favoured
(Haraux & de Kouchkovsky 1998: Rich 1988) an high CO₂ concentrations. On the other hand an H⁺/ATP appears to be only a small amount of light-dependent O₂ ratio of 4 together with Q-cycle activity are now favoured uptake when compared with C₃ higher plants, b \bigcup these assumptions very little extra electron flux is actually (Haraux & de Kouchkovsky 1998; Rich 1988) and with
these assumptions very little extra electron flux is actually
required at high CO_2 . At the CO_2 compensation point,
these required flows increase to 23% and 9% r these assumptions very little extra electron flux is actually
required at high CO_2 . At the CO_2 compensation point,
these required flows increase to 23% and 9%, respec-
tively. The observations that O_2 untake at the required at high CO_2 . At the CO_2 compensation point,
these required flows increase to 23% and 9%, respec-
tively. The observations that O_2 uptake at the compensa-
tion point was almost solely accounted for by rubis these required flows increase to 23% and 9%, respectively. The observations that O_2 uptake at the compensation point was almost solely accounted for by rubisco oxygenase (figure 2) activity would support the latter tively. The observations that O_2 uptake at the compensa-
tion point was almost solely accounted for by rubisco
oxygenase (figure 2) activity would support the latter
assumption of 4 H^+ per ATP and O-cycle activit tion point was almost solely accounted for by rubisco
oxygenase (figure 2) activity would support the latter
assumption of 4 H^+ per ATP and Q-cycle activity with
little involvement of Mebler activity. % oxygenase (figure 2) activity would
assumption of 4 H^+ per ATP and Q
little involvement of Mehler activity. **(d)** *Higher plant conclusions*

(d) *Higher plant conclusions*
Based on the above, the following general conclusions may be inferred. In C_3 and CAM plants, a Mehler O_2 Based on the above, the following general conclusions
may be inferred. In C_3 and CAM plants, a Mehler O_2
uptake reaction is unlikely to support a significant flow of
electron transport (probably less than 10%). I may be inferred. In C_3 and CAM plants, a Mehler O_2 uptake reaction is unlikely to support a significant flow of electron transport (probably less than 10%). In addition, *Phil. Trans. R. Soc. Lond.* B (2000) **Phil.** Trans. *R. Soc. Lond.* B (2000)

if Mehler reaction were present it would appear to scale with PCO and PCR cycle activity. This is supported by if Mehler reaction were present it would appear to scale
with PCO and PCR cycle activity. This is supported by
studies with reduced rubisco tobacco plants under both
low and high temperatures and high light, as well as with PCO and PCR cycle activity. This is supported by
studies with reduced rubisco tobacco plants under both
low and high temperatures and high light, as well as
studies with potatoes grapes and madrone during water studies with reduced rubisco tobacco plants under both
low and high temperatures and high light, as well as
studies with potatoes, grapes and madrone during water
stress. The lack of a significant Mebler reaction in these low and high temperatures and high light, as well as studies with potatoes, grapes and madrone during water stress. The lack of a significant Mehler reaction in these plants directly argues for a strong control of Mehler r studies with potatoes, grapes and madrone during water stress. The lack of a significant Mehler reaction in these
plants directly argues for a strong control of Mehler reac-
tion in the absence of ATP consumption by the PCR and
PCO cycles. This control is most probably exerted plants directly argues for a strong control of Mehler reaction in the absence of ATP consumption by the PCR and
PCO cycles. This control is most probably exerted via an
increase in ApH and a regulation of electron flow tion in the absence of ATP consumption by the PCR and PCO cycles. This control is most probably exerted via an increase in ΔpH and a regulation of electron flow through the cytochrome h , f complex. Considering this PCO cycles. This control is most probably exerted via an increase in ΔpH and a regulation of electron flow through the cytochrome $b_6 f$ complex. Considering this, the potential for energy dissipation at high light thr increase in Δ pH and a regulation of electron flow
through the cytochrome $b_{6}f$ complex. Considering this,
the potential for energy dissipation at high light through
Mebler reaction electron flow appears limited Under through the cytochrome b_6f complex. Considering this,
the potential for energy dissipation at high light through
Mehler reaction electron flow appears limited. Under the potential for energy dissipation at high light through
Mehler reaction electron flow appears limited. Under
water-stress conditions, when stomata and CO_2 may limit
rubisco carboxylation electron flow to rubisco oxyg Mehler reaction electron flow appears limited. Under
water-stress conditions, when stomata and CO_2 may limit
rubisco carboxylation, electron flow to rubisco oxygenase
is probably by far the most important energy dissipa water-stress conditions, when stomata and $CO₂$ may limit
rubisco carboxylation, electron flow to rubisco oxygenase
is probably by far the most important energy dissipative
electron flow. However, it is still much le rubisco carboxylation, electron flow to rubisco oxygenase is probably by far the most important energy dissipative electron flow. However, it is still much less than the nonelectron flow may still play a role in energizing the formation of a large Δ pH, as has previously been suggested (Neubauer & Yamamoto 1992; Schreiber & Neubauer 1990).

(e) *Algae*

The potential for various types of photosynthetic O_2 exchange in algae have been previously reviewed (Badger The potential for various types of photosynthetic O_2
exchange in algae have been previously reviewed (Badger
1985), showing a number of similarities with higher
plants. However, more recent measurements on a wider exchange in algae have been previously reviewed (Badger
1985), showing a number of similarities with higher
plants. However, more recent measurements on a wider
range of species than previously studied (L. Franklin and 1985), showing a number of similarities with higher
plants. However, more recent measurements on a wider
range of species than previously studied (L. Franklin and
M. R. Badger, unpublished data: Badger et al. 1998) plants. However, more recent measurements on a wider range of species than previously studied (L. Franklin and M. R. Badger, unpublished data; Badger *et al.* 1998), range of species than previously studied (L. Franklin and M. R. Badger, unpublished data; Badger *et al.* 1998), together with a greater understanding of the evolution of the kinetic properties of rubisco, leads to the con M. R. Badger, unpublished data; Badger *et al.* 1998), together with a greater understanding of the evolution of the kinetic properties of rubisco, leads to the conclusion that some re-appraisel of initial conclusions may together with a greater understanding of the evolution of
the kinetic properties of rubisco, leads to the conclusion
that some re-appraisal of initial conclusions may be
needed needed. that some re-appraisal of initial conclusions may be

The different rates of ATP and NADPH consumption
the PCR and PCO cycles in C_3 plants and the C_4 CO₂ tion in a number of non-green algal species is shown in Measurements of photosynthetic O_2 uptake and evolufigure 4, together with the effects of a carbonic anhydrase tion in a number of non-green algal species is shown in
figure 4, together with the effects of a carbonic anhydrase
inhibitor, ethoxyzolamide (EZA), that decreases the effec-
tiveness of any CO, concentrating mechanism. Th figure 4, together with the effects of a carbonic anhydrase
inhibitor, ethoxyzolamide (EZA), that decreases the effec-
tiveness of any CO_2 concentrating mechanism. These
data, have been previously presented and discusse inhibitor, ethoxyzolamide (EZA), that decreases the effec-
tiveness of any CO_2 concentrating mechanism. These
data have been previously presented and discussed
(Badger et al. 1998: Legast et al. 1999) and serve to bightiveness of any CO_2 concentrating mechanism. These data have been previously presented and discussed (Badger *et al.* 1998; Leggat *et al.* 1999) and serve to high-
light a number of the intriguing and different aspects data have been previously presented and discussed (Badger *et al.* 1998; Leggat *et al.* 1999) and serve to high-
light a number of the intriguing and different aspects of
photosynthetic Ω , untake and its interpretation (Badger *et al.* 1998; Leggat *et al.* 1999) and serve to high-
light a number of the intriguing and different aspects of
photosynthetic O₂ uptake and its interpretation in algae.
For three of the species *Isochrysis* (light a number of the intriguing and different aspects of photosynthetic O_2 uptake and its interpretation in algae.
For three of the species, *Isochrysis* (Chrysophyta) and *Porphyridium* and *Gonniotrichopsis* (Rhodop photosynthetic O₂ uptake and its interpretation in algae.
For three of the species, *Isochrysis* (Chrysophyta) and
Porphyridium and *Gonniotrichopsis* (Rhodophyta), there
appears to be only a small amount of light-depe For three of the species, *Isochrysis* (Chrysophyta) and
 Porphyridium and *Gonniotrichopsis* (Rhodophyta), there

appears to be only a small amount of light-dependent O_2

untake when compared with C_2 bigher plant uptake when compared with C_3 higher plants, being appears to be only a small amount of light-dependent O_2
uptake when compared with C_3 higher plants, being
more similar to C_4 plants in this regard. Accounting for
dark respiration, the maximum light stimulated O uptake when compared with C_3 higher plants, being
more similar to C_4 plants in this regard. Accounting for
dark respiration, the maximum light stimulated O_2
uptake represents between seven and 14% of CO, satumore similar to C_4 plants in this regard. Accounting
dark respiration, the maximum light stimulated
uptake represents between seven and 14% of CO_2 sa
rated electron transport at what would be consider uptake represents between seven and 14% of CO_2 satudark respiration, the maximum light stimulated O_2 uptake represents between seven and 14% of CO_2 saturated electron transport at what would be considered high light intensities. This compares with values of rated electron transport at what would be considered
high light intensities. This compares with values of
30–50% for C₃ plants (Canvin *et al.* 1980; Gerbaud &
Andre 1980) and 20–30% for *Chlamydononas reinhardtii* high light intensities. This compares with values of 30–50% for C_3 plants (Canvin *et al.* 1980; Gerbaud & Andre 1980) and 20–30% for *Chlamydomonas reinhardtii*

(Sültemeyer *et al.* 1986–1993) and a number of other $30-50\%$ for C_3 plants (Canvin *et al.* 1980; Gerbaud & Andre 1980) and $20-30\%$ for *Chlamydomonas reinhardtii* (Sültemeyer *et al.* 1986, 1993) and a number of other green algae (for a review see Badger 1985) Oxyge Andre 1980) and $20-30\%$ for *Chlamydomonas reinhardtii* (Sültemeyer *et al.* 1986, 1993) and a number of other green algae (for a review, see Badger 1985). Oxygen uptake rates of around 25% have also been seen with a red macro-alga *Chondrus crispus* (Brechignac & Andre 1984, 1985) and in our laboratory with a red red macro-alga *Chondrus crispus* (Brechignac & Andre
1984, 1985) and in our laboratory with a red
(*Porphyra columbina*), a brown (*Zonaria crenata*) and a green
(*Ulna australis*) macro-alga (I Franklin and M R 1984, 1985) and in our laboratory with a red
(*Ulva australis*) macro-alga (L. Franklin and M. R.
Radger unpublished data) In addition to the lower O (*Porphyra columbina*), a brown (*Zonaria crenata*) and a green (*Ulva australis*) macro-alga (L. Franklin and M. R. Badger, unpublished data). In addition to the lower O_2

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Figure 4. Photosynthesis in four species of non-green algae, (*a*) *Isochrysis galbana*, (*b*) *Porphyrium purpureum*, (*c*) *Symbiodinium* sp.,
(*d*) *Gonniotrichopsis sublittoralis*, in response to external Ci (inorganic Figure 4. Photosynthesis in four species of non-green algae, (a) Isochrysis galbana, (b) Porphyrium purpureum, (c) Symbiodinium sp.,
(d) Gonniotrichapsis sublittoralis, in response to external Ci (inorganic carbon). The a uptake and net O_2 evolution are shown together with O_2 uptake in the dark. The carbonic anhydrase inhibitor ethoxyzolamide (EZA) was added where indicated at 500 μ M.

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 (22.1) was added where maleaded at 500 μ m.
uptake, as for C₄ plants, the uptake is relatively insensitive
to CO₁ limitation, even when EZA is applied and photouptake, as for C_4 plants, the uptake is relatively insensitive
to CO_2 limitation, even when EZA is applied and photo-
synthesis, is, clearly, limited, by, CO_2 , availability, This uptake, as for C_4 plants, the uptake is relatively insensitive
to CO_2 limitation, even when EZA is applied and photo-
synthesis is clearly limited by CO_2 availability. This
apparent insensitivity is also seen in *C* to CO_2 limitation, even when EZA is applied and photosynthesis is clearly limited by CO_2 availability. This apparent insensitivity is also seen in *Chondrus crispus* (Brechignac & Andre 1984; 1985) and the species synthesis is clearly limited by CO_2 availability. This
apparent insensitivity is also seen in *Chondrus crispus*
(Brechignac & Andre 1984; 1985) and the species
studied by I. Franklin and M.R. Badger (unpublished (Brechignac & Andre 1984; 1985) and the species
studied by L. Franklin and M. R. Badger (unpublished
data). In addition, the green alga *C. reinhardtii* O₂ uptake
is also relatively insensitive to CO (Sültemeyer *et al* studied by L. Franklin and M. R. Badger (unpublished data). In addition, the green alga *C. reinhardtii* O₂ uptake is also relatively insensitive to CO_2 (Sültemeyer *et al.* 1987), although it is stimulated considerab is also relatively insensitive to CO_2 (Sültemeyer *et al.* 1987), although it is stimulated considerably by increasing light intensities (Sültemeyer *et al.* 1986).

light intensities (Sültemeyer *et al.* 1986).
The O_2 uptake in the dinoflagellate *Symbiodinium*
species is much larger and intriguing (figure 4). The
maximum O uptake cancity represents some $35-45\%$ The O_2 uptake in the dinoflagellate *Symbiodinium* (Bespecies is much larger and intriguing (figure 4). The T
maximum O_2 uptake capacity represents some $35-45%$ The
of maximum O_2 evolution and was relatively ins species is much larger and intriguing (figure 4). The
maximum O_2 uptake capacity represents some 35–45%
of maximum O_2 evolution and was relatively insensitive
to changing CO conditions and inhibition by $EZ\Delta$ maximum O_2 uptake capacity represents some 35–45%
of maximum O_2 evolution and was relatively insensitive
to changing CO_2 conditions and inhibition by EZA.
There was even evidence for stimulation by increasing of maximum O_2 evolution and was relatively insensitive
to changing CO_2 conditions and inhibition by EZA.
There was even evidence for stimulation by increasing
CO. In addition to this the O. untake observed at both to changing CO_2 conditions and inhibition by EZA.
There was even evidence for stimulation by increasing CO_2 . In addition to this, the O_2 uptake observed at both high and low CO_2 appears to be saturated by as litt There was even evidence for stimulation by increasing CO_2 . In addition to this, the O_2 uptake observed at both high and low CO_2 appears to be saturated by as little as 10% O (Legrat et al. 1999) $CO₂$. In addition to this, the vertical high and low $CO₂$ appears to 10% O₂ (Leggat *et al.* 1999). gh and low CO_2 appears to be saturated by as little as
 $\%$ O_2 (Leggat *et al.* 1999).

In trying to explain the photosynthetic O_2 uptake

proposes a number of possibilities can be raised. In many

non-green algae, such as Chrysophyta, Rhodophyta and responses a number of possibilities can be raised. In many
non-green algae, such as Chrysophyta, Rhodophyta and
Phaeophyta, the form I rubiscos (L_8S_8 —with small sub-
units) show considerably different kinetic properti non-green algae, such as Chrysophyta, Rhodophyta and
Phaeophyta, the form I rubiscos $(L_8S_8$ —with small sub-
units) show considerably different kinetic properties to
those of higher plants and chlorophyte algae (for a Phaeophyta, the form I rubiscos $(L_8S_8$ —with small sub-
units) show considerably different kinetic properties to
those of higher plants and chlorophyte algae (for a
review see Badgaer et al. 1998). These kinetics mean th units) show considerably different kinetic properties to
those of higher plants and chlorophyte algae (for a
review, see Badger *et al.* 1998). These kinetics mean that at
atmospheric levels of Ω . little overcase activi those of higher plants and chlorophyte algae (for a review, see Badger *et al.* 1998). These kinetics mean that at atmospheric levels of O_2 , little oxygenase activity may atmospheric levels of O_2 , little oxygenase activity may *Phil. Trans. R. Soc. Lond.* B (2000)

apparent insensitivity is also seen in *Chondrus crispus* complete photorespiratory cycle (Husic *et al.* 1987), the (Brechignac & Andre 1984; 1985) and the species net result in many algae may be low potential for lightht intensities (Sültemeyer *et al.* 1986).
The O₂ uptake in the dinoflagellate *Symbiodinium* (Bennoun 1994). occur (Badger *et al.* 1998). When this is combined with a
CO concentrating mechanism (Badger & Spalding occur (Badger *et al.* 1998). When this is combined with a CO_2 concentrating mechanism (Badger & Spalding 2000: Kaplan & Reinhold 1999) and the lack of a occur (Badger *et al.* 1998). When this is combined with a CO_2 concentrating mechanism (Badger & Spalding 2000; Kaplan & Reinhold 1999) and the lack of a complete photorespiratory cycle (Husic *et al.* 1987) the CO₂ concentrating mechanism (Badger & Spalding 2000; Kaplan & Reinhold 1999) and the lack of a complete photorespiratory cycle (Husic *et al.* 1987), the net result in many algae may be low potential for light-2000; Kaplan & Reinhold 1999) and the lack of a complete photorespiratory cycle (Husic *et al.* 1987), the
net result in many algae may be low potential for light-
dependent O_2 uptake and with little sensitivity to O_2 . The
reduced amount of O uptake that is obs net result in many algae may be low potential for light-
dependent O_2 uptake and with little sensitivity to O_2 . The
reduced amount of O_2 uptake that is observed is probably
due to some rubisco oxygenase. Mebler O dependent O_2 uptake and with little sensitivity to O_2 . The reduced amount of O_2 uptake that is observed is probably
due to some rubisco oxygenase, Mehler O_2 photoreduc-
tion and possibly chlororespiration that reduced amount of O_2 uptake that is observed is probably
due to some rubisco oxygenase, Mehler O_2 photoreduc-
tion and possibly chlororespiration that is much better
developed in algae compared with higher plants due to some rubisco oxygenase, Mehler O_2 photoreduction and possibly chlororespiration that is much better veloped in algae compared with higher plants
ennoun 1994).
The *Symbiodinium* data need further investigation.

10% O_2 (Leggat *et al.* 1999).

In trying to explain the photosynthetic O_2 uptake exchange being due to rubisco oxygenase. Perhaps an responses a number of possibilities can be raised. In many explanation lies in ch (Bennoun 1994).
The *Symbiodinium* data need further investigation.
There was an initial expectation that this alga with a
form II rubisco (I —without small subunits) (Whitney There was an initial expectation that this alga with a form II rubisco (L_2 —without small subunits) (Whitney There was an initial expectation that this alga with a form II rubisco $(L_2$ —without small subunits) (Whitney *et al.* 1995; Whitney & Yellowlees 1995) with a potentially hetter developed oxygenses activity may show evide form II rubisco (L_2 —without small subunits) (Whitney *et al.* 1995; Whitney & Yellowlees 1995) with a potentially better developed oxygenase activity may show evidence for this in its Ω . exchange However the insensi *et al.* 1995; Whitney & Yellowlees 1995) with a potentially better developed oxygenase activity may show evidence for this in its O_2 exchange. However, the insensitivity of the untake to decreasing CO, and increasing better developed oxygenase activity may show evidence
for this in its O_2 exchange. However, the insensitivity of
the uptake to decreasing CO_2 and increasing O_2 is not
consistent, with higher rates of photosyntheti for this in its O_2 exchange. However, the insensitivity of
the uptake to decreasing CO_2 and increasing O_2 is not
consistent with higher rates of photosynthetic O_2
exchange being due to rubisco oxygenase. Perhap the uptake to decreasing CO_2 and increasing O_2 is not
consistent with higher rates of photosynthetic O_2
exchange being due to rubisco oxygenase. Perhaps an
explanation lies in chlororespiration and Mebler reaction consistent with higher rates of photosynthetic O_2 explanation lies in chlororespiration and Mehler reaction.
(f) **Cyanobacteria**

Experiments with cyanobacteria over recent years have $\begin{pmatrix} f & Cyanobacteria \\ \text{Experiments with cyanobacteria over recent years have} \\ \text{shown a number of interesting features of photosynthetic} \\ \text{O. exchange that indicate some differences from a large number of interest.} \end{pmatrix}$ Experiments with cyanobacteria over recent years have
shown a number of interesting features of photosynthetic
 O_2 exchange that indicate some differences from algae
and bigher plants. Similar to non-green algae describ shown a number of interesting features of photosynthetic O_2 exchange that indicate some differences from algae described and higher plants. Similar to non-green algae described

 $\frac{1}{\beta}$ Percentage of maximal O₂ evolution at high CO₂ and amb
^bO₂ uptake at low CO₂ relative to O₂ uptake at high CO₂.

^a Percentage of maximal O₂ evolution at high CO₂ and ambient O₂.
^bO₂ uptake at low CO₂ relative to O₂ uptake at high CO₂.
^e Potential to act as electron acceptor.
^dAn indication of the potential rate d^{d} An indication of the potential rates for Mehler (
 ^{e} Relative contribution of non-radiative energy

energy incident on light-harvesting complexes.

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energy incident on light-harvesting complexes.

above (§5(e)), photosynthetic O_2 exchange at high CO_2

may represent between 10 and 20% of maximum electron above (§5(e)), photosynthetic O_2 exchange at high CO_2
may represent between 10 and 20% of maximum electron
transport rates (Li & Capyin 1997a: Miller et al. 1988) above (§5(e)), photosynthetic O_2 exchange at high CO_2
may represent between 10 and 20% of maximum electron
transport rates (Li & Canvin 1997*a*; Miller *et al.* 1988),
although this may increase to in excess of 30% a may represent between 10 and 20% of maximum electron
transport rates (Li & Canvin 1997a; Miller *et al.* 1988),
although this may increase to in excess of 30% at high
irradiances (Kana 1992: Li & Canvin 1997c). This untak transport rates (Li & Canvin 1997*a*; Miller *et al.* 1988), although this may increase to in excess of 30% at high irradiances (Kana 1992; Li & Canvin 1997*c*). This uptake is relatively insensitive to CO_z althoug although this may increase to in excess of 30% at high
irradiances (Kana 1992; Li & Canvin 1997*c*). This uptake
is relatively insensitive to CO_2 , although rates may be
slightly stimulated at low CO_2 . (Li & Canvin 199 irradiances (Kana 1992; Li & Canvin 1997*c*). This uptake
is relatively insensitive to CO_2 , although rates may be
slightly stimulated at low CO_2 (Li & Canvin 1997*a*).
However, when carbon fixation is inhibited by is relatively insensitive to CO_2 , although rates may be
slightly stimulated at low CO_2 (Li & Canvin 1997*a*).
However, when carbon fixation is inhibited by
compounds such as glycolaldeby and iodoacetamide slightly stimulated at low CO_2 (Li & Canvin 1997*a*).
However, when carbon fixation is inhibited by compounds such as glycolaldehyde and iodoacetamide, some cyanobacteria show the ability to undertake high some cyanobacteria show the ability to undertake high
rates of electron transport to O_2 approaching those seen
for saturating CO_2 conditions (Goosney & Miller 1997;
Li & Canvin 1997a) Photosynthetic O, untake under rates of electron transport to O_2 approaching those seen
for saturating CO_2 conditions (Goosney & Miller 1997;
Li & Canvin 1997*a*). Photosynthetic O_2 uptake under
both inhibited and uninhibited conditions shows a rates of electron transport to O_2 approaching those seen for saturating CO_2 conditions (Goosney & Miller 1997;
Li & Canvin 1997a). Photosynthetic O_2 uptake under
both inhibited and uninhibited conditions shows a low
affinity for O_2 requiring in excess of 400 uM for half Li & Canvin 1997a). Photosynthetic O_2 uptake under
both inhibited and uninhibited conditions shows a low
affinity for O_2 requiring in excess of 400 μ M for half
saturation (Li & Canvin 1997c) both inhibited and uninhibited conditions shows a low
affinity for O_2 requiring in excess of $400 \mu M$ for half
saturation (Li & Canvin 1997*c*).
An interesting feature of O_2 photoreduction, and inity for O_2 requiring in excess of $400 \mu M$ for half
curation (Li & Canvin 1997*c*).
An interesting feature of O_2 photoreduction, and
deed whole chain electron transport is that in the **BIOLOGICAL**
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saturation (Li & Canvin 1997*c*).

An interesting feature of O_2 photoreduction, and

indeed whole chain electron transport, is that in the

absence of CO rates of untake and evolution are An interesting feature of O_2 photoreduction, and
indeed whole chain electron transport, is that in the
absence of CO_2 , rates of uptake and evolution are
restricted to varying degrees (Badger & Schreiber 1993. indeed whole chain electron transport, is that in the absence of CO_2 , rates of uptake and evolution are restricted to varying degrees (Badger & Schreiber 1993; Goosney & Miller 1997 I i & Capyin 1997*a*: Miller *et al* absence of CO₂, rates of uptake and evolution are restricted to varying degrees (Badger & Schreiber 1993; Goosney & Miller 1997; Li & Canvin 1997*a*; Miller *et al.* 1988). Such restrictions are seen in the presence of a Goosney & Miller 1997; Li & Canvin 1997*a*; Miller *et al.* 1988). Such restrictions are seen in the presence of any PS I acceptor and clearly implicate some role for inorganic carbon in controlling the rate of intersystem 1988). Such restrictions are seen in the presence of any PS
I acceptor and clearly implicate some role for inorganic
carbon in controlling the rate of intersystem electron
transport (I i & Capyin 1997b). How this occurs r I acceptor and clearly implicate some role for inorganic
carbon in controlling the rate of intersystem electron
transport (Li & Canvin 1997*b*). How this occurs remains
unclear but recent work understanding the role of the carbon in controlling the rate of intersystem electron
transport (Li & Canvin 1997*b*). How this occurs remains
unclear but recent work understanding the role of the
thylakoid NADPH debydrogenase complex on catalysing transport (Li & Canvin 1997*b*). How this occurs remains
unclear but recent work understanding the role of the
thylakoid NADPH dehydrogenase complex on catalysing
active CO, untake by cyanohacterial cells may provide an unclear but recent work understanding the role of the
thylakoid NADPH dehydrogenase complex on catalysing
active CO_2 uptake by cyanobacterial cells may provide an
explanation (Kaplan & Reinhold 1999; Klugbammer *et* thylakoid NADPH dehydrogenase complex on catalysing
 \Box active CO₂ uptake by cyanobacterial cells may provide an
 \Box explanation (Kaplan & Reinhold 1999; Klughammer *et al*. 1999). Such an explanation would suppose that elecexplanation (Kaplan & Reinhold 1999; Klughammer *et al.* 1999). Such an explanation would suppose that electron transport through the cytochrome $b_6 f$ complex was controlled not by the ApH of the thylakoid membrane al. 1999). Such an explanation would suppose that electron transport through the cytochrome $b_6 f$ complex was controlled not by the ΔpH of the thylakoid membrane but by stromal side interactions of the NADPH complex tron transport through the cytochrome $b_6 f$ complex was
controlled not by the ΔpH of the thylakoid membrane
but by stromal side interactions of the NADPH complex
with CO. The fact that whole chain electron transport controlled not by the Δ pH of the thylakoid membrane
but by stromal side interactions of the NADPH complex
with CO_2 . The fact that whole chain electron transport
can occur at high rates in the absence of CO . fixation but by stromal side interactions of the NADPH complex
with CO_2 . The fact that whole chain electron transport
can occur at high rates in the absence of CO_2 fixation
implies that electron flow is not tightly coupled to with CO_2 . The fact that whole chain electron transport
can occur at high rates in the absence of CO_2 fixation
implies that electron flow is not tightly coupled to a thyla-
koid proton gradient, as is the case in bighe can occur at high rates in the absence of CO_2 fixation
implies that electron flow is not tightly coupled to a thyla-
koid proton gradient, as is the case in higher plants. This
has also been shown through the lack of ef implies that electron flow is not tightly coupled to a thyla-
koid proton gradient, as is the case in higher plants. This
has also been shown through the lack of effect of an
uncoupler ECCP (carbonyl cyanide p-(trifluorome

koid proton gradient, as is the case in higher plants. This
has also been shown through the lack of effect of an
uncoupler, FCCP (carbonyl cyanide p-(trifluoromethoxy)
phenylbydrazone) on electron transport to an artificia has also been shown through the lack of effect of an uncoupler, FCCP (carbonyl cyanide p-(trifluoromethoxy) phenylhydrazone), on electron transport to an artificial PS I acceptor (Badger & Schreiber 1993). Some aspects of uncoupler, FCCP (carbonyl cyanide p-(trifluoromethoxy)
phenylhydrazone), on electron transport to an artificial
PS I acceptor (Badger & Schreiber 1993). Some aspects of
a similar uncoupling of electron transport from ATP phenylhydrazone), on electron transport to an artificial
PS I acceptor (Badger & Schreiber 1993). Some aspects of
a similar uncoupling of electron transport from ATP
synthesis have been seen in the green also *Scendesmus* PS I acceptor (Badger & Schreiber 1993). Some aspects of
a similar uncoupling of electron transport from ATP
synthesis have been seen in the green alga *Scenedesmus* in *Phil. Trans. R. Soc. Lond.* B (2000)
Phil. Trans. R. Soc. Lond. B (2000)

the presence of PCO and PCR cycle inhibitors (Radmer & Kok 1976; Radmer & Ollinger 1978) the presence of PCO and PCR cycle inh
& Kok 1976; Radmer & Ollinger 1978).
In interpreting O, untake in eva Exercise of PCO and PCR cycle inhibitors (Radmer Kok 1976; Radmer & Ollinger 1978).

In interpreting O₂ uptake in cyanobacteria, the

lowing can be concluded Under normal photosynthetic

However, when carbon fixation is inhibited by photoreduction, depending on the extent to which CO_2 compounds such as glycolaldehyde and iodoacetamide, can serve as the normal electron acceptor from PS I.
some cyanobacte & Kok 1976; Radmer & Ollinger 1978).

In interpreting O_2 uptake in cyanobacteria, the

following can be concluded. Under normal photosynthetic

conditions a limited rubisco oxygenase activity may In interpreting O_2 uptake in cyanobacteria, the following can be concluded. Under normal photosynthetic conditions a limited rubisco oxygenase activity may occur due to the poor O_2 affinity of cyanobacteria oxygeneo following can be concluded. Under normal photosynthetic
conditions a limited rubisco oxygenase activity may
occur due to the poor O_2 affinity of cyanobacteria oxy-
genase. There exists, however a strong potential for conditions a limited rubisco oxygenase activity may
occur due to the poor O_2 affinity of cyanobacteria oxygenase. There exists, however a strong potential for O_2 occur due to the poor O_2 affinity of cyanobacteria oxy-
genase. There exists, however a strong potential for O_2
photoreduction, depending on the extent to which CO_2
can serve as the normal electron acceptor from P genase. There exists, however a strong potential for O_2
photoreduction, depending on the extent to which CO_2
can serve as the normal electron acceptor from PS I.
Ovvern photoreduction therefore has the potential to photoreduction, depending on the extent to which CO_2
can serve as the normal electron acceptor from PS I.
Oxygen photoreduction therefore has the potential to
increase at light intensities above those required to satucan serve as the normal electron acceptor from PS I. Oxygen photoreduction therefore has the potential to increase at light intensities above those required to saturate CO_2 fixation and would be stimulated significantly at low CO . if it were not for the inhibitory effect increase at light intensities above those required to satu-
rate CO_2 fixation and would be stimulated significantly
at low CO_2 if it were not for the inhibitory effects of low
 CO on the potential for whole-chain elec rate CO_2 fixation and would be stimulated significantly
at low CO_2 if it were not for the inhibitory effects of low
 CO_2 on the potential for whole-chain electron transport.
A confounding factor in evangelecteria is at low CO_2 if it were not for the inhibitory effects of low CO_2 on the potential for whole-chain electron transport.
A confounding factor in cyanobacteria is the relatively high rates of cyclic electron transport, muc $CO₂$ on the potential for whole-chain electron transport. A confounding factor in cyanobacteria is the relatively
high rates of cyclic electron transport, much of which
may proceed through the NDH1 complex and chloro-
respiration (Mi et al. 1994-1995) high rates of cyclic electron tran
may proceed through the NDH1
respiration (Mi *et al.* 1994, 1995). **(g)** *Algal and cyanobacterial conclusions*

Algae show a range of light-dependent O_2 uptake rates, similar to C_4 plants. However, there is some variation, as Algae show a range of light-dependent O_2 uptake rates,
similar to C_4 plants. However, there is some variation, as
evidenced by the increased O_2 uptake observed in the
dinoflagellate Symbiodinium (forme 4) However similar to C_4 plants. However, there is some variation, as
evidenced by the increased O_2 uptake observed in the
dinoflagellate *Symbiodinium* (figure 4). However, our
current understanding is limited by the low numb evidenced by the increased O_2 uptake observed in the dinoflagellate *Symbiodinium* (figure 4). However, our current understanding is limited by the low number of species that have actually been studied. As in C, plants dinoflagellate *Symbiodinium* (figure 4). However, our current understanding is limited by the low number of species that have actually been studied. As in C_4 plants, the O_2 untake appears to be largely insensitive current understanding is limited by the low number of
species that have actually been studied. As in C_4 plants,
the O_2 uptake appears to be largely insensitive to CO_2 ,
even in species that lack a CO₂ concentrati species that have actually been studied. As in C_4 plants, the O_2 uptake appears to be largely insensitive to CO_2 , even in species that lack a CO_2 concentrating mechanism and under conditions that are clearly limiting with even in species that lack a CO_2 concentrating mechanism
and under conditions that are clearly limiting with
respect to inorganic carbon supply. A partial explanation
for this could lie in the fact that many algal rubisc and under conditions that are clearly limiting with
respect to inorganic carbon supply. A partial explanation
for this could lie in the fact that many algal rubiscos may
have considerably different oxygenase kinetic proper respect to inorganic carbon supply. A partial explanation
for this could lie in the fact that many algal rubiscos may
have considerably different oxygenase kinetic properties
and exhibit for less oxygenase potential in air for this could lie in the fact that many algal rubiscos may
have considerably different oxygenase kinetic properties
and exhibit far less oxygenase potential in air. This leads have considerably different oxygenase kinetic properties
and exhibit far less oxygenase potential in air. This leads
to the conclusion that perhaps a greater proportion of the
observed Ω , untake may be due to a Mebler r and exhibit far less oxygenase potential in air. This leads
to the conclusion that perhaps a greater proportion of the
observed O_2 uptake may be due to a Mehler reaction and
less to rubisco, compared with C , plants to the conclusion that perhaps a greater probserved O_2 uptake may be due to a Mehl
less to rubisco, compared with C_3 plants.
In contrast, to both algae and bigher served O_2 uptake may be due to a Mehler reaction and
s to rubisco, compared with C_3 plants.
In contrast to both algae and higher plants, cyano-
cteria annear to have a high canacity for Mehler O_2 .

less to rubisco, compared with C_3 plants.
In contrast to both algae and higher plants, cyano-
bacteria appear to have a high capacity for Mehler O_2
untake which appears not well coupled or limited by In contrast to both algae and higher plants, cyano-
bacteria appear to have a high capacity for Mehler O_2
uptake, which appears not well coupled or limited by
ATP consumption. However, the potential for Mehler bacteria appear to have a high capacity for Mehler O_2 uptake, which appears not well coupled or limited by ATP consumption. However, the potential for Mehler uptake, which appears not well coupled or limited by ATP consumption. However, the potential for Mehler reaction may be controlled by inorganic carbon, in that intersystem electron transport appears to be limited by ATP consumption. However, the potential for Mehler
reaction may be controlled by inorganic carbon, in that
intersystem electron transport appears to be limited by
the absence of inorganic carbon reaction may be controlled by in
intersystem electron transport ap
the absence of inorganic carbon.

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6. A CONCLUDING COMPARISON

Table 1 shows a qualitative comparison of the potential for photosynthetic O_2 uptake in higher plants, algae and Table 1 shows a qualitative comparison of the potential
for photosynthetic O_2 uptake in higher plants, algae and
cyanobacteria. Among all of these phototrophs, rubisco-
supported O_2 uptake is a major alternative pho for photosynthetic O_2 uptake in higher plants, algae and
cyanobacteria. Among all of these phototrophs, rubisco-
supported O_2 uptake is a major alternative photosynthetic
electron acceptor only in C higher plants eyanobacteria. Among all of these phototrophs, rubisco-
supported O_2 uptake is a major alternative photosynthetic
electron acceptor only in C_3 higher plants (and also
 CAM plants data not shown). In C plants, alga supported O_2 uptake is a major alternative photosynthetic
electron acceptor only in C_3 higher plants (and also
CAM plants, data not shown). In C_4 plants, algae and
examples term the Mebler reaction may dominate p electron acceptor only in C_3 higher plants (and also
CAM plants, data not shown). In C_4 plants, algae and
cyanobacteria, the Mehler reaction may dominate, parti-
cularly in cyanobacteria where it has the potential t CAM plants, data not shown). In C_4 plants, algae and
cyanobacteria, the Mehler reaction may dominate, parti-
cularly in cyanobacteria where it has the potential to
support up to 50% of whole-chain electron transport cyanobacteria, the Mehler reaction may dominate, particularly in cyanobacteria where it has the potential to support up to 50% of whole-chain electron transport. It is likely that in all bigher plants and algae, which have cularly in cyanobacteria where it has the potential to
support up to 50% of whole-chain electron transport. It
is likely that in all higher plants and algae, which have a
well developed non-photochemical quenching mechanis cularly in cyanobacteria where it has the potential to *Physiol.* **66**, 302–307.
support up to 50% of whole-chain electron transport. It Casano, L. M., Zapata, J. M., Martin, M. & Sabater, B. 2000
is likely that in all hig (Niyogi 1999), NRD is the major mechanism for dissiwell developed non-photochemical quenching mechanism
(Niyogi 1999), NRD is the major mechanism for dissi-
pating excess photons absorbed by the light-harvesting
complexes under stressful conditions. However, for examo-(Niyogi 1999), NRD is the major mechanism for dissipating excess photons absorbed by the light-harvesting
complexes under stressful conditions. However, for cyano-
bacteria which lack significant non-photochemical pating excess photons absorbed by the light-harvesting
complexes under stressful conditions. However, for cyano-
bacteria, which lack significant non-photochemical
quenching (Campbell et al. 1998) the situation may well complexes under stressful conditions. However, for cyano-
bacteria, which lack significant non-photochemical
quenching (Campbell *et al.* 1998), the situation may well bacteria, which lack significant non-photochemical quenching (Campbell *et al.* 1998), the situation may well be different. Under these circumstances, the high capa-
city for Mebler reaction may well serve an important ro quenching (Campbell *et al.* 1998), the situation may well
be different. Under these circumstances, the high capa-
city for Mehler reaction may well serve an important role
in the energy dissipation. Further study of thes be different. Under these circumstances, the high capacity for Mehler reaction may well serve an important role
in the energy dissipation. Further study of these prokar-
votic phototrophs is necessary to establish the exte city for Mehler reaction may well serve an important role
in the energy dissipation. Further study of these prokar-
yotic phototrophs is necessary to establish the extent to
which this serves as a photoprotective mechanism in the energy dissipation. Further study of these p
yotic phototrophs is necessary to establish the ext
which this serves as a photoprotective mechanism.

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the contribution of pseudocyclic photophosphorylation to
the energy requirement of the mechanism [for concen](http://matilde.ingentaselect.com/nw=1/rpsv/cgi-bin/linker?ext=a&reqidx=/0032-0935^28^29189L.235[aid=536415,csa=0032-0935^26vol=189^26iss=2^26firstpage=235,springer=1])the contribution of pseudocyclic photophosphorylation to
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carboxylase from two photosynthetic dinoflagellates. 3 hitney, S. M. & Yellowlees, D. 1995 Preliminary investigations
into the structure and activity of ribulose bisphosphate
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carboxylase fr
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carboxylase/oxygenase related to that of the α proteobacteria hitney, S. M., Shaw, D. C. & Yellowlees, D. 1995 Evidence
that some dinoflagellates contain a ribulose 1,5-bisphosphate
[carboxylase/oxygenase related to](http://matilde.ingentaselect.com/nw=1/rpsv/cgi-bin/linker?ext=a&reqidx=/0962-8452^28^29259L.271[aid=524506,csa=0962-8452^26vol=259^26iss=1356^26firstpage=271,nlm=7740046]) that of the α -proteobacteria.
Proc. R. Sec. Land B. 259, 271–275. *Proc. R. Soc. Londagellates contain a*
Proc. R. Soc. Lond. B 259, 271–275.

Discussion

Discussion
A. Laisk (*Institute of Molecular and Cell Biology*, *University*
of Tarty Estonia) Why did you not mention the possibility **Discussion**
 A. Laisk (*Institute of Molecular and Cell Biology*, *University*
 of Tartu, Estonia). Why did you not mention the possibility

that electrons could be transported to the mitochondria A. Laisk (*Institute of Molecular and Cell Biology*, *University* of Tartu, Estonia). Why did you not mention the possibility that electrons could be transported to the mitochondria by the malate debydrogenase shuttle and of *Tartu, Estonia*). Why did you not mention the possibility that electrons could be transported to the mitochondria by the malate dehydrogenase shuttle and be oxidized there? If this pathway was active, the flux denoted that electrons could be transported to the mitochondria
by the malate dehydrogenase shuttle and be oxidized
there? If this pathway was active, the flux denoted as
Mehler reaction in your paper would have been even by the malate dehydrogenase shuttle and be oxidized
there? If this pathway was active, the flux denoted as
Mehler reaction in your paper would have been even
lower than presented in your graphs Mehler reaction in your paper would have been even lower than presented in your graphs.

Memer reaction in your paper would nave been even
lower than presented in your graphs.
M. R. Badger. You are correct in pointing out that any
light-generated reducing equivalents transported to the light-generated in your graphs.

M. R. Badger. You are correct in pointing out that any

light-generated reducing equivalents transported to the

mitochondria and reducing oxygen via cytochrome M. R. Badger. You are correct in pointing out that any light-generated reducing equivalents transported to the mitochondria and reducing oxygen via cytochrome c oxidase would be measured in our techniques as light-
dene mitochondria and reducing oxygen via cytochrome ϵ oxidase would be measured in our techniques as light-
dependent oxygen uptake. I did not consider this for the
sake of simplifying the situation but certainly if it did oxidase would be measured in our techniques as light-
dependent oxygen uptake. I did not consider this for the
sake of simplifying the situation, but certainly if it did
occur to any significant extent it would reduce the dependent oxygen uptake. I did not consider this for the sake of simplifying the situation, but certainly if it did
occur to any significant extent it would reduce the level of
any inferred Mebler reaction in our experimen sake of simplifying the situation, but certainly if it did
occur to any significant extent it would reduce the level of
any inferred Mehler reaction in our experiments.

occur to any significant extent it would reduce the level of
any inferred Mehler reaction in our experiments.
J. F. Allen (*Department of Plant Cell Biology, Lund University*,
Steeden). Oxygen can also have a catalytic r *Sweden*). Oxygen can also have a catalytic role. Over-
Sweden). Oxygen can also have a catalytic role. Over-
reduction of evolic electron transport can be counteracted J. F. Allen (*Department of Plant Cell Biology, Lund University,*
Sweden). Oxygen can also have a catalytic role. Over-
reduction of cyclic electron transport can be counteracted
by a poising pulse of O. Do the analyses sh Sweden). Oxygen can also have a catalytic role. Over-
reduction of cyclic electron transport can be counteracted by a poising pulse of O_2 . Do the analyses shown consider reduction of cyclic electron transport can be counteracted
by a poising pulse of O_2 . Do the analyses shown consider
the vital catalytic role where the total O_2 consumption
may be small, but the Mebler reaction would by a poising pulse of O_2 . Do the analyses shown consider
the vital catalytic role where the total O_2 consumption
may be small, but the Mehler reaction would be indispen-
sable for the initiation of photosynthesis? the vital catalytic role where the total O₃
may be small, but the Mehler reaction woul
sable for the initiation of photosynthesis? may be sman, but the Mehler reaction would be indispen-
sable for the initiation of photosynthesis?
M. R. Badger. Our analyses really only deal with consid-
ering electron flows to O. during steady-state

sable for the initiation of photosynthesis?

M. R. Badger. Our analyses really only deal with considering electron flows to O_2 during steady-state

photosynthesis and our techniques have a level of error M. R. Badger. Our analyses really only deal with considering electron flows to O_2 during steady-state photosynthesis and our techniques have a level of error where it would be difficult to resolve the presence of small ering electron flows to O_2 during steady-state
photosynthesis and our techniques have a level of error
where it would be difficult to resolve the presence of small photosynthesis and our techniques have a level of error where it would be difficult to resolve the presence of small O_2 uptakes of a few per cent or less of total whole-chain electron transport. We have not studied the period during the initiation of photosynthesis from a d O_2 uptakes of a few per cent or less of total whole-chain
electron transport. We have not studied the period during
the initiation of photosynthesis from a dark period
because the light on causes thermal artefacts that electron transport. We have not studied the period during
the initiation of photosynthesis from a dark period
because the light on causes thermal artefacts that would mask any significant oxygen uptake.

Because the fight on causes thermal artefacts that would
mask any significant oxygen uptake.
K. Asada (*Department of Biotechnology, Faculty of Engineering,*
Eukuvama University, Jahan). You showed that the electron *Fukuyama University, Japan*). *Faculty of Engineering,*
Fukuyama University, Japan). You showed that the electron
Fukuyama University, Japan). You showed that the electron
flux through the water water cycle proceeds a K. Asada (Department of Biotechnology, Faculty of Engineering,

Fukuyama University, Japan). You showed that the electron

flux through the water-water cycle proceeds at appreci-

able rates in C plants eukaryotic algae an Fukuyama University, Japan). You showed that the electron
flux through the water-water cycle proceeds at appreciable rates in C_4 plants, eukaryotic algae and flux through the water-water cycle proceeds at appreciable rates in C_4 plants, eukaryotic algae and cyanobacteria. What mediator participates in the enhanced photoreduction of oxygen in algae and cyanoable rates in C_4 plants, eukaryotic algae and cyano-bacteria. What mediator participates in the enhanced photoreduction of oxygen in algae and cyano-bacteria? When the water-water cycle operates just for cyanobacteria. What mediator participates in the
enhanced photoreduction of oxygen in algae and cyano-
bacteria? When the water-water cycle operates just for
the dissination of excess photons. ATP is produced but enhanced photoreduction of oxygen in algae and cyano-
bacteria? When the water–water cycle operates just for
the dissipation of excess photons, ATP is produced but
not consumed. As Professor Heber has shown, chlorobacteria? When the water–water cycle operates just for
the dissipation of excess photons, ATP is produced but
not consumed. As Professor Heber has shown, chloro-
plasts can keep a constant level of ATP i.e. chloroplasts the dissipation of excess photons, ATP is produced but
not consumed. As Professor Heber has shown, chloro-
plasts can keep a constant level of ATP, i.e. chloroplasts
can hydrolyge ATP to keep a constant level. This is just not consumed. As Professor Heber has shown, chloro-
plasts can keep a constant level of ATP, i.e. chloroplasts
can hydrolyse ATP to keep a constant level. This is just a comment.

can nydrolyse ATP to keep a constant level. This is just a
comment.
M. R. Badger. I don't know what the mediator for oxygen
untake is in these non-higher plant systems. Reduced comment.
M. R. Badger. I don't know what the mediator for oxygen
uptake is in these non-higher plant systems. Reduced
ferredovin is a possibility, but the potential for monodebyuptake is in these non-higher plant systems. Reduced ferredoxin is a possibility, but the potential for monodehyuptake is in these non-higher plant systems. Reduced
ferredoxin is a possibility, but the potential for monodehy-
droascorbate reductase to mediate this uptake (as shown
by you in bigher plants), may be more limited due to ferredoxin is a possibility, but the potential for monodehy-
droascorbate reductase to mediate this uptake (as shown
by you in higher plants), may be more limited due to
different activities of the associate reduction and droascorbate reductase to mediate this uptake (as shown
by you in higher plants), may be more limited due to
different activities of the ascorbate reduction and
oxidation cycles in the chloroplasts of algae and cyanoby you in higher plants), may be more limited due to different activities of the ascorbate reduction and oxidation cycles in the chloroplasts of algae and cyanodifferent activities of the ascorbate reduction and oxidation cycles in the chloroplasts of algae and cyano-
bacteria (see $\S 5(e,f)$ for discussion). As pointed out by Dr
Matthiis (see next question), both algae and cyanooxidation cycles in the chloroplasts of algae and cyano-
bacteria (see $\S 5(e,f)$ for discussion). As pointed out by Dr
Matthijs (see next question), both algae and cyano-
bacteria have strong chlorogespiratory activities o bacteria (see $\S 5(e,f)$ for discussion). As pointed out by Dr
Matthijs (see next question), both algae and cyano-
bacteria have strong chlororespiratory activities on the
thylakoids that could also play a role in light-sti Matthijs (see next question), both algae and cyano-
bacteria have strong chlororespiratory activities on the
thylakoids that could also play a role in light-stimulated
oxygen untake via a cytochrome oxidase pathway bacteria have strong chlororespiratory activities of
thylakoids that could also play a role in light-stim
oxygen uptake via a cytochrome oxidase pathway.

THE ROYAL

PHILOSOPHICAL
TRANSACTIONS

BIOLOGICAL
SCIENCES

H. C. P. Matthijs (*Department of Microbiology, University of Amsterdam, The Netherlands*). I wish to address the difference
Amsterdam, The Netherlands). I wish to address the difference
in energy use, in which cyanobacteria have more electron H. C. P. Matthijs (*Department of Microbiology, University of Amsterdam, The Netherlands*). I wish to address the difference
in energy use, in which cyanobacteria have more electron
transfer (to oxygen) than plants and alg Amsterdam, The Netherlands). I wish to address the difference
in energy use, in which cyanobacteria have more electron
transfer (to oxygen) than plants and algae. You attribute
this to very high Mebler reaction in cyanobac in energy use, in which cyanobacteria have more electron
transfer (to oxygen) than plants and algae. You attribute
this to very high Mehler reaction in cyanobacteria. How
would you be able to discriminate between Mehler re transfer (to oxygen) than plants and algae. You attribute
this to very high Mehler reaction in cyanobacteria. How tion and direct PS II (transfer) to cytochrome aa_3 electron transfer? would you be able to discriminate between Mehler reac-

transier:
M. R. Badger. The truth is that we cannot distinguish
with our measurements, and the flow of electrons from PS
II to a cytochrome oxidase nathway would be observed as M. R. Badger. The truth is that we cannot distinguish
with our measurements, and the flow of electrons from PS
II to a cytochrome oxidase pathway would be observed as
light-stimulated oxygen untake. However, one consewith our measurements, and the flow of electrons from PS
II to a cytochrome oxidase pathway would be observed as
light-stimulated oxygen uptake. However, one conse-
quence of this would be that the electron flow through PS If to a cytochrome oxidase pathway would be observed as
light-stimulated oxygen uptake. However, one conse-
quence of this would be that the electron flow through PS
for as monitoring mass 34 is concerned I don't immedilight-stimulated oxygen uptake. However, one consequence of this would be that the electron flow through PS II would be in excess of PS I or else the intersystem pool would be drained of electrons. Recent measurements that quence of this would be that the electron flow through PS
II would be in excess of PS I or else the intersystem pool
would be drained of electrons. Recent measurements that
we have been doing, comparing electron flow, thro II would be in excess of PS I or else the intersystem pool
would be drained of electrons. Recent measurements that
we have been doing, comparing electron flow through
both photosystems, clearly show that PS I flow is in would be drained of electrons. Recent measurements that
we have been doing, comparing electron flow through
both photosystems, clearly show that PS I flow is in
considerable excess indicating cyclic electron flow we have been doing, comparing electron flow this both photosystems, clearly show that PS I flow considerable excess, indicating cyclic electron flow.

Frank photosystems, clearly show that PS 1 now is in

considerable excess, indicating cyclic electron flow.

H. Griffiths *(Department of Agricultural and Environment*

Science University of Newcastle UK). One possible lim *Science, University of Mercastle, UK*). One possible limitation
Science, University of Newcastle, UK). One possible limitation
of the mass spectrometer method as you mentioned Science, University of Newcastle, UK). One possible limitation ately see how this would help us to derive a measure of the mass spectrometer method as you mentioned O_2 recycling within the leaf.

would be the possibility of (oxygen) recycling. In the closed system of the cuvette, what are the likely rates of this process as the $CO₂-O₂$ ratio changes, and can you determine the extent by monitoring the m/e 34 (i.e. $^{18}O^{16}O$ appearance)?

M. R. Badger. The truth is that we cannot distinguish compartments within the leaf that are quite isolated from
with our measurements, and the flow of electrons from PS the ambient air as a result of strong diffusional lim M. R. Badger. Recycling of O_2 species is only likely in
compartments within the leaf that are quite isolated from M. R. Badger. Recycling of O_2 species is only likely in compartments within the leaf that are quite isolated from the ambient air as a result of strong diffusional limitations. M. R. Badger. Recycling of O_2 species is only likely in
compartments within the leaf that are quite isolated from
the ambient air as a result of strong diffusional limita-
tions. Even when stomata are relatively closed compartments within the leaf that are quite isolated from
the ambient air as a result of strong diffusional limita-
tions. Even when stomata are relatively closed, it is hard
to see recycling contributing more than a few p the ambient air as a result of strong diffusional limitations. Even when stomata are relatively closed, it is hard to see recycling contributing more than a few per cent to the error of estimating oxygen untake and evoluti tions. Even when stomata are relatively closed, it is hard
to see recycling contributing more than a few per cent to
the error of estimating oxygen uptake and evolution. As
far as monitoring mass 34 is concerned. I don't i to see recycling contributing more than a few per cent to
the error of estimating oxygen uptake and evolution. As
far as monitoring mass 34 is concerned, I don't immedi-
ately see how this would belp. An increased evolutio the error of estimating oxygen uptake and evolution. As
far as monitoring mass 34 is concerned, I don't immediately see how this would help. An increased evolution of
mass 34 above what could be expected as a consequence far as monitoring mass 34 is concerned, I don't immediately see how this would help. An increased evolution of mass 34, above what could be expected as a consequence of the natural isotopic abundance in water, could only ately see how this would help. An increased evolution of mass 34, above what could be expected as a consequence
of the natural isotopic abundance in water, could only
occur if the water in the leaf became relatively enriched
in 34. This could happen through diffusional restricti occur if the water in the leaf became relatively enriched placed on the water in the leaf became relatively enriched
in 34. This could happen through diffusional restrictions
placed on the evaporation of water, but I cannot immedi-
ately see how this would help us to derive a mea in 34. This could happen through diffusional restrictions
placed on the evaporation of water, but I cannot immediately see how this would help us to derive a measure of
 Ω , recycling within the leaf placed on the evaporation of v
ately see how this would help
 O_2 recycling within the leaf.

BIOLOGICAL

ROYA

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