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**PROTECTIVE MECHANISMS IN
NEW ZEALAND LIVERWORTS**

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**A thesis submitted in fulfilment of the requirements
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ABSTRACT

Liverworts were the first plants to successfully make the transition from water to land and thus had to develop morphological and physiological features to overcome novel environmental constraints. The relative simple structure of liverworts in comparison to vascular plants implies that they have to combat environmental stress at a cellular level. Liverworts are an important part of the New Zealand flora. Leafy liverworts such as *Jamesoniella colorata*, *Isotachis lyallii* and *Lepidolaena taylorii* display a spectacular range in colouration within a single population. The leaves can vary from pale green in shaded habitats to bright red in more exposed places. A thalloid species, *Monoclea forsteri*, lacks such pigmentation but it might possess some unique cellular features to deal with stressful conditions. This thesis aims to study the cellular characteristics that allow liverworts to cope with extreme environmental conditions, with emphasis on (red) auxiliary pigments.

Genetic analysis of liverwort populations revealed a highly clonal structure, which suggests that red colouration of liverwort leaves is a phenotypic response, and not a result of genotypic differences. Indeed, the red pigment could be induced in *I. lyallii* at relatively modest irradiance levels.

The red leaves absorbed about 10% more photosynthetically active radiation than green leaves from the same species. Although the chemical characteristics of the red pigment remained elusive, it has light attenuation characteristics similar to anthocyanins in vascular plants. Its cellular location inside the cell wall is ideal for intercepting potentially damaging light quanta and can thereby protect the underlying chloroplasts from high light fluxes. The light energy that is absorbed by the red pigment did not translate into an enhanced protection from chilling-stress through leaf warming.

The photosynthetic apparatus of liverworts has acclimated to the environmental conditions that these plants are most likely to experience in their habitat. Gametophytes from shady environments had lower chlorophyll *a* to *b* ratios than gametophytes found in sunnier places. This illustrates the need for a more efficient light-harvesting system in the former to collect all of the available light. In addition, plants from sunny environments had lower chlorophyll to

carotenoid ratios than plants found in shady environments, which suggests that the photo-protective properties of carotenoids are better developed in the former. This was confirmed by measurements of chlorophyll *a* fluorescence which clearly showed a greater potential for non-photochemical quenching in gametophytes from exposed habitats than gametophytes found in sheltered places, both during high light treatment and desiccation.

A better developed photo-protective system (*i.e.* non-photochemical processes and light-screening pigments) allowed the red-leaved gametophytes to better deal with high light stress as well as desiccation than their green-leaved counterparts. Measurements of photosynthetic responses revealed that red gametophytes were photoinhibited less and their recovery was more complete from a high light treatment of 1800 $\mu\text{mol}/\text{m}^2/\text{s}$ than the greens. Similarly, measurements of photosynthetic responses and oxidative damage indicated that the red morph was better protected from high light fluxes that occur during drought-stress than the green morph. Determination of cell water relations showed that the red pigment in *J. colorata* did not influence the water balance during drought.

In conclusion, this study has presented evidence that liverworts from exposed habitats are better equipped to deal with abiotic stressors such as high light and dehydration than liverworts from more sheltered environments. Changes in pigment composition, concentration and location are likely to play an important role in liverwort protection from environmental stress – most noticeably a red pigment with photo-protective attributes.

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TABLE OF CONTENTS

ABSTRACT	i
ACKNOWLEDGEMENTS	iii
TABLE OF CONTENTS	iv
LIST OF FIGURES	ix
LIST OF TABLES	xvi
ABBREVIATIONS	xviii
CHAPTER 1 – General introduction	1
1.1 Liverwort biology	1
1.1.1 Liverwort development	1
1.1.2 Liverwort structure	5
1.1.3 Liverwort ecophysiology	6
1.2 Cellular protection	8
1.3 Photosynthesis and reactive oxygen species	11
1.3.1 Reactive oxygen species	11
1.3.2 ROS formation during photosynthesis	11
1.3.3 Antioxidants	12
1.4 Photosynthesis: roles of ascorbate and photo-protection	13
1.4.1 Antioxidant activity and regeneration of ascorbate	13
1.4.2 Lipid peroxidation	15
1.4.3 The xanthophyll cycle	15
1.4.4 Chlorophyll <i>a</i> fluorescence	18
1.5 Liverworts in New Zealand	21
1.6 Plant material	22
1.6.1 <i>Monoclea forsteri</i>	22
1.6.2 <i>Jamesoniella colorata</i>	23
1.6.3 <i>Isotachis lyallii</i>	23
1.6.4 <i>Lepidolaena tatlorii</i>	24
1.7 Aims of this thesis	25

CHAPTER 2 – Genetic variability of liverwort populations	30
2.1 Introduction	30
2.1.1 Genetic variability in bryophytes	30
2.1.2 Phenotypic plasticity	30
2.1.3 Aims	32
2.2 Material and methods	33
2.2.1 Plant material	33
2.2.2 DNA extraction	34
2.2.3 RAPD methodology	35
2.2.4 Data analysis	36
2.3 Results	36
2.4 Discussion	40
2.4.1 Genetic structure of New Zealand liverwort populations	40
2.4.2 Phenotypic plasticity	41
2.5 Conclusions	42
CHAPTER 3 – Acclimation strategies of liverworts in relation to their light-environment	43
3.1 Introduction	43
3.1.1 Photosynthetic pigments	43
3.1.2 Protective strategies	44
3.1.3 Aims	46
3.2 Material and methods	46
3.2.1 Plant material	46
3.2.2 Gametophyte anatomy and morphology	46
3.2.3 Pigment extraction and determination	47
3.2.4 Optical properties	48
3.2.5 Surface reflectance properties	49
3.2.6 Environmental responses of liverwort gametophytes	49
3.2.7 Chloroplast ultrastructure	50
3.2.8 Data analysis	50
3.3 Results	50

3.3.1	Gametophyte anatomy and morphology	50
3.3.2	Photosynthetic pigments	55
3.3.3	Anthocyanins, flavonols and UV-absorbing compounds	55
3.3.4	The red pigment	55
3.3.5	Optical properties	57
3.3.6	Surface reflectance	57
3.3.7	Habitat and environmental responses	61
3.3.8	Chloroplast ultrastructure	68
3.4	Discussion	70
3.4.1	Chemical and physical properties of red pigments	70
3.4.2	Habitat characteristics	72
3.5	Conclusions	74

CHAPTER 4 – Photo-protective mechanisms of liverworts from contrasting environments at non-optimal temperatures

4.1	Introduction	75
4.1.1	Photoinhibition	75
4.1.2	Photo-protection	76
4.1.3	The effects of temperature on photosynthesis	77
4.1.4	Aims	78
4.2	Material and methods	78
4.2.1	Plant material	78
4.2.2	Light-response curves and photoinhibition at different temperatures	79
4.2.3	Lipid peroxidation	80
4.2.4	Determination of ascorbate and dehydroascorbate	81
4.2.5	Diurnal patterns of chlorophyll <i>a</i> fluorescence in <i>Jamesoniella colorata</i>	81
4.2.6	Data analysis	82
4.3	Results	82
4.3.1	Light curves at different temperatures	82
4.3.2	Photoinhibition at different temperatures	87
4.3.3	Oxidative damage	91
4.3.4	Diurnal patterns of chlorophyll <i>a</i> fluorescence in <i>Jamesoniella colorata</i>	94

4.4	Discussion	98
4.4.1	Photo-protection	98
4.4.2	Effects of temperature on photosynthesis	99
4.4.3	Oxidative damage	101
4.4.4	Diurnal patterns of photosynthesis in <i>Jamesoniella colorata</i> on Rangitoto Island	102
4.5	Conclusions	103
CHAPTER 5 – Desiccation-tolerance of liverworts from contrasting environments		104
5.1	Introduction	104
5.1.1	Membrane integrity	104
5.1.2	Oxidative damage	106
5.1.3	Ecological considerations	108
5.1.4	Aims	110
5.2	Material and methods	110
5.2.1	Plant material	110
5.2.2	Water content	111
5.2.3	Rate of water loss	111
5.2.4	Isopiestic psychrometry	111
5.2.5	Chlorophyll <i>a</i> fluorescence measurements	112
5.2.6	Determination of ascorbate and dehydroascorbate	113
5.2.7	Lipid peroxidation	114
5.2.8	Pigment extraction and determination	115
5.2.9	Electrolyte leakage	115
5.2.10	Data analysis	116
5.3	Results	116
5.3.1	Kinetics of water loss during desiccation	116
5.3.2	Isopiestic psychrometry	118
5.3.3	Chlorophyll <i>a</i> fluorescence during desiccation	121
5.3.4	Recovery of <i>Jamesoniella colorata</i> after mild drought	124
5.3.5	Recovery of <i>Jamesoniella colorata</i> from severe drought	124
5.3.6	Recovery of <i>Monoclea forsteri</i> from drought	125

5.3.7	Oxidative damage in <i>Jamesoniella colorata</i> during desiccation and rehydration	129
5.3.8	Oxidative damage in <i>Monoclea forsteri</i> during desiccation	132
5.3.9	Photosynthetic pigments in <i>Jamesoniella colorata</i> during desiccation and rehydration	133
5.3.10	Electrolyte leakage in <i>Monoclea forsteri</i> during desiccation	134
5.4	Discussion	136
5.4.1	Desiccation-tolerance in <i>Jamesoniella colorata</i>	136
5.4.1.1	The importance of auxiliary pigments	136
5.4.1.2	Tolerance: desiccation vs rehydration	137
5.4.2	Desiccation-tolerance in <i>Monoclea forsteri</i>	138
5.4.3	The importance of habitat	139
5.5	Conclusions	141
CHAPTER 6 – General discussion		142
REFERENCES		148

LIST OF FIGURES

- Figure 1.1** Liverwort life-cycle (*Marchantia* spp) 3
- Figure 1.2** Sporophyte structures of liverworts. A: emerging sporophyte and calyptra tissue of *Lepidolaena taylorii*. B: sporangium of *Balantiopsis* sp. showing spiral dehiscence of the capsule. C, D: sporangium of *Cuspidatula monodon* showing dehiscence along four lines (C) and elaters with spores (D) 4
- Figure 1.3** Thylakoid-associated protective events involving ascorbate. (A) H₂O₂ removal and reactive oxygen species detoxification. (B) α -Tocopherol regeneration and alkylperoxyl radical trapping. (C) The xanthophyll cycle and non-radiative energy dissipation 17
- Figure 1.4** Characteristic fluorescence induction kinetics or ‘Kautsky curve’ of dark-acclimated and illuminated leaves 20
- Figure 1.5** Photographic details of *Monoclea forsteri*. A: 50-meter long continuous carpet of *M. forsteri* growing on the banks of a stream at Huapai University Reserve, New Zealand. B, C: extensively lobed thallus of male gametophytes showing antheridial discs on the dorsal side and rhizoids on the ventral side 26
- Figure 1.6** Photographic details of *Jamesoniella colorata*. A: patches of *J. colorata* growing on the exposed volcanic rocks of Rangitoto Island, Hauraki Golf, New Zealand. B: patch containing both red and green gametophytes. C: scanning electron micrograph of leaf surface covered with smooth dome-shaped papillae. D: inflated perianth with contracted mouth 27

Figure 1.7	Photographic details of <i>Isotachis lyallii</i> . A, B: continuous red carpet of <i>I. lyallii</i> gametophytes growing on dripping vertical rock faces along Jackson River, Westland, New Zealand. B: erect, unbranched leafy shoots showing sporophytes. C: scanning electron micrograph of leaf surface covered with elongated striae	28
Figure 1.8	Photographic details of <i>Lepidolaena taylorii</i> . A: frond of <i>L. taylorii</i> growing on the trunk of <i>Rhopalostylis sapida</i> at Colin Kerr Taylor Memorial Reserve in Waimauku, New Zealand. B: tapering pinnate frond showing a fleshy shoot calyptra (coelocaulis)	29
Figure 2.1	RAPD-banding pattern on agarose gel (1.5%) obtained with primer OPAX-10 for <i>Jamesoniella colorata</i>	38
Figure 2.2	RAPD-banding pattern on agarose gel (1.5%) obtained with primer OPAX-14 for <i>Lepidolaena taylorii</i> from Waimauku and Massey	39
Figure 2.3	RAPD-banding pattern on agarose gel (1.5%) obtained with primer OPAX-10 for the 50-meter long population of <i>Monoclea forsteri</i> at Huapai	39
Figure 3.1	Photographic details of transverse sections through a thallus of <i>Monoclea forsteri</i> . A: phase-contrast micrograph showing chloroplasts and associated starch grains on both the ventral and dorsal side, rhizoids on the ventral side, and large, thin walled cells in the centre. B: bright field micrograph of an oil body	51
Figure 3.2	Photographic details of <i>Lepidolaena taylorii</i> gametophytes. A: tapering pinnate frond showing both red and green leaves on single branchlets. B, C: bright field micrographs of an intact red (B) and green (C) leaf	52

- Figure 3.3** Photographic details of *Isotachis lyallii* gametophytes. A: leafy shoots with uniform and mixed colours. B, C: bright field micrographs of an intact red (B) and green (C) leaf, showing chloroplasts and granular oil bodies. D, E: bright field micrographs of transverse cross sections through a red (D) and green (E) leaf, showing the association of the red pigment with the cell wall 53
- Figure 3.4** Photographic details of *Jamesoniella colorata* gametophytes. A, B: leafy red (A) and green (B) shoots, both showing green apices. C, D: bright field micrographs of an intact red (C) and green (D) leaf. E-H: micrographs of transverse cross sections through a red and green leaf, top and bottom respectively, showing the association of the red pigment with the cell wall; bright field (E), filter set 02 (F), filter set 09 (G), filter set 15 (H) 54
- Figure 3.5** Spectral absorptance (A-D) of whole ‘leaves’ and spectral reflectance (E-H) of gametophyte canopies from (A, E) *Jamesoniella colorata*, (B, F) *Isotachis lyallii*, (C, G) *Lepidolaena taylorii* and (D, H) *Monoclea forsteri* 58
- Figure 3.6** Absorption ratio (red leaves / green leaves) within photosynthetically active radiation (PAR: 400-700 nm) in *Jamesoniella colorata*, *Isotachis lyallii* and *Lepidolaena taylorii* 59
- Figure 3.7** The effects of micro-climatic conditions in field situations. A: *Jamesoniella colorata* as found on volcanic rocks on Rangitoto Island in the Hauraki Golf, New Zealand, showing that red patches grow in more exposed areas than the green, which is here shown growing in a rock crevice. B: carpet of red *Isotachis lyallii* gametophytes growing on exposed vertical rock faces along Jackson River, Westland, New Zealand whereas green gametophytes occupy more sheltered places. Insert shows the green gametophytes growing under the fern leaves. C, D: patch of red *I. lyallii* gametophytes before (C) and after (D) removal of a fern leaf showing green gametophytes underneath 62

- Figure 3.8** Effect of irradiance on green gametophytes of *Isotachis lyallii*. Gametophytes were exposed to 20 $\mu\text{mol}/\text{m}^2/\text{s}$ (top), 65 $\mu\text{mol}/\text{m}^2/\text{s}$ (middle), and 200 $\mu\text{mol}/\text{m}^2/\text{s}$ (bottom) for 55 days and photographed about every 2 weeks 63
- Figure 3.9** Effect of irradiance on green gametophytes of *Isotachis lyallii*. A, B: before exposure. C, D: 55 days after exposure to 65 $\mu\text{mol}/\text{m}^2/\text{s}$ (C) and 200 $\mu\text{mol}/\text{m}^2/\text{s}$ (D). E, F: 14 days after exposure to 20 $\mu\text{mol}/\text{m}^2/\text{s}$ following high light treatment of 65 $\mu\text{mol}/\text{m}^2/\text{s}$ (E) and 200 $\mu\text{mol}/\text{m}^2/\text{s}$ (F) 64
- Figure 3.10** Effect of irradiance on red gametophytes of *Isotachis lyallii*. Gametophytes were exposed to 20 $\mu\text{mol}/\text{m}^2/\text{s}$ (top), 65 $\mu\text{mol}/\text{m}^2/\text{s}$ (middle), and 200 $\mu\text{mol}/\text{m}^2/\text{s}$ (bottom) 55 days and photographed about every 2 weeks 65
- Figure 3.11** Effect of irradiance on green gametophytes of *Jamesoniella colorata*. Gametophytes were exposed to 20 $\mu\text{mol}/\text{m}^2/\text{s}$ (top), 65 $\mu\text{mol}/\text{m}^2/\text{s}$ (middle), and 200 $\mu\text{mol}/\text{m}^2/\text{s}$ (bottom) for 55 days and photographed about every 2 weeks 66
- Figure 3.12** Effect of irradiance on red gametophytes of *Jamesoniella colorata*. Gametophytes were exposed to 20 $\mu\text{mol}/\text{m}^2/\text{s}$ (top), 65 $\mu\text{mol}/\text{m}^2/\text{s}$ (middle), and 200 $\mu\text{mol}/\text{m}^2/\text{s}$ (bottom) for 55 days and photographed about every 2 weeks 67
- Figure 3.13** Effects of irradiance and desiccation-rehydration cycles on green (A, B) and red (C, D) gametophytes of *Jamesoniella colorata*. Before (A, C) and after (B, D) exposure to 200 $\mu\text{mol}/\text{m}^2/\text{s}$ for 55 days, while being rehydrated once every four days 68

Figure 3.14	Transmission electron micrographs of chloroplasts from <i>Jamesoniella colorata</i> . A, B: transverse section through chloroplasts from red (A) and green (B) leaves. C, D: chloroplasts of green leaves showing variability in ultrastructure	69
Figure 3.15	Transmission electron micrographs of chloroplasts from <i>Isotachis lyallii</i> . A, B: transverse section through chloroplasts from red (A) and green (B) leaves showing differences in size	69
Figure 4.1	Photosynthetic responses of <i>Jamesoniella colorata</i> at 5°C (A, C, E) and 20°C (B, D, F) for red and green gametophytes; (A, B) photosynthetic efficiency (Φ_{PSII}), (C, D) photochemical quenching (qP) and (E, F) non-photochemical quenching (NPQ)	84
Figure 4.2	Photosynthetic responses of <i>Isotachis lyallii</i> at 5°C (A, C, E) and 20°C (B, D, F) for red and green gametophytes; (A, B) photosynthetic efficiency (Φ_{PSII}), (C, D) photochemical quenching (qP) and (E, F) non-photochemical quenching (NPQ)	85
Figure 4.3	Photosynthetic responses of <i>Monoclea forsteri</i> at 5°C and 20°C; (A) photosynthetic efficiency (Φ_{PSII}), (B) photochemical quenching (qP) and (C) non-photochemical quenching (NPQ)	86
Figure 4.4	Recovery of maximum photosynthetic efficiency (F_v/F_m) in the dark in red and green gametophytes of <i>Jamesoniella colorata</i> after photoinhibition treatment of 1800 $\mu\text{mol}/\text{m}^2/\text{s}$ at 5°C (A), 20°C (B), and 35°C (C)	88
Figure 4.5	Recovery of maximum photosynthetic efficiency (F_v/F_m) in the dark in red and green gametophytes of <i>Isotachis lyallii</i> after photoinhibition treatment of 1800 $\mu\text{mol}/\text{m}^2/\text{s}$ at 5°C (A) and 20°C (B)	89

Figure 4.6	Recovery of maximum photosynthetic efficiency (F_v/F_m) in the dark in <i>Monoclea forsteri</i> after photoinhibition treatment of 1800 $\mu\text{mol}/\text{m}^2/\text{s}$ at 5°C, 20°C, and 35°C	90
Figure 4.7	Malondialdehyde (MDA) content before and after photoinhibition treatment of 1500 $\mu\text{mol}/\text{m}^2/\text{s}$ in gametophytes of (A) <i>Jamesoniella colorata</i> , (B) <i>Isotachis lyallii</i> and (C) <i>Monoclea forsteri</i>	92
Figure 4.8	Response of ascorbate to photoinhibition treatment of 1500 $\mu\text{mol}/\text{m}^2/\text{s}$ in (A) <i>Jamesoniella colorata</i> and (B) <i>Isotachis lyallii</i>	93
Figure 4.9	Diurnal changes in photosynthetic efficiency (Φ_{PSII}) and photosynthetically active radiation (PAR) at the end of summer (A, B) (March 5 th , 2003) and winter (C, D) (August 6 th , 2003) in representatives of green (A, C) and red (B, D) gametophytes of <i>Jamesoniella colorata</i> on Rangitoto Island	96
Figure 4.10	Diurnal changes in (A) patch temperature and (B) photosynthetically active radiation (PAR) at March 5 th , 2003 and August 6 th , 2003 in green and red gametophytes of <i>Jamesoniella colorata</i> on Rangitoto Island	97
Figure 5.1	Surface conductances of (A) <i>Monoclea forsteri</i> , and (B) red and green gametophytes of <i>Jamesoniella colorata</i>	117
Figure 5.2	Water losses in <i>Monoclea forsteri</i> , and in red and green gametophytes of <i>Jamesoniella colorata</i>	117
Figure 5.3	Pressure-volume curves of representatives from (A) red and green gametophytes of <i>Jamesoniella colorata</i> and (B) <i>Monoclea forsteri</i>	119
Figure 5.4	Effects of water-stress on symplast osmotic potential ($\Psi\pi_s$) in <i>Monoclea forsteri</i> , and in red and green gametophytes of <i>Jamesoniella colorata</i>	120

Figure 5.5	Turgor pressure (Ψ_p) as a function of cell water deficit in <i>Monoclea forsteri</i> , and in red and green gametophytes of <i>Jamesoniella colorata</i>	120
Figure 5.6	Changes in (A) photosynthetic efficiency of photosystem II (Φ_{PSII}) and (B) non-photochemical quenching (NPQ) in response to desiccation in red and green gametophytes of <i>Jamesoniella colorata</i>	122
Figure 5.7	Changes in (A) photosynthetic efficiency of photosystem II (Φ_{PSII}) and (B) non-photochemical quenching (NPQ) in response to desiccation in <i>Monoclea forsteri</i> 123	123
Figure 5.8	Changes in (A) photosynthetic efficiency of photosystem II (Φ_{PSII}) and (B) non-photochemical quenching (NPQ) in response to rehydration of red and green gametophytes of <i>Jamesoniella colorata</i> after mild drought	126
Figure 5.9	Changes in (A) photosynthetic efficiency of photosystem II (Φ_{PSII}) and (B) non-photochemical quenching (NPQ) in response to rehydration of red and green gametophytes of <i>Jamesoniella colorata</i> after one week severe drought	127
Figure 5.10	Changes in photosynthetic efficiencies of photosystem II (Φ_{PSII}) in response to rehydration of <i>Monoclea forsteri</i> gametophytes after different degrees of desiccation	128
Figure 5.11	Effects of desiccation and rehydration on (A) reduced ascorbate (AsA) content, (B) oxidized ascorbate (DHA) content and (C) the DHA / AsA ratio in red and green of <i>Jamesoniella colorata</i> gametophytes	130
Figure 5.12	Effects of dehydration and rehydration on malondialdehyde (MDA) content in red and green morphs of <i>Jamesoniella colorata</i>	131

Figure 5.13 Effects of desiccation on (A) ascorbate (AsA) and dehydroascorbate (DHA) content and (B) malondialdehyde (MDA) content in *Monoclea forsteri* 132

Figure 5.14 Effect of desiccation on relative electrolyte leakage (REL) in *Monoclea forsteri*
... 134

LIST OF TABLES

Table 2.1	Base sequence of 10-mer primers that were used for RAPD analysis	36
Table 2.2	Total number of RAPD amplification products and polymorphic products generated by each primer in <i>Monoclea forsteri</i> , <i>Jamesoniella colorata</i> and <i>Lepidolaena taylorii</i>	37
Table 2.3	Inter-population analysis of molecular variance (AMOVA) based on RAPD data from <i>Jamesoniella colorata</i> , <i>Lepidolaena taylorii</i> and <i>Monoclea forsteri</i> . .	37
Table 2.4	Intra-population analysis of molecular variance (AMOVA) based on RAPD data from <i>Jamesoniella colorata</i> , <i>Lepidolaena taylorii</i> and <i>Monoclea forsteri</i> . .	38
Table 3.1	Concentrations of chlorophylls (<i>a + b</i>), carotenoids (<i>xanthophylls + carotenes</i>), chlorophyll <i>a</i> to <i>b</i> ratio, and chlorophyll to carotenoid ratio in gametophytes of <i>Jamesoniella colorata</i> , <i>Isotachis lyallii</i> , <i>Lepidolaena taylorii</i> and <i>Monoclea forsteri</i>	56
Table 3.2	Concentrations of extractable anthocyanins, flavonol glycosides and UV-absorbing compounds in <i>Jamesoniella colorata</i> , <i>Isotachis lyallii</i> , <i>Lepidolaena taylorii</i> and <i>Monoclea forsteri</i>	56
Table 3.3	‘Leaf’ optical properties of <i>Jamesoniella colorata</i> , <i>Isotachis lyallii</i> , <i>Lepidolaena taylorii</i> and <i>Monoclea forsteri</i>	59
Table 3.4	Surface reflectance properties from canopies of <i>Jamesoniella colorata</i> , <i>Isotachis lyallii</i> , <i>Lepidolaena taylorii</i> and <i>Monoclea forsteri</i>	60

Table 3.5	Reflectance properties from gametophyte canopies of <i>Jamesoniella colorata</i> , <i>Isotachis lyallii</i> , <i>Lepidolaena taylorii</i> and <i>Monoclea forsteri</i> measured as photochemical reflectance index (PRI), anthocyanin reflectance index (ARI) and red / green ratio (R_{red} / R_{green})	60
Table 4.1	Non-photochemical quenching capacity and its components for liverwort species that were exposed to an irradiance of 1800 $\mu\text{mol}/\text{m}^2/\text{s}$ for 30 mins at different temperatures	91
Table 4.2	Decline in diurnal photosynthetic efficiency of photosystem II (Φ_{PSII}) in red and green gametophytes of <i>Jamesoniella colorata</i> on Rangitoto Island during summer and winter	95
Table 4.3	Average diurnal patch temperature and photosynthetically active radiation (PAR) in red and green gametophytes of <i>Jamesoniella colorata</i> on Rangitoto Island during summer and winter	95
Table 5.1	Water relations parameters in <i>Monoclea forsteri</i> and in red and green gametophytes of <i>Jamesoniella colorata</i> , obtained from pressure-volume (P-V) curves according to Proctor <i>et al.</i> (1998)	118
Table 5.2	Concentrations of chlorophylls ($a + b$), carotenoids (<i>xanthophylls + carotenes</i>), chlorophyll a / b ratio and chlorophyll / carotenoid ratio in red and green gametophytes of <i>Jamesoniella colorata</i> after dehydration and rehydration. .	133
Table 5.3	Response of relative electrolyte leakage (REL) to dehydration and 5 minutes after rehydration in <i>Monoclea forsteri</i>	135
Table 5.4	Response of relative electrolyte leakage (REL) to dehydration and 1 hour after rehydration in <i>Monoclea forsteri</i>	135

ABBREVIATIONS

SI (Système Internationale) abbreviations are used for chemical elements. Other abbreviations are listed below:

°C	degrees Celsius
³ Chl*	triplet (excited) chlorophyll
ε	extinction coefficient
μg	microgram(s)
μl	micro litre(s)
μM	micro molar
μmol	micromole(s)
Φ _{PSII}	efficiency of photochemistry within photosystem II
Ψ _p	turgor pressure
Ψ _w	water potential
Ψ _π	osmotic potential
Ψ _{π,s}	symplast osmotic potential
<	smaller-than
>	greater-than
≤	smaller-than or equal to
≥	greater-than or equal to
≈	almost equal to
A	absorbance
ABA	abscisic acid
AMOVA	analysis of molecular variance
ANOVA	analysis of variance
APX	ascorbate peroxidase
ARI	anthocyanin reflectance index
AsA	ascorbate
ATP	adenosine triphosphate
BHT	butylated hydroxytoluene

bp	base pair(s)
<i>c</i>	circa
cm	centimetre(s)
DHA	dehydroascorbate
DHAR	dehydroascorbate reductase
DNA	deoxyribonucleic acid
dNTPs	2'-deoxynucleotide 5'-triphosphate
D_{st}	average gene diversity over loci
DTT	dithiothreitol
DW	dry weight
EDTA	ethylene diamine tetra-acetic acid
etc	etcetera
Fd	ferredoxin
fig(s)	figure(s)
F_m	maximal chlorophyll <i>a</i> fluorescence of dark acclimated tissue
F_m'	maximal chlorophyll <i>a</i> fluorescence of light acclimated tissue
F_o	minimal chlorophyll <i>a</i> fluorescence of dark acclimated tissue
F_o'	minimal chlorophyll <i>a</i> fluorescence of light acclimated tissue
F_s	stable chlorophyll <i>a</i> fluorescence of light acclimated tissue
F_v	variable chlorophyll <i>a</i> fluorescence of dark acclimated tissue
F_v/F_m	maximum quantum efficiency of photosystem II
FW	fresh weight
g	gram(s)
<i>g</i>	gravitational acceleration
GR	glutathione reductase
GSH	glutathione
GSSH	glutathione disulfide
H ₂ O ₂	hydrogen peroxide
hr(s)	hour(s)
Kb	kilo base(s)
km	kilometre(s)
<i>lea</i>	late-embryogenesis-abundant

m	meter(s)
M	molar (moles / litre)
MDA	malondialdehyde
MDA [•]	monodehydroascorbate radical
MDAR	monodehydroascorbate reductase
mg	milligram(s)
min(s)	minute(s)
ml	millilitre(s)
mm	millimetre(s)
mM	milli molar
MPa	mega Pascal(s)
NADP ⁺	nicotinamide adenine dinucleotide phosphate
NADPH	protonated form of nicotinamide adenine dinucleotide phosphate
n.d.	not detectable
ng	nanogram(s)
nm	nanometre(s)
NPQ	non-photochemical quenching
O ₂	molecular oxygen
O ₂ ^{•-}	superoxide
¹ O ₂	singlet oxygen
•OH	hydroxyl radical
PAR	photosynthetically active radiation (400-700 nm)
PCR	polymerase chain reaction
PRI	photochemical reflectance index
PSI	photosystem I
PSII	photosystem II
P-V	pressure-volume
Q _A	plastoquinone
qP	photochemical quenching
R	reflectance
R'a	apoplast volume
RAPDs	random amplified polymorphic DNA

REL	relative electrolyte leakage
RFLPs	restricted fragment length polymorphisms
RNA	ribonucleic acid
ROO [•]	lipid peroxy radical
ROS	reactive oxygen species
R _{red} / R _{green}	red / green reflectance ratio
Rubisco	ribulose biphosphate carboxylase / oxygenase
RWC	relative water content
s	second(s)
SEM	scanning electron microscopy
SOD	superoxide dismutase
sp	species (singular)
spp	species (plural)
SW	saturated weight
TBA	thiobarbituric acid
TBARS	thiobarbituric acid reactive substances
TBE	Tris-boric acid-EDTA
TCA	trichloroacetic acid
TEM	transmission electron microscopy
UV	ultraviolet
UV-B	ultraviolet-B (280-320 nm)
UV-VIS	ultraviolet-visible
^v / _v	volume / volume
W	Watt
^w / _v	weight / volume