

Towards an understanding of the photosynthetic anomalies of the unusual Tasmanian alpine shrub *Ozothamnus ledifolius*

Anthony N. Mann

KPA378 Plant Science Research
School of Plant Science

Mentor: Dr. Mark J. Hovenden

Abstract

Alpine plants are continually subject to low temperatures and high irradiance, conditions that promote photoinhibition. *Ozothamnus ledifolius* (Asteraceae) has been shown to exhibit unusually high photosynthetic light use efficiency and therefore low requirement for dissipation of excess light during such conditions (Williams *et al.* 2003). This study was designed to increase our understanding of the species' photosynthetic anomalies, as well as to examine its photosynthetic response to these conditions during winter, a season not previously sampled. Chlorophyll fluorescence was measured *in situ*, providing values for pre-dawn and midday F_v/F_m , as well as 9am and midday photochemical quantum yield, for both *O. ledifolius* and a control species, *Epacris serpyllifolia* (Epacridaceae). From this, chronic, dynamic and total photoinhibition were calculated. Growth cabinet experiments allowed examination of carbon assimilation rates over a temperature range of between 16 to 24°C (max.) and -9 to +4°C (min.). *In situ* carbon assimilation of *O. ledifolius* was also measured. Results showed that *O. ledifolius* was not severely photoinhibited, with a mean value of only 17.3%, compared to *E. serpyllifolia* with a mean of 70.8%. F_v/F_m was significantly higher in *O. ledifolius* than *E. impressa*, whereas yield showed no interspecific difference. Growth cabinet experiments showed a significant difference in optimal temperature for photosynthesis, with a mean of 6.0°C for *O. ledifolius* and 13.3°C for *E. serpyllifolia*. *O. ledifolius* also showed a significantly higher carbon assimilation rate (5.64 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than *E. serpyllifolia* (2.67 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). The study confirms *O. ledifolius*' unique ability to maintain high carbon assimilation rates during an alpine winter, as well as an abnormal efficiency in photosynthetic light utilisation. This work contributes towards the ecological understanding of an unusual alpine shrub, and once fully understood, the mechanisms driving this species' photosynthetic capabilities may be applied in practices such as horticulture, silviculture, and agriculture (Ball *et al.* 1995).

Introduction

Photosynthesis has been described as “the most fundamental life process on earth” (Raghavendra 1998). It has been the primary focus of many studies in plant biology, agriculture, horticulture, biotechnology (Raghavendra 1998), and global climate change (e.g. Drake *et al.* 1998). In alpine areas where plants are subject to low temperatures and high light intensity, photosynthetic pathways may become disrupted, leading to physiological complications and ecological stress (Oliveira & Peñuelas 2001). This state is known as photoinhibition.

Hurry *et al.* (1998) define photoinhibition as “the light induced loss of photosynthetic efficiency”, and it is Photosystem II (PS II) that is primarily affected (Berry & Björkman 1980, Critchley 1998, Hurry *et al.* 1998). During photoinhibitory conditions, high irradiance means PS II receives an abundant supply of photons and its efficiency is decreased, whilst low temperatures slow enzymes such as Rubisco (e.g. Kubien *et al.* 2003, Kubien & Sage 2004). If no photoprotective mechanisms are employed, photodamage occurs, including inactivation of, and subsequent damage to, PS II (Hopkins 1999), production of superoxide radicals and the resulting photooxidative bleaching of chlorophyll (Wise 1995), and the suppression of repair to damaged proteins (Streb *et al.* 1998).

Two types of photoinhibition have been described (Werner *et al.* 1998). Dynamic photoinhibition is the short-term response to light stress, whereby excess light energy is dissipated to prevent photodamage. It is important to note that this type of photoinhibition is rapidly reversible and non-damaging, meaning that plants showing a high proportion of dynamic photoinhibition are able to downregulate photosynthesis during high photoinhibitory stress, and rapidly relax this should environmental conditions suddenly become more favourable (Critchley 1998). As the alpine environment is characterised by extremes in temperature and light fluctuations (Körner 1999), a high capacity for dynamic photoinhibition is clearly advantageous to alpine plants. In contrast, chronic photoinhibition is a more long-term state arising from more permanent stress, and often results in photodamage (Hurry *et al.* 1998). This type is reversible only after extended periods of time (Critchley 1998), and thus plants with high chronic photoinhibition are forced into long-term downregulation of photosynthesis. Martinez-Ferri *et al.* (2004) showed that chronic photoinhibition increases during winter, as temperatures decrease and potential for photodamage increases, and one might assume this trend to be typical of alpine plants.

A number of methods are employed by plants to prevent photodamage by photoinhibition (e.g. Adams *et al.* 2002). Williams *et al.* (2003) found that six species growing in photoinhibitory conditions in alpine Tasmania use three main photoprotective strategies. Firstly, light harvesting can be maximised under low temperatures through a large capacity for light energy utilisation. This is usually attainable by 'cold hardening', whereby plants acclimate to photoinhibitory conditions as they become more severe (i.e. during the onset of winter). Oquist & Huner (1993) showed that cold-hardened individuals of winter rye (*Secale cereale*) at risk of photoinhibition had a higher photosynthetic capacity than non-hardened individuals. Warren *et al.* (1998) achieved the same result with their study on *Eucalyptus* species. The second photoprotective strategy involves the dissipation of thermal energy, often through the xanthophyll cycle. By trapping and dissipating surplus excitation energy through this cycle, photooxidative damage to PS II can be prevented (Hopkins 1999). Demmig-Adams & Adams (1996) explain the significant relationship between presence of xanthophylls and thermal energy dissipation. The third strategy recognised by Williams *et al.* (2003) involves a reduction in the proportion of light that reaches the light-harvesting complex. This is mostly attained through morphological adaptation, such as leaf pubescence (e.g. Bisba *et al.* 1997), epicuticular waxes (e.g. Robinson *et al.* 1993), and foliar anthocyanins (e.g. Gould *et al.* 2000).

One species that has shown a high degree of resistance to photoinhibition is *Ozothamnus ledifolius* (Asteraceae) (Williams *et al.* 2003). It has crowded yellow-green leaves, suggesting low anthocyanin content, with recurved margins (Kirkpatrick 1997), an indication of morphological adaptation to photoinhibitory conditions (Lebkuecher & Eickmeier 1993). In Williams *et al.*'s (2003) comparative study on six Tasmanian alpine species, *O. ledifolius* showed a relatively low level of both dynamic and chronic photoinhibition in autumn (April) and spring (November). As well as low levels of photoinhibition, use of photoprotective mechanisms was minimal: *O. ledifolius* exhibited low carotenoid pigment content, xanthophyll content, and anthocyanin content when compared to other Tasmanian alpine species. Perhaps most interestingly, PS II efficiency in *O. ledifolius* was nearly double that of its co-occurring species. Results led Williams *et al.* (2003) to suggest that this species is an efficient harvester of light energy, requiring only a small xanthophyll pool as photoprotection. Williams *et al.* (2003) have recommended an extensive analysis into the photosynthetic anomalies of *O. ledifolius*, in order to understand its ability to resist photoinhibition.

This descriptive study was designed to attain baseline data on the photosynthetic properties of *O. ledifolius* during winter, a sampling period not included in Williams *et al.* (2003), and one that frequently presents photoinhibitory stress on alpine plants. Particular attention will be paid to the species' carbon assimilation rates at various temperatures, as this work has not been performed



previously. Braun *et al.* (2002) states that an optimal temperature exists for photosynthesis, as well as upper and lower temperature limits. These limits are unknown for *O. ledifolius*. Thus results from this work will contribute significantly to our understanding of the species' unusual photosynthetic characteristics. In a more applied sense, the information will give an insight into the mechanisms employed by plants to successfully avoid, or cope with, high levels of light stress. This, in turn, may prove useful to those interested in avoidance strategies of photodamage adopted by plants, in particular plant ecologists and managers of agricultural or silvicultural production (e.g. Ball *et al.* 1995).

Materials and Methods

O. ledifolius was analysed during winter 2004 for several of its photosynthetic attributes. Comparisons were made with another Tasmanian alpine shrub, *Epacris serpyllifolia* (Epacridaceae), which has shown a more typical response to photoinhibitory conditions (Williams *et al.* 2003).

Study Site

In situ measurements were undertaken on the summit plateau of Mt. Wellington (42.9°S, 147.2°E, 1270m A.S.L.), an area with a negligible slope and exposure to full sunlight. Soils are derived from Jurassic dolerite. Conditions at the site are typical of temperate alpine zones, with cold to freezing winter temperatures (mean max. = 2.7°C, mean min. = -1.4°C), and extreme exposure to wind, rain, snow and sunlight irradiance (BOM 2004). The vegetation type is alpine heath, typical of Tasmanian alpine zones, and is dominated by *Ozothamnus ledifolius* (Kirkpatrick 1997). There were two components to this study:

1. *Photoinhibition and chlorophyll fluorescence measurements (in situ)*, and
2. *Carbon assimilation parameters (in situ and ex situ)*.

1. Photoinhibition and chlorophyll fluorescence parameters (in situ) (29th July and 19th August 2004)

Individuals of both species were randomly selected to determine chronic, dynamic, and total photoinhibition levels as well as photosynthetic yield, on cold, sunny, cloudless mornings. Chlorophyll fluorescence parameters were measured using a portable fluorometer (PAM-2000 (Heinz Walz Gmb, Effeltrich, Germany), with attached leaf clip 2030-B (see Maxwell & Johnson 2000 for a comprehensive review on chlorophyll fluorescence analysis). Pre-dawn levels of photochemical efficiency ($F_v/F_{m\text{PD}}$) were recorded within an hour before sunrise, and midday levels ($F_v/F_{m\text{mid}}$) recorded within half an hour of 12:00 noon. The latter followed from 15 minutes of dark-adaptation whereby individual plants were covered with a shade cloth, following Werner *et al.* (2002) and Williams *et al.* (2003). Maximum photochemical efficiency ($F_v/F_{m\text{max}}$) was taken as the highest recorded F_v/F_m for each species, from the present work and from Williams *et al.* (2003). $F_v/F_{m\text{max}}$ values used were 0.794 for *O. ledifolius*, and 0.721 for *E. serpyllifolia*. Calculation of dynamic (PI_{dyn}) and chronic (PI_{chr}) photoinhibition follows Werner *et al.* (2002), with the result expressed as a percentage reduction in $F_v/F_{m\text{max}}$. Total photoinhibition (PI_{tot}) was measured as the sum of dynamic and chronic photoinhibition.

$$PI_{\text{dyn}} = ((F_v/F_{m\text{PD}} - F_v/F_{m\text{mid}}) / F_v/F_{m\text{max}}) \times 100$$

$$PI_{\text{chr}} = ((F_v/F_{m\text{max}} - F_v/F_{m\text{PD}}) / F_v/F_{m\text{max}}) \times 100$$

$$PI_{\text{tot}} = PI_{\text{dyn}} + PI_{\text{chr}}$$

Photochemical quantum yield was measured at 9am and midday, also using the PAM-2000. The objective of this was to detect differences in photosynthetic downregulation between pre-dawn and midday.

2. Carbon assimilation (ex situ and in situ)

Ex situ photosynthesis at controlled temperatures (growth cabinet)

Seedlings grown at a local nursery (approx. 350m A.S.L.) were selected at random for *ex situ* examination of carbon assimilation, at temperatures controlled by growth cabinets. Two types of Infra-Red Gas Analysers (IRGAs) with attached chambers were used for these measurements.

Licor LI-6400 Portable Photosynthesis System

The conifer chamber attached to this IRGA was positioned within the growth cabinet, and one branch of the plant placed inside the chamber. Photosynthetic photon flux density (PPFD) of the growth chamber was maintained at approximately $400 \mu\text{mol m}^{-2} \text{s}^{-1}$. Growth cabinet and conifer chamber temperatures were then reduced steadily from 16-24°C down to 0-4°C over a period of several hours, during which time carbon assimilation was measured. This was repeated for a total of 3 replicates of *O. ledifolius* and 4 replicates of *E. serpyllifolia*. To ensure that plants were respiring as well as photosynthesising, lights were switched off and the response observed. A decrease in photosynthesis to a negative value confirmed that plants were respiring.

Walz CMS400 Minicuvette System

Two individuals of *O. ledifolius* were measured for carbon assimilation using this IRGA, which enables analysis of photosynthesis at sub-zero temperatures. Methods were as above, with temperatures taken to minima of -9°C and -1.2°C.

In situ photosynthesis (18th October 2004)

The Licor LI-6400 was used to measure *in situ* photosynthesis of *O. ledifolius* exposed to photoinhibitory conditions. Measurements were taken on a cold (ambient temperature = 2.7°C), sunny, cloudless morning from 8:45 am until 9:05 am. PPFD was estimated as approximately $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$. Mean carbon assimilation rate and mean EBT_{ff} were measured, and compared to analogous *ex situ* values.

Data Analysis

One-way ANOVAs were used to detect for significant differences ($\alpha = 0.05$) between the two species.

Results

1. Photoinhibition and chlorophyll fluorescence parameters

Total photoinhibition (PI_{tot}) was very low in *O. ledifolius* (17.3%), in particular when compared to *E. serpyllifolia* (70.8%), showing a highly significant difference ($P < 0.0001$). PI_{chr} also showed a significant difference between the two species ($P < 0.0001$), whereas PI_{dyn} showed no significant difference ($P = 0.423$). PI_{dyn} was approx. 35% of PI_{tot} in *O. ledifolius*, but less than 5% of PI_{tot} in *E. serpyllifolia* (Fig. 1). F_v/F_m ratios showed significant differences between species both at pre-dawn ($F_v/F_{m\text{PD}}$) ($P < 0.0001$) and at midday ($F_v/F_{m\text{mid}}$) ($P < 0.0001$) (Fig. 2). Conversely, quantum efficiency of PS II (yield) was not significantly different between species, neither at 9am ($P = 0.897$) nor at midday ($P = 0.786$) (Fig. 2).



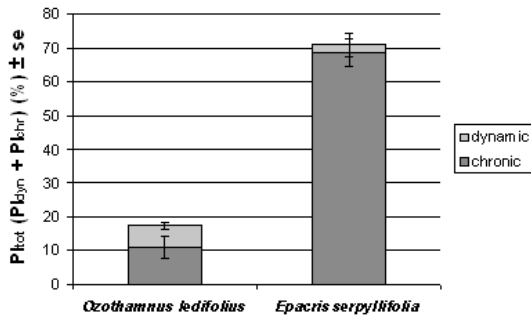


Figure 1. Chronic, dynamic and total photoinhibition of *O. ledifolius* and *E. serpyllifolia* in winter

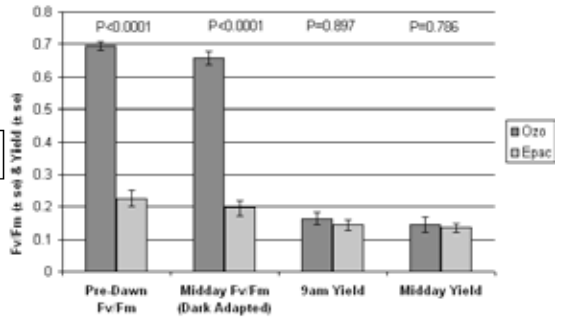
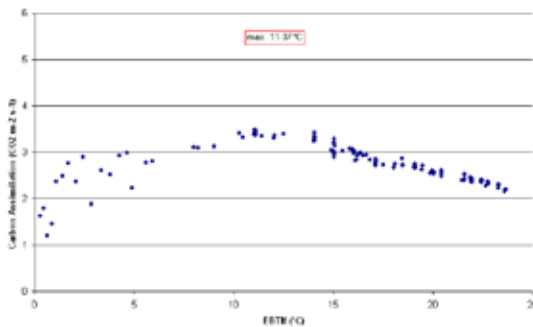


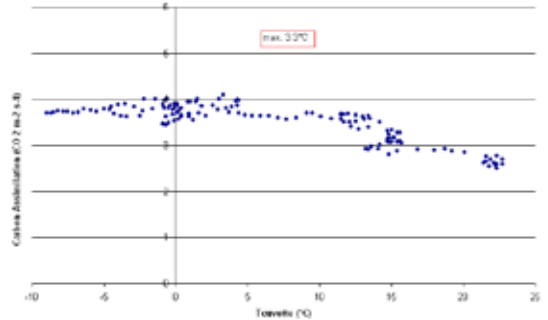
Figure 2. Chlorophyll fluorescence parameters for *Ozothamnus ledifolius* and *Epacris serpyllifolia*

2. Carbon assimilation

Temperature/photosynthesis curves from growth cabinet experiments revealed varied responses from both species, with individuals of both species displaying both flat and peaked curves (Fig. 3). Carbon assimilation rates, however, were significantly higher ($P=0.003$) in *O. ledifolius* (mean max. = $5.64 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than in *E. serpyllifolia* (mean max. = $\mu\text{mol } 2.67 \text{ CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) (Fig. 4). In addition, the temperature at which this rate occurred was significantly lower ($P=0.01$) in *O. ledifolius* (6.0°C) than in *E. serpyllifolia* (13.3°C) (Fig. 4).



3 a)



3 b)

Figure 3. Examples of temperature/carbon assimilation curves generated from ex situ growth experiments: a) *Epacris serpyllifolia* (leaf temperature estimated from energy balance equations $[\text{EBT}_{\text{pl}}]$, measured with the Licor LI-6400), and b) *Ozothamnus ledifolius*. (measured with the Walz CMS400. Due to a malfunction in its leaf temperature probe, cuvette temperature $[\text{T}_{\text{cuvette}}]$ was used as the independent variable with this apparatus). ‘max.’ indicates the temperature at which photosynthetic maximum was attained.

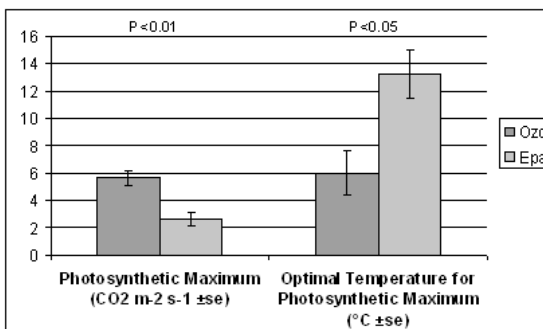


Figure 4. Carbon assimilation rates and temperature at mean photosynthetic maximum for *Ozothamnus ledifolius* and *Epacris serpyllifolia*, derived from ex situ growth experiments

Mean *in situ* carbon assimilation of *O. ledifolius*

was $2.96 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, which occurred at a temperature of 11.44°C . Mean *ex situ* (growth experiment) carbon assimilation at a similar mean temperature was $4.97 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. *In situ* carbon assimilation rate for *E. serpyllifolia* was not measured.

Discussion

Combining results from this work and Williams *et al.* (2003), there is now information on photosynthesis patterns of *O. ledifolius* during three seasons: autumn, winter and spring. This provides more than just a comparison of photosynthetic parameters between seasons. The results clearly show that *O. ledifolius* is able to cope with extreme photoinhibitory conditions, confirming the unusual and unique status of this species in its ability to maintain a high capacity for light utilisation during winter, unlike its co-occurring species.

Winter photoinhibition (PI_{tot}) was high for *E. serpyllifolia*, with photosynthesis downregulating by over 70%, compared to 17.3% for *O. ledifolius*. When compared to Williams *et al.* (2003), *E. serpyllifolia* showed much higher photoinhibition in winter than in spring or autumn, whilst levels for *O. ledifolius* remained virtually unchanged throughout the three seasons. Chronic photoinhibition was only slightly higher in winter than in autumn and spring for *O. ledifolius*, but much higher for *E. serpyllifolia* (Williams *et al.* 2003), and dynamic photoinhibition was low for both. The significance of this information lies in *O. ledifolius*' low total and chronic photoinhibition. In the beginning of this work it was stated that chronic photoinhibition is a semi-permanent state, an indication of long-term stress (Critchley 1998), making it clear that *O. ledifolius* has low levels of long-term photoinhibitory stress. *E. serpyllifolia*, on the other hand, with its significantly higher chronic photoinhibition rate, requires downregulation of photosynthesis to a much higher degree, and for a longer period, in order to survive a harsh alpine winter. Interestingly, its low dynamic photoinhibition levels indicate it has little ability to rapidly reverse any downregulation of PS II during such conditions. Again, *O. ledifolius* has more plasticity in this regard, and is able to change its degree of photosynthetic down regulation more rapidly. This is advantageous in conditions where cloud cover and temperature change frequently and rapidly, a situation characteristic of the alpine zone (Körner 1999).

Morphology has also been shown to affect levels of chronic and dynamic photoinhibition. Werner *et al.* (2002) state that the extent of photoinhibition is largely species-specific, but also suggest that leaf orientation may play some role, an attribute that showed pronounced seasonal variation in semi-deciduous species, and little variation in evergreen sclerophylls (less than 10° change in angle). As *O. ledifolius* and *E. serpyllifolia* fall into the latter category, it is believed that their leaf angle changes little throughout the year, thereby discounting any significant effect of leaf angle on photoinhibition. Further work of this type on *O. ledifolius* may confirm this suggestion.

Figure 2 displays the chlorophyll fluorescence parameters of the two species over winter, and the difference in photosynthetic patterns between them is once again highlighted. $F_v/F_{m\text{PD}}$ values were lower for *E. serpyllifolia* in winter than previous values obtained in autumn and spring (Williams *et al.* 2003). In the same work, little variation was found in *O. ledifolius* $F_v/F_{m\text{PD}}$ values (approx. 0.8) and $F_v/F_{m\text{mid}}$ values (approx. 0.7) between the two seasons. However, the current work shows that *O. ledifolius* does, in fact, exhibit slightly lower $F_v/F_{m\text{PD}}$ (mean = 0.71) and $F_v/F_{m\text{mid}}$ (mean = 0.66) values during winter, yet this difference is negligible. Photosynthetic yield, on the other hand, is considerably lower in winter than in autumn and spring (Williams *et al.* 2003). The high F_v/F_m (after dark adaptation), and low yield (full sun) values indicate that *O. ledifolius* is rapidly altering its photosynthetic responses, according to the influx of available light. This becomes more evident from the large proportion of dynamic (rapidly reversing) photoinhibition (over one-third of total photoinhibition) shown by *O. ledifolius* (Fig. 1). The small proportion of dynamic to total photoinhibition in *E. serpyllifolia* offers an explanation for the low F_v/F_m and yield values: without the ability to rapidly reverse photoinhibition, it is forced to down-regulate photosynthesis more



permanently, so that regardless of light levels, its carbon assimilation rates remain low. The growth experiments present the first work on photosynthetic response to temperature of any Tasmanian alpine plant species, and again, *O. ledifolius* has shown its abilities to withstand photoinhibitory conditions to a remarkable extent. Even with its leaf temperature taken to -9°C , one individual of *O. ledifolius* still managed to photosynthesise at just over 90% its maximum rate (at 3.3°C) (Fig. 3a). One of the temperature curves, however, did exhibit a pronounced decline in carbon assimilation at around 7°C (Fig. 3a). This is thought to be due to a fault in the *Walz CMS400* thermocouple that occurred with that particular individual, and thus not expected to be indicative of the photosynthetic response to temperature. The significantly high carbon assimilation rate shown by *O. ledifolius* also indicates its ability to thrive during winter conditions, when its co-occurring species are forced into downregulating their photosynthetic rate. The lower carbon assimilation rate found at the Mt. Wellington site is most likely due to some environmental effect, such as lower *in situ* nutrient availability, or higher *in situ* PPFD, an attribute that is inversely related to photosynthetic efficiency (Schreiber *et al.* 1998). Further work is needed to examine temperature response curves of this species below -9°C and above 24°C to determine the critical limits for photosynthesis mentioned by Braun *et al.* (2002). PPFD levels above $400\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ (e.g. Manuel *et al.* 1999) should be used in conjunction with this, as Braun *et al.* (2003) found that PS II efficiency is severely reduced with PPFD values higher than $900\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$.

Williams *et al.* (2003) showed that photoprotective pigment content, in the form of anthocyanins, and xanthophyll pool size in *O. ledifolius*, were low in both autumn and spring. *E. serpyllifolia* showed not only higher values, but also significant differences between seasons, in response to environmental changes in photoinhibitory variables. Winter analyses on these should be undertaken to build on the knowledge of photoprotection in *O. ledifolius*, and to determine whether or not it is able to sustain these low anthocyanin and xanthophyll pool sizes during winter.

This study has confirmed the unique ability of *O. ledifolius* to maintain a high capacity for light utilisation during photoinhibitory conditions, an ability not observed to this extent by any other plant. The apparent plasticity of its photosynthetic apparatus enables rapid response to the frequently changing temperatures and light irradiance characteristic of the alpine environment, and its ability to sustain high carbon assimilation rates at low temperatures ensure continued growth during the colder winter months. More detailed work is required on this species before we can completely understand its unusual photosynthetic capabilities. Other alpine species from the same genus, such as *Ozothamnus hookeri* and *Ozothamnus rodwayi* have not yet been examined for their photosynthetic properties, and may in fact exhibit similar anomalies. In addition, further studies should examine *O. ledifolius* populations in alpine regions other than Mt. Wellington. If other populations have similar attributes, such studies will increase power in the results found here. If not, it may be the Mt. Wellington population that is unique, in which case genetic factors such as polyploidy (see Warner & Edwards 1993) may be controlling the species' unusual photosynthetic characteristics. Eventually, the information included in this work will lead to increased understanding of the alternative mechanisms used to avoid photodamage, as well as those outlined by Adams *et al.* (2002). This will also have practical applications for forestry, horticultural and agricultural bodies (Ball *et al.* 1995).

Acknowledgements

Sincere gratitude goes to Dr. Mark Hovenden for his enthusiastic supervision of this project, despite both of our patience levels being tested by the IRGA gods! Stephen Kern provided valuable advice and assistance, as well as good company during very early (not to mention cold!) fieldwork on Mt. Wellington. He also provided some of the data used in this report. I also thank Dr. John Ross for his encouragement in publishing this work.

References

- Adams III W.W., Demmig-Adams B., Rosenstiel T.N., Brightwell A.K. & Ebbert V. (2002). Photosynthesis and photoprotection in overwintering plants. *Plant Biology*. **4**, pp. 545-557
- Ball M.C., Butterworth J.A., Roden J.S., Christian R. & Egerton J.J.G. (1995). The applications of chlorophyll fluorescence to forest ecology. *Australian Journal of Plant Physiology*. **22** (2), pp. 311-319
- Berry J. & Björkman O. (1980). **Photosynthetic response and adaptation to temperature in higher plants.** *Annual Review of Plant Physiology*. **31**, pp. 491-543
- Bisba A., Petropoulou Y & Manetas Y. (1997). The transiently pubescent young leaves of plane (*Platanus orientalis*) are deficient in photodissipative capacity. *Physiologia Plantarum*. **101**, pp. 373-378
- BOM (Bureau of Meteorology) (2004). *Climate Averages for Mount Wellington*. http://www.bom.gov.au/climate/averages/tables/cw_094087.shtml. Accessed 27th October 2004
- Braun V., Buchner O. & Neuner G. (2002). Thermotolerance of photosystem 2 of three alpine plant species under field conditions. *Photosynthetica*. **40** (4), pp. 587-595
- Critchley C. (1998). Photoinhibition. In Raghavendra A.S. (Ed.). *Photosynthesis: A Comprehensive Treatise*. Cambridge University Press, U.K.
- Demmig-Adams B. & Adams III W.W. (1996). The role of xanthophyll cycle carotenoids in the protection of photosynthesis. *Trends in Plant Science*. **1**, pp. 21-26
- Drake B.G., Jacob J. & González-Meler M.A. (1998). In Raghavendra A.S. (Ed.). *Photosynthesis: A Comprehensive Treatise*. Cambridge University Press, U.K.
- Gould K.S., Markham K.R., Smith R.H. & Goris J.J. (2000). Functional role of anthocyanins in the leaves of *Quintinia serrata* A. Cunn. *Journal of Experimental Botany*. **51** (347), pp. 1107-1115
- Hopkins W.G. (1999). *Introduction to Plant Physiology*. John Wiley & Sons, Inc. New York, U.S.A.
- Hurry V., Huner N., Selstam E., Gardeström P. & Öquist G. (1998). In Raghavendra A.S. (Ed.). *Photosynthesis: A Comprehensive Treatise*. Cambridge University Press, U.K.
- Kirkpatrick J.B. (1997). *Alpine Tasmania: An Illustrated Guide to the Flora and Vegetation*. Oxford University Press, Melbourne
- Körner C. (1999). *Alpine Plant Life: Functional Plant Ecology of High Mountain Plants*. Springer. Berlin, Germany.
- Kubien D.S. & Sage R.F. (2004). Low-temperature photosynthetic performance of a C-4 grass and a co-occurring C-3 grass native to high latitudes. *Plant, Cell & Environment*. **27** (7), pp. 907-916
- Kubien D.S., von Caemmerer S., Furbank R.T. & Sage R.F. (2003). C₄ photosynthesis at low temperature. A study using transgenic plants with reduced amounts of Rubisco. *Plant Physiology*. **132**, pp. 1577-1585



Lebkuecher J.G. & Eickmeier W.G. (1993). Physiological benefits of stem curling for resurrection plants in the field. *Ecology*. **74** (4), pp. 1073-1080

Manuel N., Cornic G., Aubert S., Choler P., Bligny R & Heber U. (1999). Protection against photoinhibition in the alpine plant *Geum montanum*. *Oecologia*. **119**, pp. 149-158

Martinez-Ferri E., Manrique E. Valladares F. & Balaguer L. (2004). Winter photoinhibition in the field involves different processes in four co-occurring Mediterranean tree species. *Tree Physiology*. **24** (9), pp. 981-990

Maxwell K. & Johnson G.N. (2000). Chlorophyll fluorescence – a practical guide. *Journal of Experimental Botany*. **51** (345), pp. 659-668

Oliveira G. & Peñuelas J. (2001). Allocation of absorbed light energy into photochemistry and dissipation in a semi-deciduous and an evergreen Mediterranean woody species during winter. *Australian Journal of Plant Physiology*. **28**, pp. 471-480

Oquist G. & Huner N.P.A. (1993). Cold-hardening-induced resistance to photoinhibition of photosynthesis in winter rye is dependent upon an increased capacity for photosynthesis. *Planta*. **189** (1), pp. 150-156

Raghavendra A.S. (Ed.) (1998). *Photosynthesis: A Comprehensive Treatise*. Cambridge University Press, U.K.

Robinson S.A., Lovelock C.E. & Osmond C.B. (1993). Wax as a mechanism for protection against photoinhibition - a study of *Cotyledon orbiculata*. *Botanica Acta*. **106** (4), pp. 307-312

Schreiber U., Bilger W., Hormann H. & Neubauer C. (1998). Chlorophyll fluorescence as a diagnostic tool: basics and some aspects of practical relevance. In Raghavendra A.S. (Ed.). *Photosynthesis: A Comprehensive Treatise*. Cambridge University Press, U.K.

Streb P., Shang W., Feierabend J. & Bligny R. (1998). Divergent strategies of photoprotection in high-mountain plants. *Planta*. **207**, pp. 313-324

Warren C.R., Hovenden M.J., Davidson N.J. & Beadle C.L. (1998). Cold hardening reduces photoinhibition of *Eucalypts nitens* and *E. pauciflora* at frost temperatures. *Oecologia*. **113**, pp. 350-359

Werner C., Correia O. & Beyschlag W. (2002). Characteristic patterns of chronic and dynamic photoinhibition of different functional groups in a Mediterranean exosystem. *Functional Plant Biology*. **29**, pp. 999-1011

Williams E.L., Hovenden M.J. & Close D.C. (2003). Strategies of light energy utilisation, dissipation and attenuation in six co-occurring alpine heath species in Tasmania. *Functional Plant Biology*. **30**, pp. 1205-1218

Wise R.R. (1995). Chilling-enhanced photooxidation: the production, action and study of reactive oxygen species produced during chilling in the light. *Photosynthesis Research*. **45**, pp. 79-97

Warner D.A. & Edwards G.E. (1993). Effects of polyploidy on photosynthesis. *Photosynthesis Research*. **35** (2), pp. 135-147