LICHEN THERMAL SENSITIVITIES, MOISTURE INTERCEPTION AND ELEMENTAL ACCUMULATION IN AN ARID SOUTH AFRICAN ECOSYSTEM

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A thesis submitted in partial fulfillment of the requirements for the degree of Magister Scientiae in the Department of Biodiversity and Conservation Biology, University of the Western Cape.

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October 2010

To Azwifaneli and Mpho

Keywords

Climate warming
Diurnal measurements
Effective temperature
Elemental concentrations
Fog and dew precipitation
Lethal temperature
Lichens
Moisture uptake
Photosynthetic quantum yield
Respiration

Abstract

Elevated temperatures accompanying climate warming are expected to have adverse effects on sensitive lichen species. This premise was examined by measuring the sensitivity of different lichen species to elevated temperatures in the laboratory and in the field. Laboratory studies involved the exposure of nine hydrated lichen species (*Xanthoparmelia austro-africana, X. hyporhytida, Xanthoparmelia* sp., *Xanthomaculina hottentotta, Teloschistes capensis, Ramalina* sp., *Flavopuntelia caperata, Lasallia papulosa, Parmotrema austrosinensis)* collected from sites of different aridity and mean annual temperature for 2 hourly intervals to temperatures ranging from 24ºC to 48ºC in a forced daft oven and measuring their respiration rates and maximum quantum yield of PSII. Field studies involved simultaneous hourly measurements of ground surface air temperatures and Lichen effective quantum yield of PSII of hydrated lichen species populations under ambient and artificially modified environmental conditions. Artificial modification of the ambient environment (2.1^{o}C - 3.8^{o}C increase; 31.9% - 46.1% precipitation decrease), approximating future climate change scenarios, was achieved by covering lichen populations at a hot arid and warm coastal site with transparent hexagonal open-top chambers. All lichen species displayed diminished maximum quantum yield of PSII with elevated temperatures. The temperatures limiting lichen maximum quantum yield of PSII were condsiderably lower than those limiting respiration. They were higher in lichens from hot arid than cool motane sites, with limiting photosynthetic temperatures under natural conditions also substantially (up to 20 ^{o}C) lower than those under laboratory conditions. Under natural conditions, all lichen species displayed early morning peaks in photosynthetic quantum yield which subsequently declined with increasing temperatures towards midday with a second phase of elevated photosynthetic quantum yield also apparent in the cooler late afternoon. All these findings indicated that even small increases in temperature, especially during early morning and late afternoon periods of peak photosynthetic activity, or just a shift from a winter to summer precipitation pattern, could negatively affect the carbon balance of lichens resulting in localized extinctions.

In addition to the studies of lichen thermal sensitivity, moisture interception and elemental accumulation by lichens in a coastal subtropical desert were investigated. Two dominant lichen species (*T. capensis* and *Ramalina* sp.) were cultivated on their gypsum substrates in automated weighing micro-lysimeters which measured at hourly intervals their changes in mass due to fog and dew interception and loss from which net daily, monthly and annual amounts were computed. Also, samples of lichen tissue were collected monthly for analysis of eleven elemental concentrations. *T. capensis* with its thinner thallus displayed larger daily fluctuations in moisture gain and loss and intercepted greater net amounts of fog and dew annually (502.3 mm a^{-1}) than *Ramalina* sp. (372.4 mm a^{-1}), both of which were up to ten times greater than the rainfall amount of 42.6 mm a^{-1}. Measured elemental concentrations in the two lichens were in the range of background concentrations reported in other lichen species, except Fe, Mg and Na which more closely approximated concentration ranges reported for lichens in other seashore ecosystems. Rainfall appeared a more important source of elements for the lichens than fog and dewfall as it was positively correlated with Ca, N and B concentrations in these lichens compared with fog and dewfall correspondence with only K concentrations.

Declaration

I declare that *Lichen Thermal Sensitivities, Moisture Interception and Elemental Accumulation in an Arid South African Ecosystem* is my own work, that it has not been submitted for any degree or examination at any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

Khumbudzo Walter Maphangwa October 2010

Signed:………………………………………………………..…

Acknowledgment

I would like to thank my supervisor, Professor Charles F. Musil for guiding me throughout this study. His encouragement, guidance and support enabled me to develop an understanding of the subject. He was always accessible and willing to advise me whenever I needed help. I would like to thank Professor Lincoln Raitt for reviewing my chapters. I would also like to thank Dr. Luciana Zedda for helping me with the identification of lichens and reviewing my chapters. Professor Gerhard Rambold is thanked for helping me with lichen identifications and allowing me to use his laboratory. I would also like to thank Mr. Leslie Powrie for helping me with the maps. All my colleagues at the Climate Change and Bio-adaptation Divisions made it a friendly place to work. In particular, I would like to thank Judith Arnolds, Ignatious Matimati, Justine Nyaga, Ruwanza Sheunesu and Thabiso Mokotjomela. Special mention goes to Stanley Snyders who assisted me with most of the technical work in the field. I would also like to extend my heartfelt gratitude to the South African National Biodiversity Institute for funding this study, providing office space, vehicles and internet facilities. I am grateful to the German Federal Ministry of Education and Research under BIOTA Southern Africa Phase III for funding my trip to Germany for training on lichen identification using modern chemical assay. My deepest gratitude goes to my parents, Alfred and Selinah Maphangwa for their care and love. My brothers, sisters and Lucas Chauke are thanked for their support. Last but not least, I would like to thank Azwifaneli Traider Makungo and Mpho Maphangwa for their love, support and encouragement.

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A review of lichen biology

1.1. Introduction

Lichens are by definition symbiotic organisms, usually composed of a fungal partner, the mycobiont, and one or more photosynthetic partners, the photobiont, which is most often either a green alga or cyanobacterium (Nash, 2008). Each partner contributes in different ways to the symbiosis. The fungus protects the photobiont from intense isolation and dehydration, and absorbs mineral nutrients from the substratum and the atmosphere. The photobionts synthesize organic compounds by the photosynthesis process and cyanobacteria are able to produce organic nitrogen compounds by nitrogen fixation (Zedda & Rambold, 2006). These organisms are perennials and maintain a uniform morphology over time. They grow slowly, have a large-scale dependence upon the environment for their nutrition, and in contrast to vascular plants they do not shed their parts during growth (Nash, 2008).

1.2. Morphology

Lichens are traditionally classified into three main growth forms: crustose, foliose and fruiticose. These forms, which are in no sense natural divisions, are at best points on a scale of continuous differentiation from primitive to highly structured thalli with many intermediates. Each form is characterized by a particular arrangement of cortical, algal and medullary tissues and by different modes of attachment to the substrate (Hale, 1983).

The simplest crustose lichen growth forms, the leprose one, lack an organized thallus which is composed of an indeterminate hyphal mat which entraps and encloses algal colonies (Hale, 1983), while other crustose forms are tightly adhered to substrates and extremely difficult to remove. Lichens of this grow-form are often found in extreme habitats such as bare, exposed rock surfaces or arid soils and very common in semiarid and arid regions of the world (Zedda & Rambold, 2006).

Typical foliose lichens differ from the crustose type in being dorsiventral with distinct upper and lower surfaces free of the substrate but usually attached to it by rhyzines. The thallus is typically divided into branching lobes, and most commonly represented in the genera *Anaptychia, Cetraria, Heterodermia*, *Parmelia* s.l., *Physcia*, and *Xanthoria*. This highly developed form has given rise to a great range of thallus size and diversity (Hale, 1983).

Fruiticose lichens are hair-like, shrubby, finger-like, or strap shaped with a wide range in size, i.e. from minute thalli of *Siphula* only a few mm tall to strands of *Usnea* up to several meters long. Their internal structure can be radial with a dense outer cortex, a thin algal layer, a medulla and a more or less hollow centre or a dense central cord. The thallus may be round or flattened and often richly branched. Fruticose lichens are anchored by basal rhizoidal strands derived from the cortex, although many species are without any attachment to the substrate (Hale, 1983).

Among the various species, a wide range of subtypes can be observed within this major growth type however crustose lichens can have a powdery surface, or present squamulose or peltate structures, or can even have some lobes at thallus border (placoid). Foliose lichen may be umbilicate, the more or less circular thalli being attached to the substrate by a central umbilicus of the lower surface (Zedda & Rambold, 2006). Lichens grow on bark, leaves and wood, rock and soil, (Ahmadjian & Hale, 1973).

1.3. Identification

Morphological and anatomical traits, especially lichen growth form, the type of photobiont and its pigmentation, mycobiont fruiting bodies, spores and conidia and chemical analyses of secondary metabolites present in lichens are all used for their identification (Hale, 1983). Colour tests and fluorescence analysis give indications of which groups of compounds might be present in a lichen sample and microcrystalization, chromatography and mass spectrometry techniques are used for their tentative identification (Ahmadjian & Hale, 1973). Thin layer chromatography (TLC) and high performance liquid chromatography (HPLC) are usually applied for a more precise identification of lichens substances with gas-liquid chromatography also applied in some cases (Ahmadjian & Hale, 1973).

Four colour tests are used routinely in lichen identification. These include: application of 1. pure bleach, 2. 10% potassium hydroxide individually or in combination with bleach, 3. paraphenylenediamine and 4. 50 % nitric acid. These colour tests are performed by applying the appropriate reagent to lichen fragments by means of a pointed glass rod and observing the colour changes with hand lens or under binocular microscope. The lichen cortex and medulla are usually tested separately (Ahmadjian & Hale, 1973).

Examination of lichen specimens under UV light also provides valuable clues to the presence or absence of certain compounds (Hale, 1956) such as anthraquinones, pulvinic-acid derivatives and xanthones. Some depsides and depsidones fluoresce bright white to bluish or greenish white under UV light (Ahmadjian & Hale, 1973).

1.4. Southern African lichen species

Lists of lichen species collected in South Africa have been published by Massalongo (1861), Crombie (1876a; 1876b), Doidge (1950), Almborn (1988), Jürgens & Niebel-Lohmann (1995), Schultz *et al*. (2009), Zedda & Rambold (2004, 2009), Zedda *et al*. (2010)

and numerous taxonomical revisions have been carried by different authors. A checklist of South African lichens has been published by Feuerer & Zedda (2001). However, wide regions of Southern Africa are still lichenologically unexplored. A brief overview of lichenological activities in South Africa was recently published given by Crous *et al*. (2006) who concluded that much work needs to be done, especially among microlichens, the major obstacle being a lack of critical checklists of sterile specimens.

1.5. Ecological importance

Lichens cover about 8% of the Earth's land surface and are the dominant vegetative form in extreme habitats, like the arctic tundra and fog deserts, where they can cover several square kilometers. As a consequence, they are important carbon sinks through their consumption of atmospheric carbon dioxide during photosynthesis and therefore have an important role in mitigating climate warming. Lichens also contribute to soil formation through physical and chemical breakdown of rock minerals, and enrich the soil with nutrients and organic matters. Physical breakdown occurs through the immense turgor pressure exerted by hyphae and rhizines in penetrating rocks. Chemical breakdown occurs in various ways, namely through secretion of oxalic acids which react with mineral components of rocks to form various metal oxalates and acidic polysaccharides which dissolve the cementing material in sandstones releasing the quartz crystals (Nash, 2008). Examples include the characteristic dark-brown stain caused by iron oxalates associated with the lichen *Lecidea lactea* colonizing dunite rock (Purvis, 2000) and the abundant calcium oxalates associated with lichens such as *Dirina massiliensis* f. *sorediata* colonizing limestones (Purvis, 2000).

Lichens accumulate large amounts of elements from wet and dry deposition sources (Nash, 1996) that mostly exceed their physiological requirements (Nash, 2008) making them useful biomonitors of the environment (Puckett, 1988; Garty, 2001). Wet deposition of elements by fog and dew precipitation is more important than that of intermittent rainfall events as it contains higher undiluted elemental concentrations (Nash, 2008). Dry deposition of elements is by sedimentation, impaction, and gaseous absorption (Knops *et al*., 1991). The influence of substrate on elemental accumulation by lichens has been studied extensively (Nieboer *et al*., 1978; Prussia & Killingbeck, 1991). Elevated concentrations of some elements in lichen tissues suggest that lichens may accumulate substrate elements (Lawrey & Rudolph, 1975; Goyal & Seaward, 1981; Garty *et al*., 1986; Garty & Ammann, 1987). De Bruin & Hackenitz (1986) and Sloof & Wolterbeek (1993), for example, showed that lichens may absorb small amounts of some elements such as Ca, Mn, Zn, Cd, and B from bark, and *Acarospora clauzadeana* restricted to gypsum substrates has been reported to accumulate calcium and sulphate ions (Nash, 2008). Also, soil particles are readily incorporated into intracellular spaces within lichen thalli resulting in relatively high concentrations of Al, Fe, Sc, Ti, and other elements of lithic origin (Nash, 2008). The surface characteristics of lichen thalli, such as the incidence of cilia, pits, isidia, and its rugosity determine the efficiency of particle entrapment (Puckett & Finegan, 1980). Also, lichen morphological and structural features (Chiarenzelli, *et al*., 1977; Clair, *et al*., 2002) determine the quantity of elements accumulated by lichens with several examples of foliose lichens with thin flat thalli, which provide a high ratio of surface area to dry weight (Nieboer *et al*., 1972), being more effective at accumulating elements in airborne particles than fruticose lichens (Lawrey & Hale, 1981; Gough *et al*., 1998; Glenn *et al*., 1995; Garty, 2001). These elemental accumulations play a crucial role in ecosystems by incorporating atmospheric nitrogen through N-fixation by photobionts of some lichen species and other elements into nutrient poor soils (Kallio 1975; Crittenden, 1983; Nash 1996; Longton, 1997), by contributing to nutrient cycling (Crittenden 1983; Crittenden 1989; Nash 1996; Kielland 1997; Longton 1997), by improving seedling establishment (Brown & Mikola, 1974; Kershaw, 1985) and acting as carbon sinks (Nash, 1996; Lange *et al*., 1998)

High ground cover of terricolous lichens prevents water loss and soil erosion, even in arid to semiarid habitats (Purvis, 2000; Belnap & Lange 2001). Also, the release by decomposing lichens of nitrogen fixed by cyanobacterial symbionts and other nutrients accumulated during growth are essential for plant growth on nutrient poor soils. Soil growing lichens are also an important component of arid to semi-arid ecosystems where they contribute, together with bryophytes, algae, cynobacteria and non-lichenized fungi, to the formation of biological soil crust and to soil formation by building up organic matter (Zedda & Rambold, 2009).

Lichens provide an important food source for many animals. *Cladonia* species are consumed by many small vertebrates (Kershaw & Alvin, 1963), including reindeer (*Rangifer tarandus*), black tail deer (*Odocoileus hemionus)* and Chinese musk deer (*Moschus moschiferus)* as well as birds such as spruce grouse (*Canachites canadensis)* and wild turkey (*Meleagris gallopavo)* in North America. Sheep in Lybian deserts graze extensively on the subfoliose *lichen Rhizoplaca (Lecanora) esculenta* which is the fabled manna of the ancient Israelites (Hale, 1967, 1983). Birds also use lichen material to build their nests. Typical examples are the Madagascar olive-headed weaver (*Ploceus olivaceiceps*) and the European goldfinch (*Carduelis spinus)* which both construct their nests entirely from *Usnea* species (Purvis, 2000). Northern flying squirrels, *Glaucomys sabrinus*, use the beard-lichen *Bryoria fremontii* as a nesting material and food, and many birds, rodent and invertebrate species also use pendulous, hair-like lichens for nesting materials and shelter (Hayward & Rosentreter, 1994; Pettersson *et al*., 1995). Humming birds in Colombia and in Arizona and gnat catchers in Virginia both cover the outside of their nests with the foliose lichen *Parmotrema reticulatum* (Hale, 1983). Also several insects, such as the peppered moth (*Biston betularia*) and the grey dagger moth (*Acronicta psi*) use lichens for camouflage, and some butterflies store lichen compounds in their tissues for chemical defence (Purvis, 2000).

1.6. Economic importance

The most important use of lichens has been in the production of dyes, perfumes, cosmetics and medicines. The lichens traditionally most used for dying wool and clothes in Europe and North America belong to the genera *Roccella, Evernia, Ochrolechia* and *Parmelia*. The most characteristic pigmentations are reddish purple (orchil), orange, yellow and brown (Hale, 1983).

Since the 16th century, lichens such as *Evernia prenastri* and *Pseudevrnia furfuracea* have been used as raw materials for the production of perfumes which are highly valued for their musk like fragrances and often used in scenting soaps (Hale, 1983; Purvis, 2000; Nash, 2008).

Lichens have persisted in folk medicine into recent times and illustrated in early herbals, for example Gerad's Herball 1597. Some species, like *Cetraria islandica, Lobaria pulmonaria, Parmelia sulcata* and *Usnea* are still used in the Northern Hemisphere, for treating respiratory diseases and other kinds of maladies (Kershaw & Alvin, 1963; Hale, 1983; Purvis, 2000). In southern Africa, species of *Parmelia* ("Klipblomme") are used as medicines in rural areas in the Cape against different diseases, and *Xanthomaculina hottentotta* is used as deodorant or perfume in Namibia. Some lichens are also used as dye source for colouring wool in the Cape (Van Wyk & Gerike, 2000). Recently a number of substances found in lichens have been shown to have antibiotic properties. One example is the yellowish usnic acid found in *Usnea* and in certain other lichens which is effective as an ointment for wounds and burns and in the treatment of infections, and for some purpose has been found to be more effective than penicillin (Kershaw & Alvin, 1963).

1.7. Lichens responses to the environment

Lichens possess certain anatomical and physiological characteristics which render them highly sensitive to environmental changes. These include: 1. the absence of stomata and a protective cuticle allowing little control over gas and moisture exchange and diffusion of atmospheric pollutants concentrated in fog and dew, a major source of water for lichens, into the sensitive photobiont layer (Rope & Pearson, 1990; Nash, 2008), 2. an elevated metabolic rate under hydrated conditions which persists even at low temperatures, 3. a high susceptibility to persistent damage due to a slow growth rate which restrains injury repair, and 4. long-lived perennial bodies which concentrate elements absorbed from their environment (Nimis *et al*., 1990; Purvis, 2000; Conti & Cecchetti, 2001; Zedda & Rambold, 2006; Tiwari, 2008).

Lichen responses to environmental changes have been determined from measurements of thallus size and fertility, thallus bleaching and convolution, photosynthetic and respiration rate (Sigal & Nash, 1983; Conti & Cecchetti, 2001; Bartók *et al*., 1992; Garty *et al*., 2000; Egger *et al*., 1994), rate of nitrogen fixation by blue green algal photobionts (Hawksworth & Rose, 1976; Sigal & Nash, 1983), ATP levels (Kardish *et al*., 1987; Garty *et al*., 1988), concentration of stress ethylene (Epstein *et al*., 1986; Garty *et al*., 2000) leakage of electrolytes (Silberstein *et al*., 1996a), glutathionine and amino acid content (Silberstein *et al*., 1996b), reduction of 2,3,5-triphenyltetrazolium chloride to triphenyl formazan (Bačkor & Fahselt, 2005), chlorophyll concentration and degree of phaeophytinization (Ronen & Galun, 1984; Garty *et al*., 1992; Chettri *et al*., 1998) and chlorophyll a fluorescenece (Garty *et a*l., 2000).

In foliose lichens the centre often dies first leaving an arc of marginal lobes. A 32% reduction in thallus expansion has been reported in *Parmelia saxatilis* at a polluted site over a three year period as well decreases in thallus size and ascocarp production along transects from unpolluted to polluted areas (Sanz *et al*., 1992). Also, diminished photosynthetic and respiration rates have been reported in lichens at polluted sites (Sanz *et al*., 1992) with photosynthesis more sensitive to pollution than respiration (Hale, 1983) and nitrogen fixation by blue green algal photobionts markedly reduced by pollution. The latter exemplified by an observed 80-90% reduction in N_2 fixation over 3 to 4 week period by lichens transplanted into an urban polluted area (Hawksworth & Rose, 1976; Sigal & Nash, 1983).

In addition to rain, lichens utilize a variety of water sources, such as fog, dew and even elevated water vapour, to activate gas exchange. There is an abundance of lichens in coastal deserts where rainfall is minimal and sporadic, but fog, dew and elevated humidity's occur very frequently (Kappen, 1988). The utilization of water vapour alone as a moisture source by lichens is remarkable (Butin, 1954; Lange & Bertsch, 1965) and as a consequence lichens are successful colonizers of the deserts of the world, because they do not rely on rain but can become active after moistening by fog, dew, or even high air humidity alone (Matthes-Sears *&* Nash, 1986). Lange *et al*. (1990) reported that *Teloschistes capensis* is able to collect sufficient fog and early morning dewfall to sustain positive net photosynthesis for a considerable portion of the day. Dew and fog favours lichen productivity also in other climatic regions, such as in the Alps, in Mediterranean-climate areas and in temperate zones (Nash, 2008). The importance of non precipitation sources of water is well demonstrated by the abundance of lichens in coastal deserts where precipitation is minimal, but fog, dew, or elevated relative humidity's occur almost daily (Kappen, 1988).

The uptake of water from unsaturated atmospheres by lichens is extraordinary as it represents essentially the reverse of evaporation and is a process that does not occur in the relatively homoiohydric vascular plants. The water moves between the lichen and the air along a decreasing water potential gradient (Rundel, 1982, 1988; Nash *et al*., 1990) until the lichen water content has equilibrated with the surrounding environment. The lichen will absorb water when the water potential of the lichen (matrix þ solute) is lower than the water potential of the air (Nash, 2008). Although it has yet to be quantified, the interception of fog and dew water by lichens in coastal deserts may well represent a significant fraction of hydrological inputs to those systems, particularly in regions where precipitation rarely occurs, such as the Atacama Desert of South America. In interior arid and semi-arid regions lichens occur commonly as part of the cryptogamic crusts that are particularly extensive on undisturbed soils. These crusts not only intercept precipitation, but also facilitate infiltration of water into the soil, which, in the absence of the cryptogams, frequently has an impervious $CaCO_3$ layer at or near the soil surface (Harper & Marble, 1988). Lichens are particularly effective at capturing both dew and fog and these sources are frequently richer in nutrients than rain (Nash, 2008).

Lichens in the hydrated state have also been reported more susceptible to environmental stress than in a dehydrated state. This exemplified by 16%, 13% and 18% greater reductions in chlorophyll contents measured in *Cladonia coniocraea, C. cristatella* and *Parmelia rudecta* respectively in hydrated than dehydrated states when fumigated with SO_2 (Nash, 1973). Fruticose lichens are well established as being the most sensitive to environmental stress, foliose lichens of intermediate sensitivity and crustose lichens the least sensitive (Zeran *et al*., 2007; Tiwari, 2008). However, under natural conditions lichens are potentially able to avoid adverse environmental conditions through their production of large number of minute diaspores which are known to be dispersed over large distances (van Herk *et al.*, 2002).

1.8. Lichen responses to atmospheric pollution

Lichens were recognized as potential indicators of air pollution as early as the 1860's in Britain and Europe where a progressive loss of lichens in major European cities was noticed (Hale, 1967). Since then, lichens have played prominent roles as indicators of sulfur dioxide air pollution throughout the world (Tiwari, 2008). Several authors maintain that SO_2 pollution is the primary cause of death of lichens in most urban and industrial areas (Gilbert, 1970; Tiwari, 2008) though some species are resistant to this pollutant (Conti & Cecchetti, 2001; Zeran *et al.*, 2007). The observed adverse effects of SO_2 pollution on sensitive lichens include decrease in respiration and photosynthesis, with photosynthesis more sensitive than respiration (Showman, 1972; Beekley & Hoffman, 1981), increase in membrane permeability, K^+ influx and loss of ions, and ultra structural changes (Belnap *et al*., 1993). Photosynthetic depression by SO_2 is due mainly to chlorophyll breakdown with chlorophyll damage most severe under moist conditions at low pH of 3.2 to 4.4 (Hawksworth & Rose, 1976).

The United Kingdom clean air act of 1956 and changes in energy policy compliant with directives set by European Economic Community (European Union) have dramatically reduced emissions of SO_2 by 80% since 1982. As a consequence, lichens are again colonizing young native oak trees in London (Larsen *et al*., 2007), a trend mirrored in other cities throughout the world (Eversman, 1978; Aarrestad & Aamlid, 1999). For example, the famous Jardin du Lexembourg in Paris, where in 1866 William Nylander made his first pioneering observation on the decline of lichens, today supports a wide range of lichen species. Seventy-two lichens were recorded recently from Kew Gardens in London where previously fewer than six were reported (Purvis, 2000). The slow rate of lichen colonization of trees in urban areas has been attributed partly to acidification persisting on the bark of older trees. For example, lichens sensitive of acidic conditions, such as *Pseudevernia furfuracea* and *Bryoria species,* have been confined to trees with alkaline barks, such as ash (*Fraxinus excelsior)*, which may neutralizing acidification caused by SO_2 pollution (Purvis, 2000). However, despite the reductions in SO_2 levels other atmospheric pollutants such as ammonia have appeared, this exemplified by the proliferation of the nitrophilous lichen *Xanthorion* in the Netherlands. Noteworthy, in this regard is the decline in the pollution lichen *Lecanora conizaeoides*, formerly ubiquitous in many industrial areas of Europe (Purvis, 2000).

Apart from SO_2, there is a large variety of elements and chemicals compounds present in the atmosphere that affect lichen growth and distribution. These include nitrous oxides and fluoride and other secondary pollutants formed through chemical reactions in the atmosphere such as ozone, peroxy-acetyl nitrate, sulphuric and nitric acids (Tiwari, 2008). Nitrous oxides produced by coal burning and by automobile emissions have been reported to reduce chlorophyll concentrations in the crustose lichen *Lecanora chrysoleuca*, the foliose lichens *Anaptychia neoleucomelaena* and *Paremelia praesignis* as well as the fruticose lichen (*Usnea cavernosa)* at concentrations of only 4 ppm NO_2 (Nash, 1976; Tiwari, 2008). Also, many lichens are adversely affected by high levels of fluoride emanating from aluminum smelters and brickworks which causes chlorosis, necrosis and thallus disintegration (Nash, 1971, 2008; Hawksworth & Rose, 1976). Differential lichen species sensitivity to fluoride often results in zonation patterns developing around fluoride sources. Generally, visible damage to lichens begins at fluoride concentrations of 50-70 ppm (Hale, 1983). Studies of the fluoride content of lichen thalli in zonation patterns around a fluoride source at Fort Williams in Scotland have shown the affected area restricted to an ellipse ranging from 1 km to 4 km from the source. This localized effect is apparent around other aluminum smelters in the United Kingdom such as at Holyhead, Invergordon and Kinlochleven (Hawksworth & Rose, 1976).

1.9. Lichen responses to global warming

Reductions in lichen cover and diversity in response to experimental warming have been reported in the Alaskan arctic tundra (Wahren *et al*., 2005), these changes qualitatively similar to those measured in standardized warming experiments at several other locations across the arctic tundra (Walker *et al*., 2006), with proportionally greater reductions in lichen cover and diversity observed in dry than moist sites (Wahren *et al*., 2005). Also, there is increasing evidence that lichens are responding to climate warming in Western Europe with observed changes in the distribution and ecology of epiphytic and terricolous lichens seemingly affected by global warming (Aptroot & van Herk, 2007). In Denmark and in the Netherlands, growth rates of *Flavoparmelia caperata*, a drought resistant, warm temperate lichen, have increased over the last 100 years. This appears to be linked to the increase of temperatures during the last 20 years (Søchting, 2004; van Herk & Aptroot, 1996, 2004). A recent study in the Netherlands has identified major changes in epiphytic lichen distributions since 1979. Warm-temperate species such as *Candelariella reflexa, Lecidella flavosorediata, Parmelia borreri* and *P. soredians* have increased in frequency, while species characteristic of colder environment have either decreased or disappeared (van Herk *et al*., 2002; Hauck, 2009). One striking example is *Flavoparmelia soredians*, a drought resistant, warm temperate lichen species presently common in the Netherlands (van Herk & Aptroot, 1996, 2004). This species was absent from the Netherlands prior to 1900, rare in the Netherlands prior to 1987, and until recently had its northernmost limit in Southern England (Seaward & Coppins, 2004). Also, several new epiphytic lichen species such as *Protoparmelia hypotremella* (Aptroot *et al*., 1997) and *Fellhanera viridisorediata* (Aptroot *et al*., 1998) have recently been documented in the Netherlands. In contrast, lichen species preferring colder environments, such as *Peltigera leucophlebia, Peltigera malacea* and *Stereocaulon tomentosum,* have declined in numbers, though not at the same rate as increases in those preferring warmer environments (Hauck, 2009). Lichen species responding positively to climate warming contain the alga *Trentepohlia* as photobionts suggesting these may be the most useful as indicators of global warming (Aptroot & van Herk, 2007).

Reports on the effects of on-going climatic warming on lichen and other non-vascular epiphyte distributions from the tropics are scant. However, two experimental studies show pronounced short-term effects. In a recent study in Bolivia, branches with dense bryophyte cover transplanted to warmer and drier climates at lower altitudes resulted in changes in the relative species abundance after a 2 year period (Jacome *et al*., 2010). In a similar study in Costa Rica, where epiphyte mats were transplanted, the fate of the abundant mosses and lichens were not quantified (Nadkarni & Solano, 2002), but after 1 year a clear deterioration of the entire epiphyte mat was apparent (Zotz & Bader, 2009). For poikilohydric plants like bryophytes and lichens, the effects of warming will interact strongly with effects of altered precipitation. Increased temperatures affect poikilohydric organisms through direct effects on metabolic rates and by increasing evaporation, thereby reducing activity time or increasing desiccation damage in sensitive species. Increasing temperatures could shift species distributions to cooler and moister habitats. However, in tropical lowland forests no better heat-adapted bryophytes and lichens are available to replace those species that may disappear. Similarly, in cloud forests no wetter habitats are available for species to escape to. This is a specific example of a much more general issue (Williams *et al*., 2007), namely the fate of ecosystems in novel climates and species in disappearing climates.

The reasons for the limited development of non-vascular epiphytes in tropical lowlands are not known with certainty, but a popular hypothesis involves a combination of high night temperatures causing strong carbon losses to respiration and high day temperatures causing dehydration, thereby restricting the time available for carbon gain by photosynthesis (Zotz, 1999). Thus, two crucial factors are night time temperature and day-time activity time. CO_2-exchange data from tropical lowland bryophytes are not available, while two foliose lowland lichen species have been studied in some detail (Zotz & Winter, 1994; Zotz *et al*., 2003). Diurnal field measurements on *Parmotrema endosulphureum* and *Leptogium azureum* showed consistently that almost the entire daily carbon gain was respired at night. A simple model developed from the temperature response of CO_2 exchange in *Parmotrema endosulphureum* indicated how future temperature change could shift this lichen's carbon balance. Assuming typical current lowland conditions, maximum net photosynthesis rates under otherwise optimal conditions are only twice as high as respiration rates. The ratio of daily carbon gain to respiration is much lower, because the former is often strongly reduced due to desiccation, while these epiphytes are usually moist and active during the entire night. Currently, *Parmotrema endosulphureum* must take up CO_2 at maximum rates for at least 40% of the light period just to balance 12-h nocturnal respiration. A predicted temperature increase of 3°C without acclimatisation would make it necessary to photosynthesize at maximum rates for more than 90% of the day to achieve a positive carbon balance. This is not feasible, since in somewhat cooler montane habitats lichens show net photosynthesis for only 30–80% of the light period, and at mostly suboptimal rates (Lange *et al*., 2004). However, assuming a shift in the temperature response of 2°C due to acclimatization, a 3°C increase would effectively represent a 1°C increase, thus requiring photosynthetic activity during “only” 50% of the day for a balanced budget. The potential for acclimatization of tropical lichens is obviously a crucial question, but completely unexplored. The conclusions are dim, since lowland lichens are arguably already living close to the edge of their physiological abilities. Thus, even a slight increase in temperature could make tropical lowlands completely uninhabitable to them.

The negative effects of warming on the carbon balance of lichens may be at least partly counteracted by increases in atmospheric CO_2 levels. In poikilohydric plants, the inability to regulate water loss limits the possible responses to CO_2 as compared to those of vascular plants, although the trade-offs related to, for instance, nitrogen allocation occur here just as much. In terrestrial bryophytes, the stimulating effect of higher CO_2 levels may be limited, because their close proximity to the respiring soil already exposes them to increased CO_2 levels (DeLucia *et al*., 2003). This could also be the case for those epiphytic lichens that grow closely attached to canopy soil or directly on living branches. For such species, increased respiration of the substrate due to higher temperatures may provide more extra CO_2 than the increased atmospheric levels (Sveinbjörnsson & Oechel, 1992; Tuba *et al*., 1999). However, generally, such epiphytes are much better coupled to the atmosphere than terrestrial species, so that global atmospheric CO_2 levels can certainly be of influence. An additional advantage of higher CO_2 levels under a warming scenario is that the temperature optimum for net photosynthesis is shifted to higher temperatures (Sveinbjörnsson & Oechel, 1992). Light compensation points are also lowered, so that species can grow at darker microsites, where they dry out more slowly and stay active for longer. Activity time is also prolonged because net photosynthesis can take place down to lower and up to higher water contents (Tuba *et al*., 1999). This can be particularly beneficial for tropical lowland species, for which it has been hypothesized, that carbon gain may become negative at higher temperatures due to lower net photosynthesis and through shorter activity times. As in vascular plants, acclimatization to high CO_2 levels can cause a return to the low-CO_2 photosynthesis rates. However, species differ in their acclimatization potential. For instance, the moss *Polytrichum formosum* clearly down-regulated its chlorophyll and RuBisCO contents after several months at 700 ppm CO_2, while the moss *Tortula ruralis* and the lichen *Cladonia convulata* maintained their positive response (Tuba *et al*., 1999). However, increased photosynthesis is also not necessarily invested in growth but in defensive phenolic compounds (Tuba *et al*., 1999).

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Chapter 2

Lichen species selection and identification, experimental site description, study objective and key questions

2.1. Selection of lichens for study

A Global Information System for the Biodiversity of Lichens and Lichenicolous Fungi lists 1730 lichen species for South Africa (http://www.biologie.uni-hamburg.de/checklists/lichens/africa/south-africa_l.htm) which comprises 9.2% of the total global list of 18 882 lichen species (Feuerer & Hawksworth, 2007; Feuerer, 2009) but exceeds the numbers of lichen species listed for surrounding countries of Angola (98), Namibia (158), Zimbabwe (262), Mozambique (171), Lesotho (55) and Swaziland (11). The Pretoria Centralized Information System data base (PRECIS) registers 1 460 quarter degree square distribution records for 412 lichen species comprising 105 genera in South Africa. Records of the 30 most collected South African lichen genera and species extracted from PRECIS are presented in Figures 2.1A & B. These show that 80% of the 105 listed genera comprise less than 20 records and 85% of the 412 listed species comprise less than 5 records. Geographical distribution records for all PRECIS registered lichen species as well as the two most common lichen genera and the most common lichen species are presented in Figures 2.2 A, B, C & D. The recorded distributions indicate a collecting bias around the major metropolitan centers of Cape Town, Pietermaritzburg, Nelspruit, Polokwane and Johannesburg which prevented the selection of lichen species for this study purely on the basis of their geographical distributions.

A stepwise regression revealed a significant ($P \leq 0.01$) correspondence between PRECIS registered lichen species records per quarter degree square and mean annual precipitation (MAP) with mean daily maximum and minimum temperature and relative humidity not corresponding significantly with total lichen species records (Table 2.1). In view of this, lichen species for this study were selected from habitats of different aridity. In total, nine lichen study species were selected, four species from a hot arid site, two species from a warm coastal site and three species from two cool montane sites.

Table 2.1. Stepwise regression of PRECIS registered lichen species records per quarter degree square against mean annual precipitation, minimum and maximum daily temperatures and humidity.

```
** Forward Selection **

Valid Number of Cases: 294, 3 Omitted
Dependent Variable: Total Lichen spp
Tolerance: 0.001
F-to-Enter: 3.8416 (5.0%)
F-to-Remove: 2.7056 (10.0%)

** Step 1: Variable Entered: MAP **

                      Multiple                      Adjusted         Change
 Standard Error    Correlation      R-squared      R-squared   in R-squared
---------------------------------------------------------------------------
         6.0540         0.1524         0.0232         0.0199         0.0232

             Due To| Sum of Squares   DoF    Mean Square      F-Stat      Signif
-------------------+------------------------------------------------------------
         Regression|        254.575     1        254.575       6.946      0.0088
              Error|      10702.065   292         36.651

          Variables|                Standard
        in Equation| Coefficient       Error t-Statistic Signif      F-to-Remove
-------------------+------------------------------------------------------------
           Constant|      2.9242
                MAP|      0.0033      0.0013      2.6355      0.0088      6.9459

          Variables|
    not in Equation|   Partial Corr      Tolerance     F-to-Enter
-------------------+---------------------------------------------
           HUMIDITY|         0.0653         0.7412         1.2447
           MIN_TEMP|         0.0060         0.9772         0.0104
           MAX_TEMP|        -0.0409         0.9478         0.4879

** Summary Table **

      |                            Multiple
  Step|  In/Out       Variable         Corr    R-squared      F-Stat      Signif
------+-------------------------------------------------------------------------
     1|      In            MAP       0.1524       0.0232      6.9459      0.0088
```

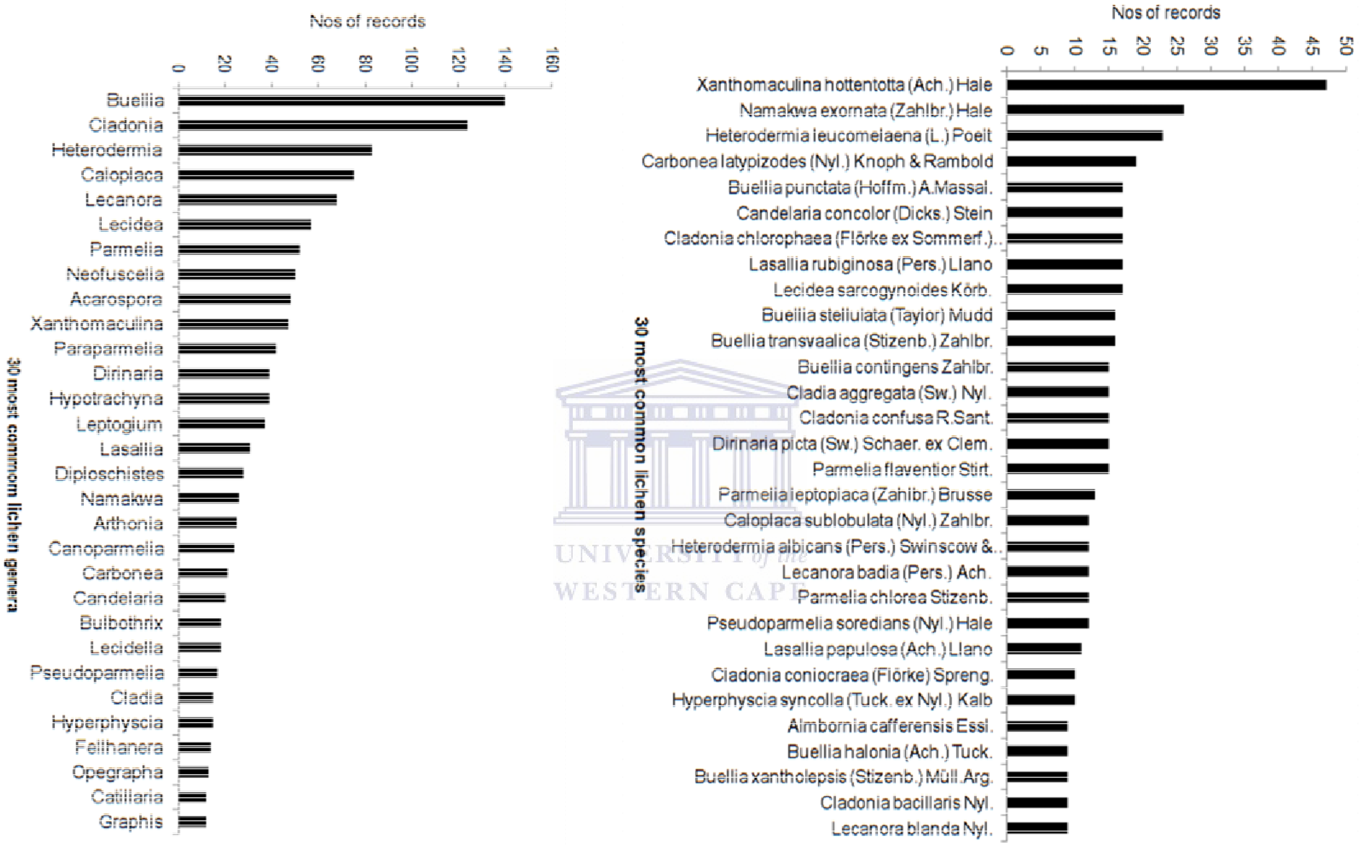

Figure 2.1. A & B. Records of 30 most common South African lichen genera and species derived from PRECIS data base.

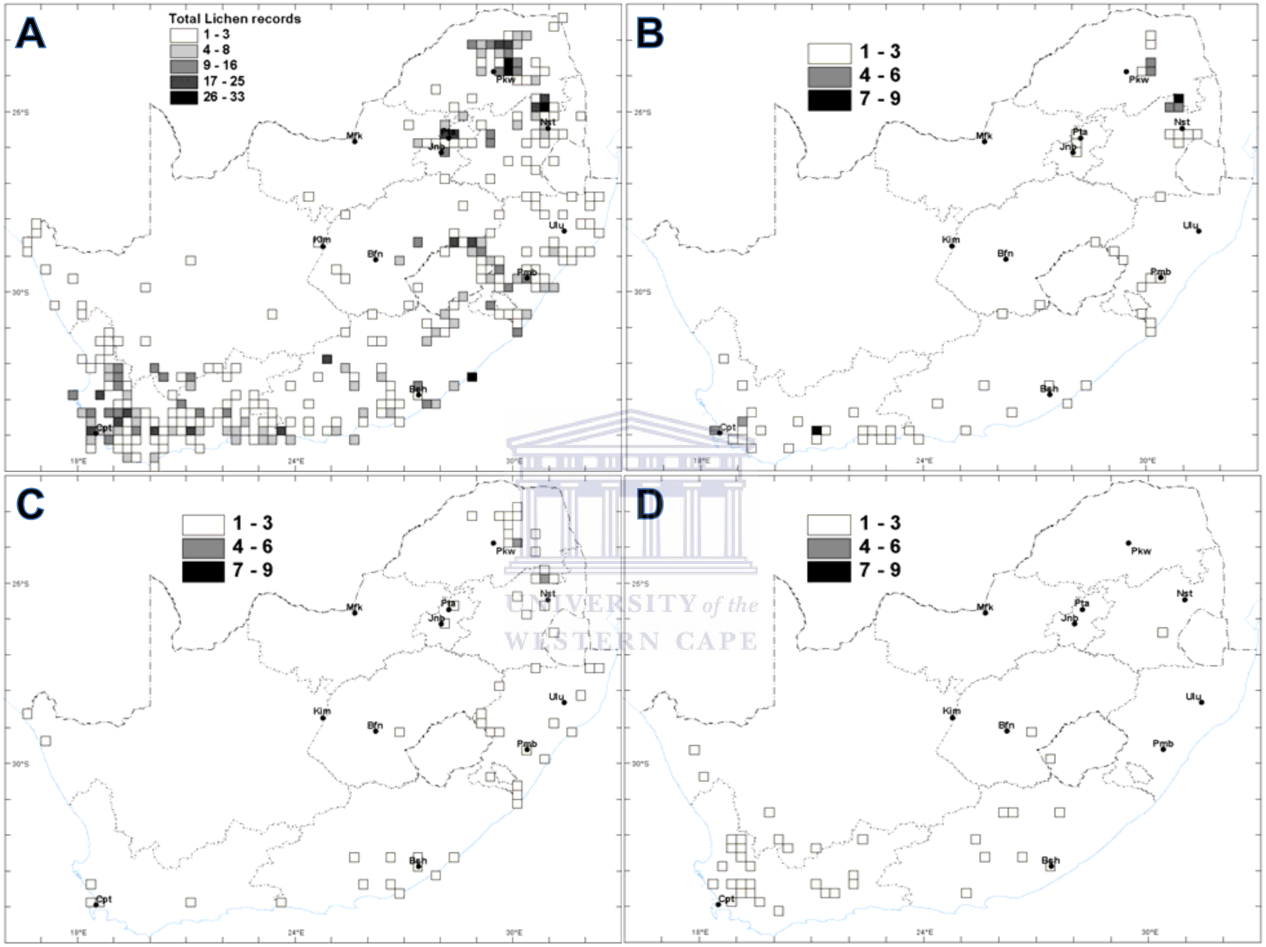

Figure 2.2 A. Distribution records for A. all lichen species, the two most common lichen genera B. *Buellia* and C. *Cladonia* and the most common lichen species D. *Xanthomaculina hottentotta* (Ach.) Hale.

2.2. Identification of selected lichens

Provisional identification of the selected study lichens was achieved by their comparison with herbarium specimens. Precise identification was performed at the universities of Bonn and Bayreuth in Germany under the guidance of Dr Luciana Zedda and Professor G. Rambold. Thin vertical slices of lichen thalli cut with a razor blade were placed in a drop of water on a microscope slide and their fruiting bodies microscopically examined (Figure 2.3A) as described by Nash *et al*. (2002). Spot tests for colour reaction of thalli were also perfomed during microscopic examination using pure bleach, 10% potassium hydroxide, paraphenylenediamine and 50% nitric acid. The lichen compounds relating to the colour reactions were identified with the database MACTABOLITES and species were identified by using the LIAS Light online identification keys computer program (http://www.lias.net) and identification keys published in Hale (1990) for *Xanthoparmelia* and *Paraparmelia*.

Thin layer chromatography was carried out on all the collected lichens which comprised the genera *Teloschistes, Xanthoparmelia, Flavopuntelia, Parmotrema, Xanthomaculina* and *Lasallia* following White & James (1985). Thin vertical slices of dry lichen material were cut with a razor blade and placed in numbered plastic phials into which cold acetone was added to extract lichen substances. Glass capillary tubes were used to transfer the acetone extracts from each phial to corresponding numbered points on the TLC plates. Three applications per spot were used. The prepared plates from each application were placed into three developing chambers each containing a different solvent (Figure 2.3B). The solvents used were toluene-dioxan-acetic acid, hexane-diethylether-formic acid and toluene-acetic acid. The plates were removed from the developing chambers when the solvent reached the terminating front line and dried with hair-drier (Figure 2.3C). Acetone extracts from voucher specimens of *Pleurosticta acetabulum, Parmelia sulcata, Physcia adscendens, Platismatia glauca* and *Evernia prunastri* were used as references for atranorin, norstictic acid and other lichen substances. The coloured spots on the dried plates were examined under natural light and also under UV-B (254 μm) and UV-A (350 μm) light. All spots illuminated under UV-B light were marked by circling the darkened area with an unbroken outline and those illuminated under UV-A light by circling the darkened area with a dotted outline. A 10% solution of sulphuric acid was brushed over the spots on one of the three plates (Figure 2.3D) which was subsequently transferred to a pre-heated oven at 110ºC for few minutes for colour development. The lichen compounds relating to the coloured spots were identified with the aid of the LIAS Light computer program.

After identification, the specimens were sealed in paper envelops and labels prepared giving the taxon name, the collection site, the collectors name, the date of collection and the name of the identifying person. Vouchers speciments were lodged in the Compton Herbarium of the South African National Biodiversity Institute.

The selected study lichens from the hot arid site in the Succulent Karoo Biome were identified as *Xanthoparmelia austro-africana* (Stirt.) Hale., *Xanthoparmelia hyporhytida* (Hale) Hale., *Xanthomaculina hottentotta* (Ach.) Hale. *and Xanthoparmelia* sp. (undescribed species). The last could not be matched with any previously described species based on colour and TLC assays. The selected study lichens from the warm coastal site in the Succulent Karoo Biome were identified as *Teloschistes capensis* (L.f.) Müll. and *Ramalina* sp. (undescribed species). The last also could not be matched with any previously described species based on colour and TLC. The selected study lichens from cool moist montane sites in the Fynbos Biome were identified as *Lasallia papulosa* (Ach.) Llano., *Parmotrema austrosinesis* (Zahlbr.) Hale. and *Flavopuntelia caperata* (L.)Hale.

Figure 2.3 A. Lichen microscopic identification, B. Developing chambers containing thin layer chromatography plates, C. Drying of plates after running in solvents; and D. Brushing of plates with a 10% solution of sulphuric acid for spot colour development.

2.3. Study sites

The farm Quaggaskop (31° 24.6' S, 18° 37.8' E) was selected as an example of a hot arid site. The site occurs in the Knersvlakte, an acknowledged centre of diversity and endemism (Hilton-Taylor 1994, 1996), in the Succulent Karoo Biome (Rutherford & Westfall, 1986), ranked among 34 global biodiversity hot spots (Myers *et al*., 2000; Mittermeier *et al*., 2000). It is situated 20 km north of the town of Vanrhynsdorp at an elevation of ±160 m and has a mean annual precipitation of 145 mm occurring mainly in winter, and mean daily maximum air temperature of 25.7°C, determined from the nearby Vredendal weather station (Climate of South Africa, 1986). The site comprises quartz-gravel fields which house a globally unique flora where specialized dwarf succulents dominate (Schmiedel & Jürgens, 1999; Schmiedel, 2001, 2002) as well as an extraordinary and peculiar diversity of lichen taxa which is even greater than that of lichen fields of the Namib Desert. Thirty-five terricolous lichen taxa have been recorded at this site, 52% of which are endemic to Namaqualand. Squamulose and crustose lichens are the most common and mostly contain green algal photobionts (Zedda & Rambold, 2009). Inter-dispersed among the quartz-gravel fields are areas devoid of quartz covered with shale, phyllite and limestone derived substrates of the Nama Group (Schmiedel & Jürgens, 1999) where larger succulent shrubs dominate (Figure 2.4).

A large lichen field situated a few kilometers South East of the mining city of Alexander Bay 3.2 km distant from the Atlantic coast (28° 37'S, 16 ° 30'E) and 4.5 km south of the Orange River delta was selected as the warm moist coastal site (Figure 2.5). The lichens at this site cover an area of approximately 75 ha forming 10 cm high dense carpets of fruticose individuals which are most prominent on west, southwest and south exposed slopes (Jürgens & Niebel-Lohmann, 1995). Thirty-one lichens species have been recorded at this site. Two lichen species are clearly visible as a well-developed, striking upslope zonation. The upper parts of the slopes, characterized by gypsum-rich topsoil, are dominated by the orange coloured lichen *Teloschistes capensis.* Further downslope, with gypsum only at deeper positions in the soil, the light green *Ramalina* sp*.* is more common. This lichen also grows abundantly as epiphyte on the very few angiosperms, such as *Asparagus capensis* (Muciana & Rutherford, 2006). The site has a mean annual temperature of 17.2° C and an erratic low rainfall of about 45 mm per annum, occurring predominately in winter. The low rainfall is supplemented by a high frequency of fog, estimated to be greater than 100 days per year. Fog carried inland by strong winds during the day makes close contact with the lichens more intensively in the range of the vegetation belts characterized by *Ramalina* sp. and *Teloschistes capensis* (Jürgens & Niebel-Lohmann, 1995).

Jonaskop and Bainskloof were selected as cool moist montane sites. Both occur in the Fynbos Biome also ranked among 34 global biodiversity hot spots (Myers *et al*., 2000; Mittermeier *et al*., 2000). Jonaskop (33°58'00 S 19°30'00 E) is located within the Riviersonderend Mountain Catchment. It is situated 23 Km SE of Worcester at elevations of between 600m and 1300m (Figure 2.6). It has a mean annual precipitation of 315 to 720 mm occurring mainly in winter and mean daily maximum and minimum air temperatures of 16.5°C and 12.1°C respectively (Muciana & Rutherford, 2006). Sixteen lichen species are listed in PRECIS in the vicinity of this site, the most common including *Lasallia papulosa* (Ach.) Llano and *Hypogymnia subphysodes* (Kremp.) Filson. Bainskloof (33° 36' 8.6 S, 19° 6' 42.2 E) is located in the Du Toitskloof and Stettyns mountains at an altitude ranging from 250-1800m. It has a mean annual rainfall of 1200 mm occurring mainly in winter (Figure 2.6) and mean daily maximum and minimum temperatures of 16.5°C and 12.5°C respectively. Twenty-nine lichen species are listed in PRECIS in the vicinity of this site the most common including *Cladonia portentosa* (Dufour) Coem. *Neofuscelia crustulosa* (Essl.) Essl. and *Cladonia portentosa* (Dufour) Coem.

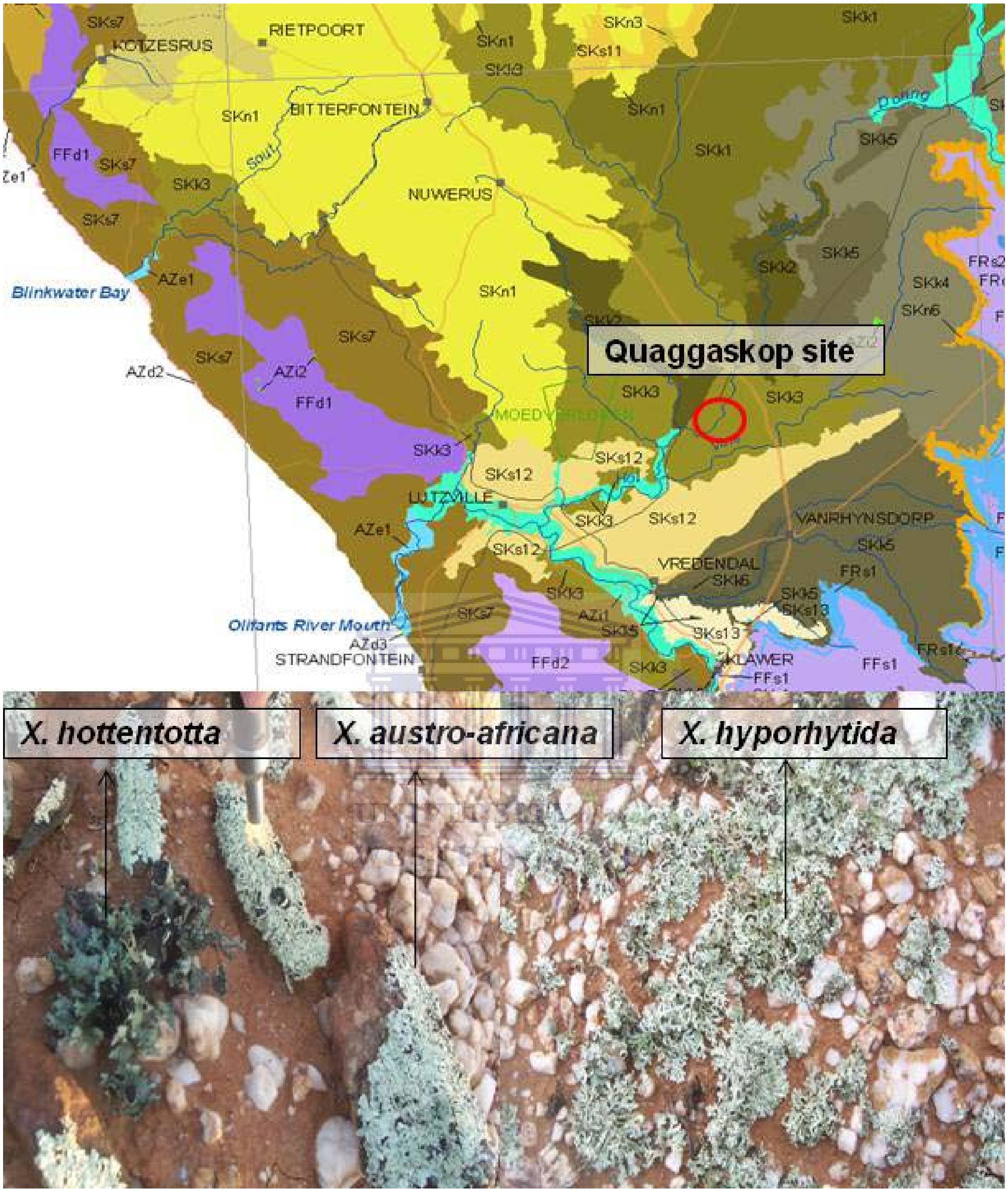

Figure 2.4. Location of the Quaggaskop experimental site and some common lichen species occurring on quartz gravel sites at the site.

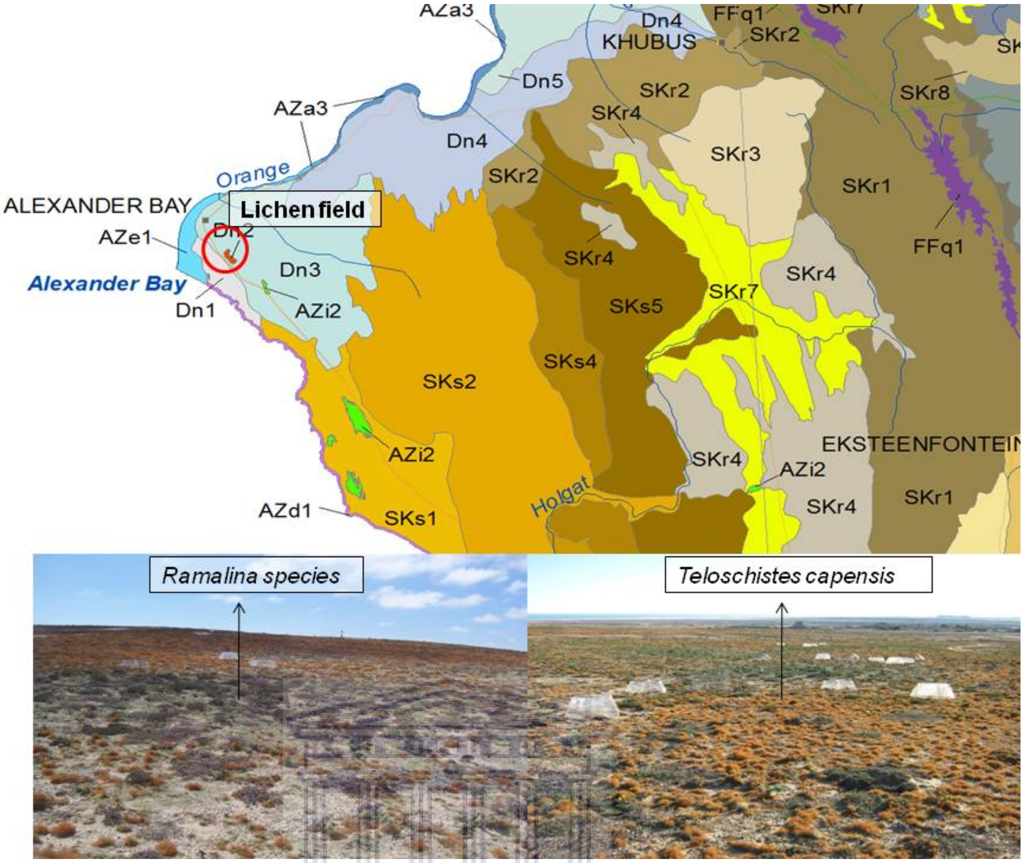

Figure 2.5. Location and typical topography of the lichen field at the Alexander Bay experimental site.

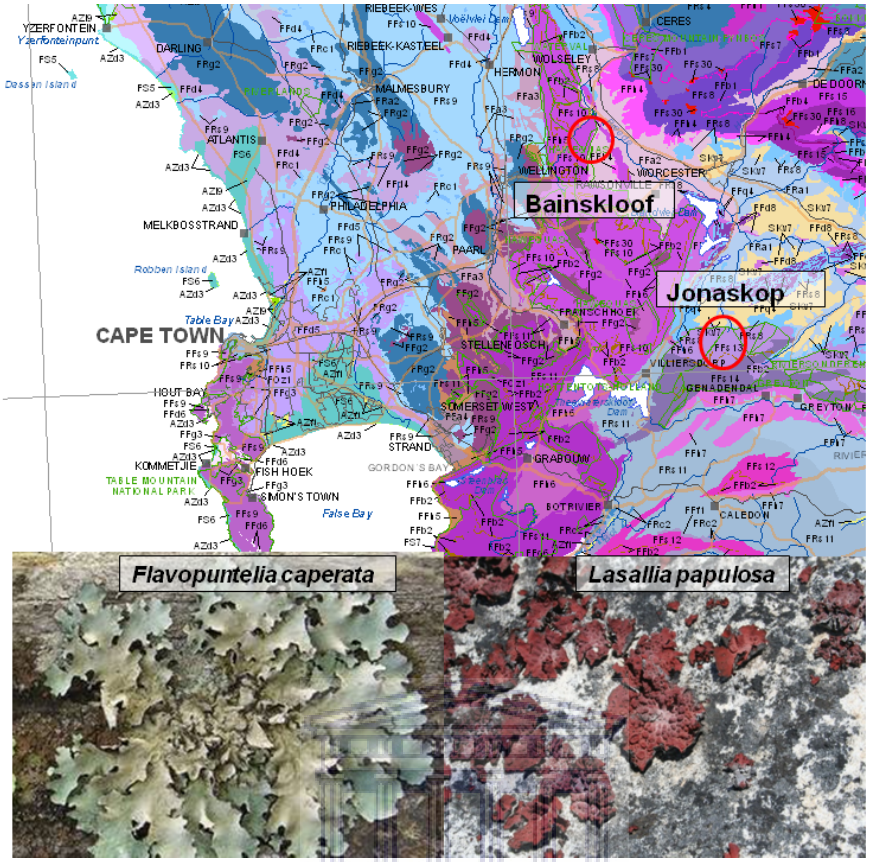

Figure 2.6. Location of the Bainskloof and Jonaskop sites and some common lichen species occurring on bark and granites.

2.4. Study objectives and hypotheses

The study's main objectives were to examine the thermal sensitivity of lichens from habitats of different aridity under laboratory and natural conditions and their interception of moisture and elements from different precipitation sources. The following key questions were addressed:

1. Is lichen photosynthesis a more sensitive indicator of heat stress than respiration?
2. Are lichens from the cooler and wetter sites more sensitive to heat stress than those from hotter and drier sites?
3. Are lichen thermal sensitivities determined under laboratory and natural conditions comparable?
4. Will future temperature increases, predicted by climate change scenarios, inhibit the lichen photosynthesis and growth of the selected species?
5. Will the selected lichens from drier sites be more severely affected by future temperature increases predicted by climate change scenarios than those from wetter sites?

6. Is fog and dew more important sources of moisture and nutrients for lichens than rainfall?

2.5. Thesis structure

The thesis comprises six chapters. The first chapter includes a comprehensive review of lichen biology based on 112 sources of reference. The second chapter presents the lichen species selected for study, the methods employed in their identification, as well as a description of the experimental site, the study objective and key questions. The third chapter describes the results obtained from measurements of the thermal sensitivities of nine different lichens species from three sites of different aridity and mean annual temperature under both laboratory and field conditions. The fourth chapter assesses the effects of experimental climate warming on lichen photosynthesis and growth under field conditions. The fifth chapter investigates moisture interception and elemental accumulation by two dominant lichen species in a South African coastal subtropical desert. The sixth chapter presents study conclusions and recommendations. Chapter three, four and five are presented as scientific manuscripts, the literature references and citations presented in accordance with provisions of the Journal of Environmental and Experimental Botany.

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Chapter 3

A comparison of the thermal sensitivities of lichens from different environments under laboratory and natural conditions

Abstract

Thermal sensitivities of nine different lichens species from three sites of different aridity and mean annual temperature were measured under laboratory and field conditions. In the laboratory studies, the 9 lichen species collected from the 3 sites were allowed to acclimatize in a growth chamber for 8 days after which they were hydrated and exposed in forced draft ovens for 2 hour intervals to 7 different temperatures ranging from 24ºC to 48ºC. Following heat exposure, the lichens were rehydrated and their respiration rates and maximum quantum yields of PSII determined. In the field studies, effective quantum yields of PSII of hydrated thalli of 6 lichen species were measured monthly at hourly intervals throughout the day at 2 sites and these matched with simultaneously recorded ground surface air temperatures. A residual maximum likelihood variance components analysis tested at which exposure temperatures lichen respiration and maximum quantum yield of PSII declined significantly from ambient, these designated effective temperatures. Exposure temperatures at which lichen respiration and maximum quantum yield of PSII ceased were designated lethal temperatures. These were derived from regression functions that quantified relationships between measured lichen respiration rate, maximum quantum yield of PSII and exposure temperature. Laboratory determined effective and lethal temperatures limiting for lichen respiration were higher than those limiting for lichen maximum quantum yield of PSII which displayed a general declining trend for lichens occurring along an environmental gradient of decreasing temperature and increasing precipitation, this extending from the hot arid site to the warm coastal site to the cool montane site. Field determined quantum yields of PSII in hydrated lichens displayed an early morning peak which subsequently declined with increasing temperatures towards midday with a second phase of elevated quantum yield of PSII also apparent in the cooler late afternoon. Field derived lethal temperatures for lichen quantum yield of PSII were similar to those determined under laboratory conditions but field derived effective temperatures for lichen quantum yield of PSII were up to 20^{o}C lower than those determined under laboratory conditions. The exceptionally low effective temperatures limiting lichen quantum yield of PSII under natural conditions suggest that even small increases in temperature, especially during early morning periods of peak photosynthetic activity, could negatively affect the carbon balance of lichens already living close to the edge of their physiological abilities.

Key words: Lichens, photosynthetic quantum yield, respiration, effective temperature, lethal temperature.

3.1. Introduction

Lichens possess certain anatomical and physiological characteristics which render them highly sensitive to environmental changes. These include 1. the absence of stomata and a protective cuticle, this causing little control over diffusion of atmospheric pollutants concentrated in fog and dew, a major source of water for lichens, into the sensitive photobiont layer (Rope & Pearson, 1990; Nash, 2008), 2. elevated metabolic rates under hydrated conditions which persist even at low temperatures, 3. high susceptibility to persistent damage due to a slow growth rate which restrains injury repair, and 4. long lived perennial bodies which concentrate elements absorbed from the environment (Nimis *et al*., 1990; Purvis, 2000; Conti & Cecchetti, 2001; Zedda & Rambold, 2006; Tiwari, 2008).

Physiological measurements used to determine changes in lichen metabolic activity and vitality in response to stress include changes in photosynthetic and respiration rate (Sigal & Nash, 1983; Bartók *et al*., 1992; Egger *et al*., 1994; Garty *et al*., 2000; Conti & Cecchetti, 2001) with photosynthesis more sensitive to stress than respiration (Hale, 1983), rate of nitrogen fixation by blue green algal photobionts (Hawksworth & Rose, 1976; Sigal & Nash, 1983), ATP levels (Kardish *et al*., 1987; Garty *et al*., 1988), concentration of stress ethylene (Epstein *et al*., 1986; Garty *et al*., 2000), leakage of electrolytes (Silberstein *et al*., 1996; Shiraz *et al*., 1996), glutathionine and amino acid content (Silberstein *et al*., 1996), reduction of 2,3,5-triphenyltetrazolium chloride to triphenyl formazan (Bačkor & Fahselt, 2005), chlorophyll concentration and degree of phaeophytinization (Ronen & Galun, 1984; Garty *et al*., 1992; Chettri *et al*., 1998) and chlorophyll a fluorescence (Garty *et al*., 2000). The latter has proved a particularly useful tool for vitality screening of lichen photosynthetic responses to extreme temperatures, light, water availability, air pollution, heavy metal contamination and ultraviolet-B radiation (Paul & Hauck, 2006; Baruffo & Tretiach, 2007; Scheidegger & Schroeter, 1995; Calatayud *et al*., 1996; Branquinho *et al*., 1997; Hájek *et al*., 2001; Garty *et al.*, 2007) both in the laboratory and in the field (Jensen, 2002; Jensen & Kricke, 2002).

Several studies have examined the responses of lichens from different environments to heat stress in dehydrated and hydrated states (Rogers, 1971; Kappen, 1973; Macfarlane & Kershaw, 1980 Larson, 1982; Larson, 1989). These have shown that lichens are more susceptible to heat stress in hydrated than dehydrated states (Larson, 1982) with those lichens from cooler sites more sensitive to heat stress than those from warmer sites (Larson, 1989). However, the exposure temperatures applied in these studies (Rogers, 1971; Larson, 1982; Larson, 1989) were considerably higher than those found under natural conditions. Since laboratory determined heat tolerance does not always reflect the injurious temperatures in the natural habitat (Kappen, 1973), this study compared the thermal sensitivities of lichens from different environments under both laboratory and natural conditions.

3.2. Methods and materials

3.2.1. Study sites and species

Lichen species for study were collected from 4 different sites. The first, a hot arid site was the farm Quaggaskop (31° 24.6’ S, 18° 37.8’ E) at an elevation ±160 m situated in the Knersvlakte, a semi-arid winter rainfall region within the South African Succulent Karoo Biome (Rutherford & Westfall, 1986) listed among 34 global biodiversity hot spots (Myers *et al.,* 2000; Mittermeier *et al.,* 2004), with a mean annual precipitation and daily maximum air temperature recorded at the nearby Vredendal weather station between 1957 and 1984 of 145 mm and 25.7°C respectively (Climate of South Africa, 1986). Lichen species examined from this site comprised the foliose *Xanthoparmelia austro-africana, X. hyporhytida, Xanthoparmelia* sp. and *Xanthomaculina hottentotta.*

The second, a warm coastal, site comprised a large lichen field (28° 37’S, 16 ° 32’E) situated a few kilometers South East of the mining city of Alexander Bay 3.2 km distant from the Atlantic coast. The site has a mean annual temperature of 17.2° C and an erratic low rainfall of 39 mm per annum (1951 – 1984 average) occurring predominately in winter, this supplemented by high frequencies of fog averaging 61 days per year and most common in May late autumn (Climate of South Africa, 1986). Of the 31 lichens species recorded at this site, two dominant fruticose lichen species were selected for study, namely *Teloschistes capensis* common on slope apices, characterized by gypsum-rich topsoil, and *Ramalina* sp. more common at the bases of slope with deeper gypsum rich soils.

The third cool, moist montane sites were Jonaskop (33° 58’ 00’’S, 19° 30’ 00’’E) and Bainskloof (33° 36’ 8.6’’S, 19° 6’ 42’’E). Jonaskop is located within the Riviersonderend Mountain Catchment situated 23 km SE of Worcester ranging at elevations of between 600m and 1300m with mean daily maximum and minimum air temperatures of 16.5°C and 12.1°C respectively and a mean annual precipitation of 315 to 720 mm occurring mainly in winter and (Muciana & Rutherford, 2006). Bainskloof is located in the Du Toitskloof and Stettyns mountains ranging in altitude from 250 -1800m with mean daily maximum and minimum temperatures of 16.5°C and 12.1°C respectively and a mean annual rainfall of 1200 mm also occurring mainly in winter. Lichen species examined from these two sites comprised *Flavopuntelia caperata, Lasallia papulosa* and *Parmotrema austrosinensis.*

3.2.2. Laboratory studies

Thirty-five thalli of each of 9 different lichen species were collected on their original substrates from the 3 different sites. The 315 lichen thalli were transferred to a growth room and allowed to acclimatize for 8 days at 18°Cday/10°C night at a 16h daily photon flux density of ca 200 µmol m^{-2} s^{-1}. During the acclimation period, the lichens were hydrated every second day by applying a fine distilled water mist spray to their thalli. Hydrated lichen thalli were exposed in forced draft ovens for 2 hour intervals to temperatures ranging from 24ºC to 48ºC at 4ºC intervals, the highest oven exposure temperature slightly above the average temperature extreme of 44.4°C recorded at the Vredendal weather station in close proximity to the Quaggaskop site between 1957 and 1984 (Climate of South Africa, 1986). The 2-hour oven exposure periods adopted corresponded with diurnal temperature maxima confined to one hour periods on either side of the solar noon. There were 5 replicated lichen thalli per species for each of the seven heat treatments. Following heat exposure, the lichens were returned to the growth room for an additional 24 hour period.

The following day the heat-treated lichens were hydrated with a fine distilled water mist spray and dark adapted for a one hour period. Subsequently, measurements of initial (F_o) and maximal (F_m) fluorescence emissions from the hydrated, heat treated lichen thalli were taken with a Plant Efficiency Analyser (PEA, Hansatech Instruments Ltd., King's Lynn, Norfolk, UK) following a 1 s saturating photosynthetic photon flux density (PPFD) of 3500 µmol m^{-2} s^{-1}. Three fluorescence measurements were performed on five thalli of each lichen species from each oven exposure temperature (15 measurements per lichen species per oven exposure temperature). Ratios of variable to maximal fluorescence (Fm-Fo/Fm), an indicator of the maximum quantum yield of Photosystem II (PSII) were computed.

Following the chlorophyll fluorescence measurements, the hydrated, heat treated lichen thalli of each species were placed in polyvinyl chloride (PVC) collars with an internal diameter of 10 cm and a length of 5cm installed on a wooden board. Measurements of lichen mycobiont and photobiont dark respiration rate (R_D) as µmol CO_2 efflux m^{-2} s^{-1} were performed on 3 randomly selected lichen thalli of each species from each oven exposure temperature (3 measurements per lichen species per oven exposure temperature) with a Li-Cor 8100 infrared gas analyzer (Li-Cor BioSciences, Lincoln, Nebraska, USA). After the respiration measurements, the lichen thalli were removed from their substrates, dried in a forced draft oven at 60°C, and weighed on a fine electronic balance. Measured respiration rates were expressed as µmol CO_2 efflux m^{-2} s^{-1} per gram of dry lichen thallus.

3.2.3. Field studies

Demarcated plots 120 cm in diameter constructed from 40 cm high steel fencing with a 5 cm diameter mesh were installed at random over populations of the four lichen species at the hot arid site and populations of the two lichen species at the warm coastal site (6 replicated plots per lichen species per site). Lichen thalli were hydrated with a fine distilled water mist spray and their effective quantum yields of PSII at a steady state (Ys = Fms-Fs/Fms = ΔF/Fm') measured with a portable modulated fluorometer (OSI-F1, Opti-Sciences Inc., Hudson, USA) following exposure to 0.8s saturating light pulses of 15 000 µE. Five replicated fluorescence measurements were taken hourly from 08h00 to 17h00 on four randomly selected thalli of each lichen species at each site. Fluorescence measurements were repeated monthly over a 12 moth monitoring period and these matched with simultaneously recorded ground surface air temperatures using radiation shielded thermocouples interfaced with miniature Watchdog Model 450 data loggers (Spectrum Technologies Inc., Plainfield, Illinois, USA)

3.2.4. Statistical analyses

Fluorescence measurements were normally distributed but respiration measurements were not and consequently were $\log_e$ transformed before statistical analysis to reduce the inequality of variance in the raw data (Figure 3.1A and B).

Both the laboratory and field trials were not fully balanced due to missing measurements. Consequently, a REML (residual maximum likelihood) variance components analysis was used to test for differences in measured lichen respiration rates and quantum yields of PSII between laboratory exposure temperatures, species and their interactions (linear mixed model) and also for differences between field exposure temperatures, corresponding with different times of the day, species and their interactions (repeated measures mixed model) using the Wald X^2 statistics generated by REML (GENSTAT Discovery Edition 3, VSL Lty, UK). In the laboratory trials, oven exposure temperature and species were fitted in the fixed model and treatment and species replications in the random model. In the field trials, lichen species and time of the day were fitted in the fixed model and monthly replications grouped into seasons in the random model. Differences exceeding twice the average standard error of differences were used to separate significantly different treatment means at $P \leq 0.05$. This based on the fact that for a normal distribution from REML estimates, the 5% two-sided critical value is two.

In the laboratory trials, the oven exposure temperatures at which respiration rate and PSII efficiency declined significantly ($P \leq 0.05$) from ambient (24°C) were designated as effective temperatures. In the field trials, the recorded temperatures corresponding with the time of the day at which PSII efficiency declined significantly ($P \leq 0.05$) from an early morning optimum were designated effective temperatures and these averaged over the 12 month recording period for each species.

In both the laboratory and field studies, least squares regressions quantified the relationships between oven and field exposure temperatures and measured respiration rates and quantum yields of PSII. A Students t-test tested the slopes and the intercepts of the linear regressions for significance at $P \leq 0.05$. The regression equations were used to compute the temperatures at which respiration rate and PSII efficiencies attained zero, which were designated as lethal temperatures.

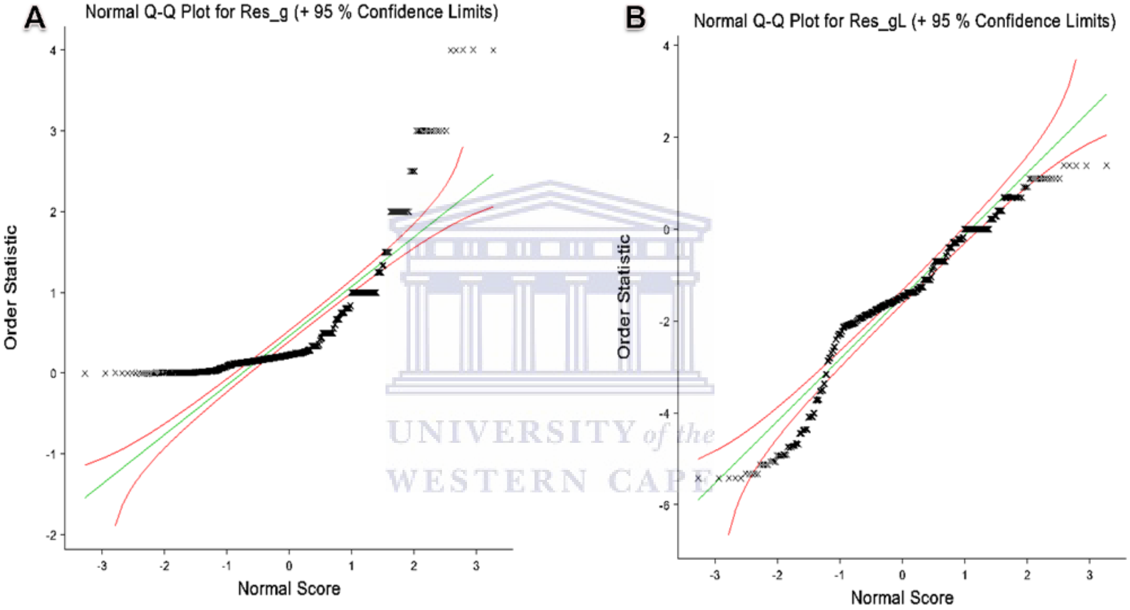

Figure 3.1. Normal plots for A. non-transformed and B. $\log_e$ transformed lichen respiration rates.

3.3. Results

3.3.1. Laboratory studies

Respiration rates and maximum quantum yields of PSII differed significantly ($P \leq 0.001$) between lichen species (Table 3.1) and decreased significantly ($P \leq 0.05$) with increased oven exposure temperature (Figure 3.2A & B). However effective temperatures (range: 40°C – 48°C) limiting for lichen respiration were higher than effective temperatures (range: 32°C - 44°C) limiting for lichen maximum quantum yield of PSII (Table 3.2). Also, there were significant ($P \leq 0.001$) species versus oven exposure temperature interactions (Table 3.1) with effective temperatures for respiration rates and maximum quantum yields of PSII differing significantly ($P \leq 0.05$) between species. The effective temperatures of 32°C to 36°C limiting for maximum quantum yield of PSII in *L. papulosa, P. austrosinesis* and *F. caperata* from cool, montane environments, for example, were significantly ($P \leq 0.05$) lower than those of 40°C to 44°C limiting for maximum quantum yield of PSII in *X. austro-africana, X. hyporhytida, X. hottentotta and Xanthoparmelia* sp. from hot arid environments.

Least squares regressions quantifying the relationships between oven exposure temperatures, respiration rates and maximum quantum yields of PSII are presented for *X. hyporhytida* in Figure 3.3A & B and for all other lichen species from the hot arid, warm coastal and cool montane sites in Appendix 3.1A to F, Appendix 3.2A to D and Appendix 3.3 A to F respectively. All 9 species had significant ($P \leq 0.001$) slopes and intercepts for respiration rate and maximum quantum yield of PSII (Table 3.3), except in *P. austrosinesis* where the slope of the regression between respiration rate and oven exposure temperature was not significant ($P \geq 0.05$) and consequently also the lethal temperature for respiration derived from the regression function for this species. Lethal temperatures for respiration and maximum quantum yield of PSII derived from the regression equations for the other lichen species were statistically significant ($P \leq 0.05$) and presented in Table 3.2. There was a general trend of declining lethal and also effective temperatures for lichen maximum quantum yield of PSII along the environmental gradient of decreasing temperatures and increasing precipitation extending from the hot arid site to the warm coastal site to the cool montane site (Table 3.2). Lethal temperatures (range: 45.7°C – 62.2°C) for lichen respiration were also substantially higher than those (range: 44.6°C – 53.0°C) limiting for lichen maximum quantum yield of PSII (Table 3.2) and did not exhibit a declining trend along the environmental gradient of decreasing temperatures and increasing precipitation.

Table 3.1. Wald statistics derived from REML (linear mixed model) which tested the effects of different oven exposure temperatures on respiration rate (R_D) and maximum quantum yield of PSII (Fv/Fm) in nine different lichen species. Values presented in bold significant at *P <0.05, **P <0.01, ***P <0.001.

		Wald χ^2 statistic	
Factor	df	R_D	Fv/Fm
Oven exposure temperature	6	**4087.7*** **	**175.4*** **
Species	8	**11037.0*** **	**1154.8*** **
Oven exposure temperature x species	48	**2367.2*** **	**2046.7*** **

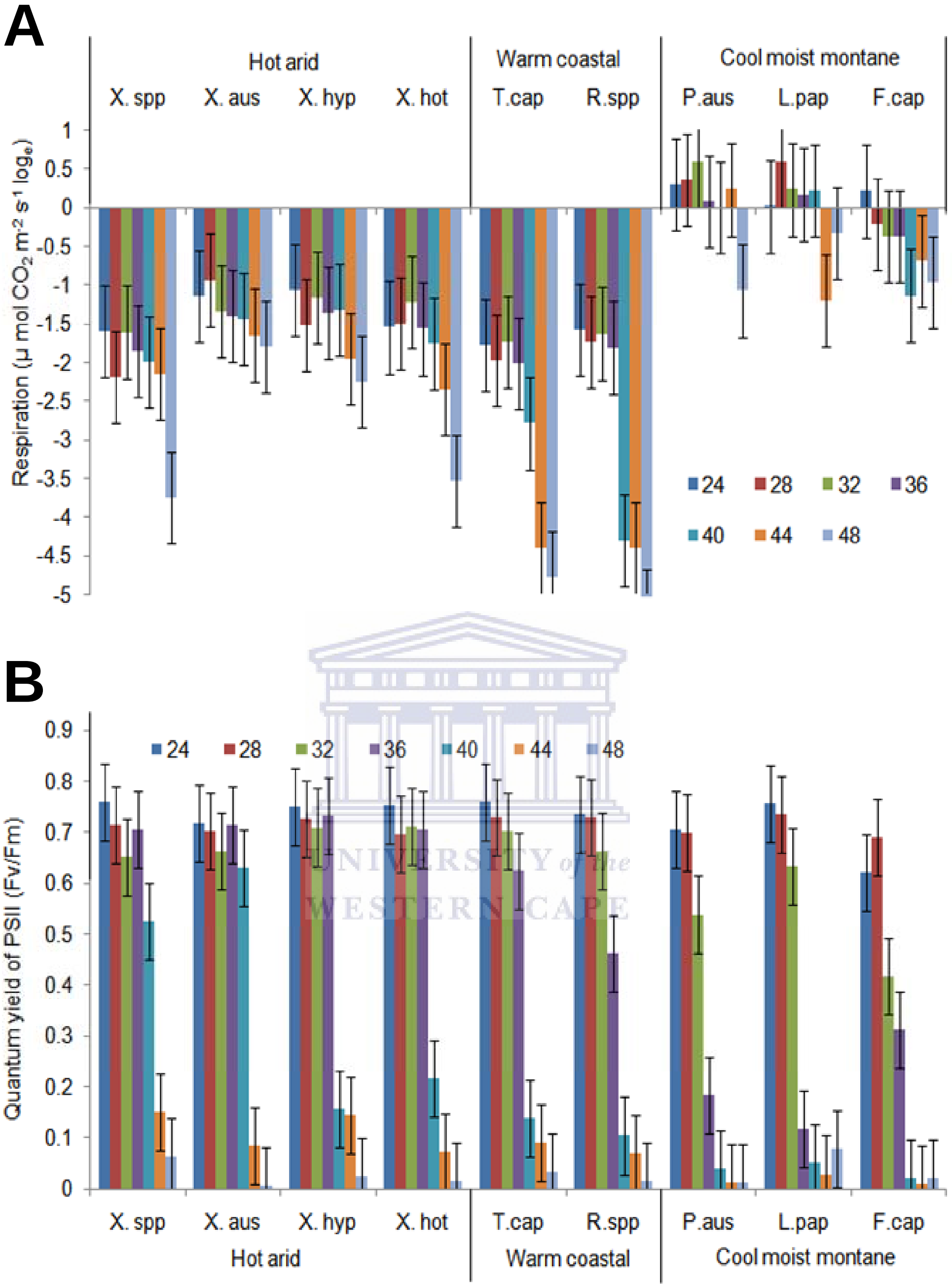

Figure 3.2. Effects of different temperatures on A, respiration and B, maximum quantum yield of PSII in nine lichen species from three different environments. Average standard errors of differences derived from REML shown by bars. Values with non-overlapping bars significantly different at $P \leq 0.05$.

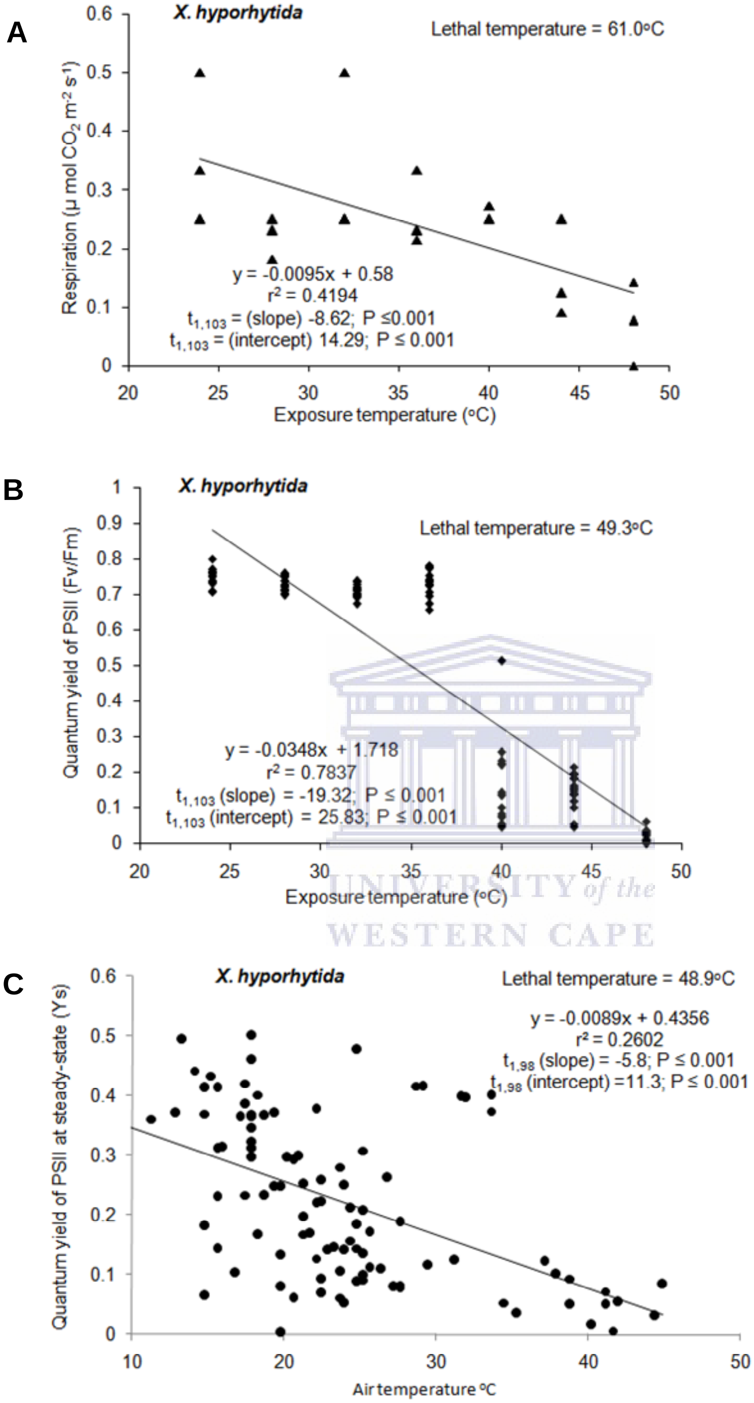

Figure 3.3. Least square regressions for (A) lichen respiration, (B) dark adapted and (C) light adapted photosynthetic quantum yields derived under laboratory and field conditions for *X. hyporhytida*.

Table 3.2. Effective and lethal temperatures for lichen respiration (RD) and maximum quantum yields of PSII derived under laboratory (Fv/Fm) and field (Ys) conditions for lichen species from different environments.

Site	Species	Effective temperature °C			Lethal temperature °C		
		Laboratory		Field	Laboratory		Field
		R_D	Fv/Fm	Ys	R_D	Fv/Fm	Ys
Hot arid site	*X. austro-africana*	48.0	44.0	25.2	58.4	52.8	49.7
	X. hottentotta	48.0	40.0	26.7	57.4	48.7	69.2
	X. hyporhytida	48.0	40.0	22.6	61.0	49.3	48.9
	Xanthoparmelia sp.	48.0	40.0	24.9	61.9	53.0	57.8
Warm coastal site	*Ramalina* sp.	40.0	36.0	21.7	47.5	46.9	42.0
	T. capensis	44.0	40.0	21.7	49.2	48.2	44.0
Cool montane site	*F. caperata*	40.0	32.0	-	55.1	45.3	-
	L. papulosa	44.0	36.0	-	62.8	45.4	-
	P. austrosinensis	48.0	32.0	-	62.2	44.6	-

Table 3.3. Coefficients of determination (r^2), degrees of freedom (df) and t-statistics (t) for slopes and intercepts of least squares regressions of exposure temperature against respiration rate (R_D) and maximum quantum yields of PSII derived under laboratory (Fv/Fm) and field (Ys) conditions for lichen species from different sites. Significant at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001.

	Hot arid site				Warm coastal site		Cool montane site		
Parameters	X. aus	X. hot	X.hyp	X.spp	R.spp	T.cap	F.cap	L.pap	P.aus
R_D									
df	19	19	19	19	19	19	19	17	19
r^2	0.4864	0.5876	0.4194	0.5138	0.8027	0.7568	0.4028	0.2679	0.1767
slope	t = -4.2***	t = -5.2***	t = -3.7**	t = -4.4***	t = -8.7***	t = -7.6***	t = -3.5**	t = -2.4*	t = -2.0
intercept	t = 6.7***	t = 8.1***	t = 6.1***	t = 7.4***	t =11.2***	t =10.2***	t = 5.35***	t = 4.2***	t = 3.4**
Fv/Fm									
df	102	103	103	103	102	103	103	103	100
r^2	0.6835	0.8026	0.7837	0.781	0.869	0.8466	0.8068	0.7944	0.8681
slope	t = -14.8***	t = -20.4***	t = -19.3***	t = -19.1***	t = -26.0***	t = -28.4***	t = -20.7***	t = -19.9***	t = -26.6***
intercept	t = 21.2***	t = 27.0***	t = 25.8***	t = 27.6***	t =33.2***	t = 31.2***	t = 25.5***	t = 24.6***	t = 31.3***
Ys									
df	98	98	98	98	91	91	-	-	-
r^2	0.2008	0.1295	0.2602	0.1529	0.2086	0.1214	-	-	-
slope	t = -4.9***	t = -3.8***	t = -11.3***	t = -4.2***	t = -4.8***	t = -3.6***	-	-	-
intercept	t = 9.7***	t = 10.5***	t = 5.8***	t = 9.7***	t = 9.1***	t = 6.9***	-	-	-

Table 3.4. Wald statistics derived from REML (repeated measures mixed model) which tested the effects of different field exposure temperatures corresponding with different times of the day in different seasons on effective quantum yield of PSII at a steady state (Ys) in lichen species from a hot arid site and a warm coastal site. Values presented in bold significant at *P <0.05, **P <0.01, ***P <0.001.

	Hot arid site		Warm coastal site	
	df	Wald χ^2 statistic	df	Wald χ^2 statistic
Main effects				
Season	3	**2809.2*** **	3	**976.8*** **
Species	3	**193.32*** **	1	**62.7*** **
Time	9	**149.4*** **	10	**202.3*** **
2-way interactions				
Season x Species	9	**82.0*** **	3	**138.4*** **
Season x Time	23	**158.3*** **	24	**134.2*** **
Species x Time	27	**73.4*** **	10	**24.2** **
3-way interactions				
Season x Species x Time	69	**136.3*** **	24	**68.3*** **

3.3.2. Field studies

Effective quantum yields of PSII (Ys) at a steady state differed significantly (P ≤ 0.001) between seasons, lichen species and time of the day at both the hot arid and warm coastal sites (Table 3.4). At hot arid site, the highest quantum yields of PSII were observed in winter (range: 0.3978 to 0.4915), followed by spring and autumn with lowest values measured in summer (range: 0.0919 to 0.1782). At the warm coastal site, the highest quantum yields of PSII were observed in winter (range: 0.3076 to 0.4585), followed autumn and spring with lowest values also measured in summer (range: 0.01397 to 0.1968). An examination of diurnal fluctuations in lichen quantum yields of PSII showed that highest values occurred in the early morning period mostly between 08h00 and 09h00 at both the hot arid site (winter range: 0.4826 to 0.5386) and the warm coastal site (winter range: 0.3522 to 0.5716), and the lowest quantum yields of PSII in the afternoon between 14h00 and 15h00 at both the hot arid site (winter range: 0.3080 to 0.4445) and the warm coastal site (winter range: 0.2680 to 0.3563) when temperatures reached their maximum levels. With decreasing temperatures towards the evening, second phases of elevated quantum yields of PSII were also apparent in the late afternoon after 16h00 (Figures 3.3 & 3.4). The magnitude of these late afternoon quantum yields of PSII increases differing with species and season. This apparent from the significant (P ≤ 0.001) interactions for quantum yield of PSII between season, lichen species and time of the day at both the hot arid and warm coastal sites (Table 3.4). Annually averaged effective temperatures limiting for effective quantum yield of PSII

(Table 3.2) for lichen species from the hot arid site (range: 22.6^{o}C – 26.7^{o}C) were higher than those limiting for quantum yield of PSII for lichen species from the warm coastal site (21.7^{o}C). Both sets of these field determined effective temperatures limiting for lichen effective quantum yield of PSII were substantially (up to 20^{o}C) lower than corresponding effective temperatures limiting for lichen maximum quantum yield of PSII determined under laboratory conditions (Table 3.2).

Least squares regressions of measured effective quantum yields of PSII at a steady state against simultaneously recorded air temperatures had significant ($P \leq 0.001$) slopes and intercepts (Table 3.3) in *X. hyporhytida* (Figure 3.2C) and in all other lichen species from the hot arid site (Appendix 3.4A to C) and the warm coastal site (Appendix 3.4D &E). Lethal temperatures derived under field conditions were only slightly different from corresponding lethal temperatures determined under laboratory conditions (0.6^{o}C to 4.9^{o}C difference) with one exception (Table 3.2).

3.4. Discussion

The measured effective temperature range of 32^{o}C to 44^{o}C limiting for lichen maximum quantum yield of PSII determined under laboratory conditions corresponded with the thermal sensitivity range of 35^{o}C to 46^{o}C reported for photosynthetic gas exchange in other hydrated lichen species exposed to artificially elevated temperatures also under laboratory conditions (Kappen, 1973; Macfarlane & Kershaw, 1978). The greatest photosynthetic resilience to an elevated temperature of 46.5^{o}C of 30 minutes duration was reported in *Cladonia rangiformis* var. *pungens* (Kappen, 1973) whereas in this study the greatest photosynthetic resilience to an elevated temperature of 44^{o}C of 2-h duration was displayed by *X. austro-africana*.

Kappen (1973) reported temperatures inhibiting for photosynthesis in the hydrated lichen *Lobaria pulmonaria* and *Umbilicaria vellea* of 35^{o}C and 36.5^{o}C respectively and for respiration of 42.5^{o}C and 44.0^{o}C respectively. This and other authors report of a greater sensitivity of lichen photosynthesis than respiration to heat stress (Macfarlane & Kershaw, 1978, 1980; Larson, 1982) which were supported by the higher effective and lethal temperatures measured for respiration than for maximum quantum yield of PSII among all 9 lichen species in this study. Also, the reported greater sensitivity to heat stress of lichens from warmer sites than those from cooler sites (Larson, 1989) was supported by the lower effective and lethal temperatures for respiration and maximum quantum yield of PSII measured in lichens from the hot arid site than in those from the cool montane site in this study.

The lethal temperatures for maximum quantum yield of PSII of 44.6^{o}C to 53.0^{o}C derived for hydrated lichens under laboratory conditions were similar to those of 42.0^{o}C to 69.2^{o}C derived for hydrated lichens under natural conditions. Both generally corresponded with lethal temperatures for photosynthetic gas exchange reported for other lichen species. Examples include 40^{o}C and 50^{o}C for hydrated *Umbilicaria vellea* and *U. mammulata* respectively, 55^{o}C for hydrated *Chondropsis semiviridis* (Rogers, 1971), 54°C for hydrated *Lobaria pulmonaria* (Gauslaa & Solhaug, 1999), 50^{o}C and 60^{o}C for hydrated *Ramalina menziesii* from cool and hot sites respectively (Larson, 1989), 50^{o}C for hydrated *Caloplaca elegantissima* and 55^{o}C for hydrated *Teloschistes capensis, Neofuscelia namibiensis* and *Xanthoparmelia walteri* (Lally & Viles, 2006). The above reported lethal temperatures for hydrated *Ramalina menziesii* and *Teloschistes capensis* were slightly higher than the lethal temperatures for maximum quantum yield of PSII of 46.9^{o}C and 48.2^{o}C derived under laboratory conditions and those of 42.0^{o}C and 44.0^{o}C derived under natural conditions for *Ramalina* sp. and *T. capensis* respectively in this study. These discrepancies possibly due to differences in habitat environments and/or heat induced reductions in PSII electron transport commencing at temperatures much lower than the threshold for de-activation of the photosynthetic gas exchange enzyme Rubisco (Musil *et al*., 2009).

Also, the lethal temperature for maximum quantum yield of PSII derived for hydrated lichens under laboratory and natural conditions in this study closely overlapped with lethal temperatures of 45.3°C and 44.1°C reported for the mosses *Plagiomnium acutum* and *Thuidium cymbifolium* (Liu *et al*., 2003) and 51°C reported for the moss *Racomitrium canescens* (Richardson, 1981). These lethal temperatures for lichen maximum quantum yield of PSII were also in the range of lethal temperatures of 50^{o}C to 55°C reported for terrestrial sun plants (Larcher, 1980), 47°C reported for wheat (Zou, 1998) and 54.6°C to 56.2°C reported for *Betula nigrahas* (Ruter, 1996), the temperature threshold of 55^{o}C considered close to the maximum tolerable by most vascular plants (Larcher, 1980; Kappen, 1981). However, the measured lethal temperatures for lichen maximum quantum yield of PSII were slightly higher than the lethal temperature of 43^{o}C reported for the aquatic fern *Salvinia molesta* (Whiteman & Room, 1991) but were mostly below those reported for succulent plants from hot arid environments. In these environments, much higher lethal temperatures of 70°C to 74°C have been reported for cacti (Nobel, 1988), 66.4^{o}C to 66.9^{o}C for rosette leafed *Haworthia* species (*H. retusa* and *H. turgida*), 68.3^{o}C to 68.7^{o}C in spherical leafed *Lithops* species (*L. leslie* and *L. turbiniformis*), and 69^{o}C to 70^{o}C in seedlings of *Ferocactus* (*F. covillei* and *F. wislizenii*) and in detached stem segments of *Opuntia* (*O. ficus-indica*) species (Smith *et al*., 1984; Nobel *et al*., 1986; Nobel, 1989).

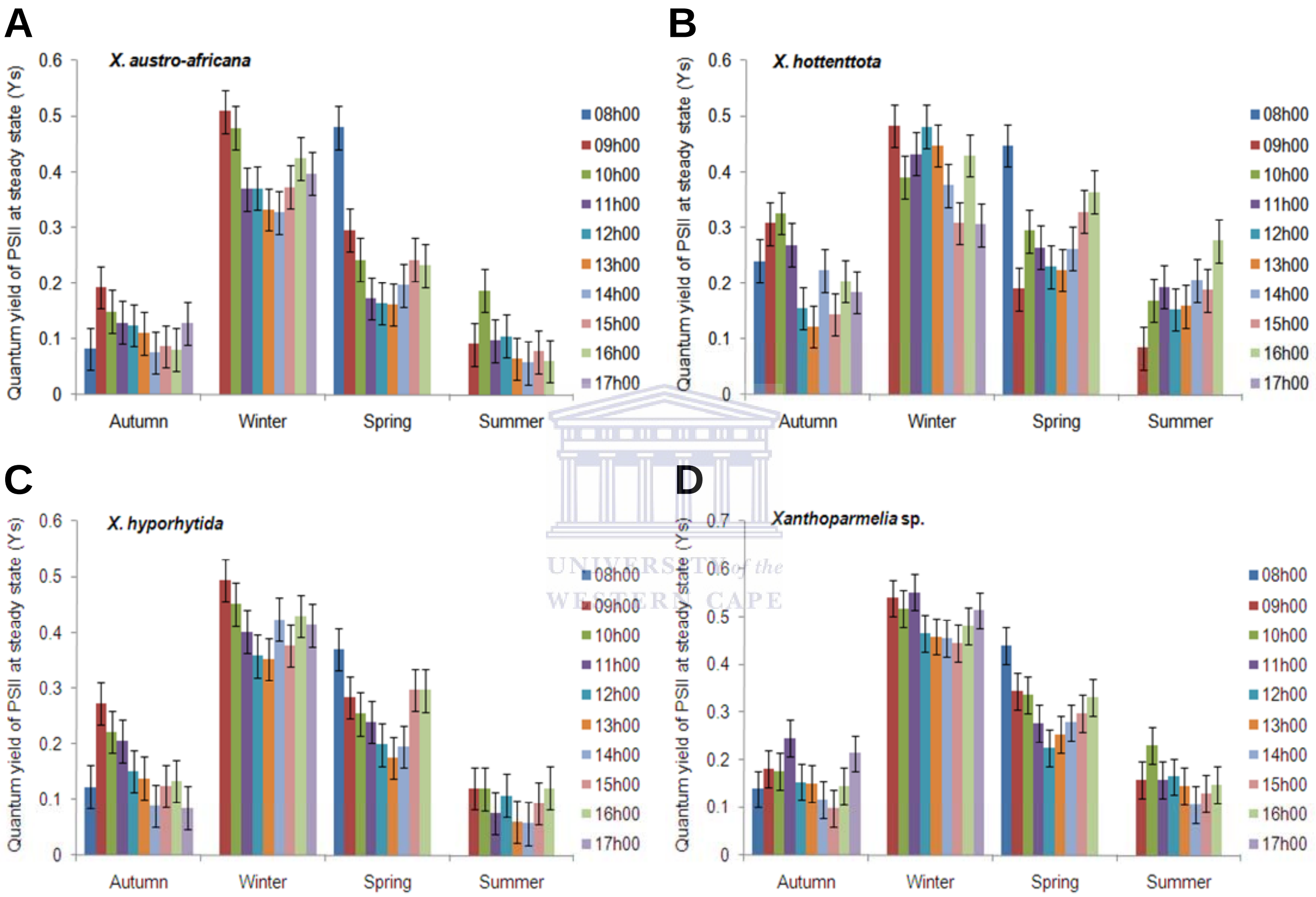

Figure 3.4. Diurnal effective quantum yields of PSII (seasonal averages) for 4 lichen species at the hot arid site. Average standard error of differences shown by bars.

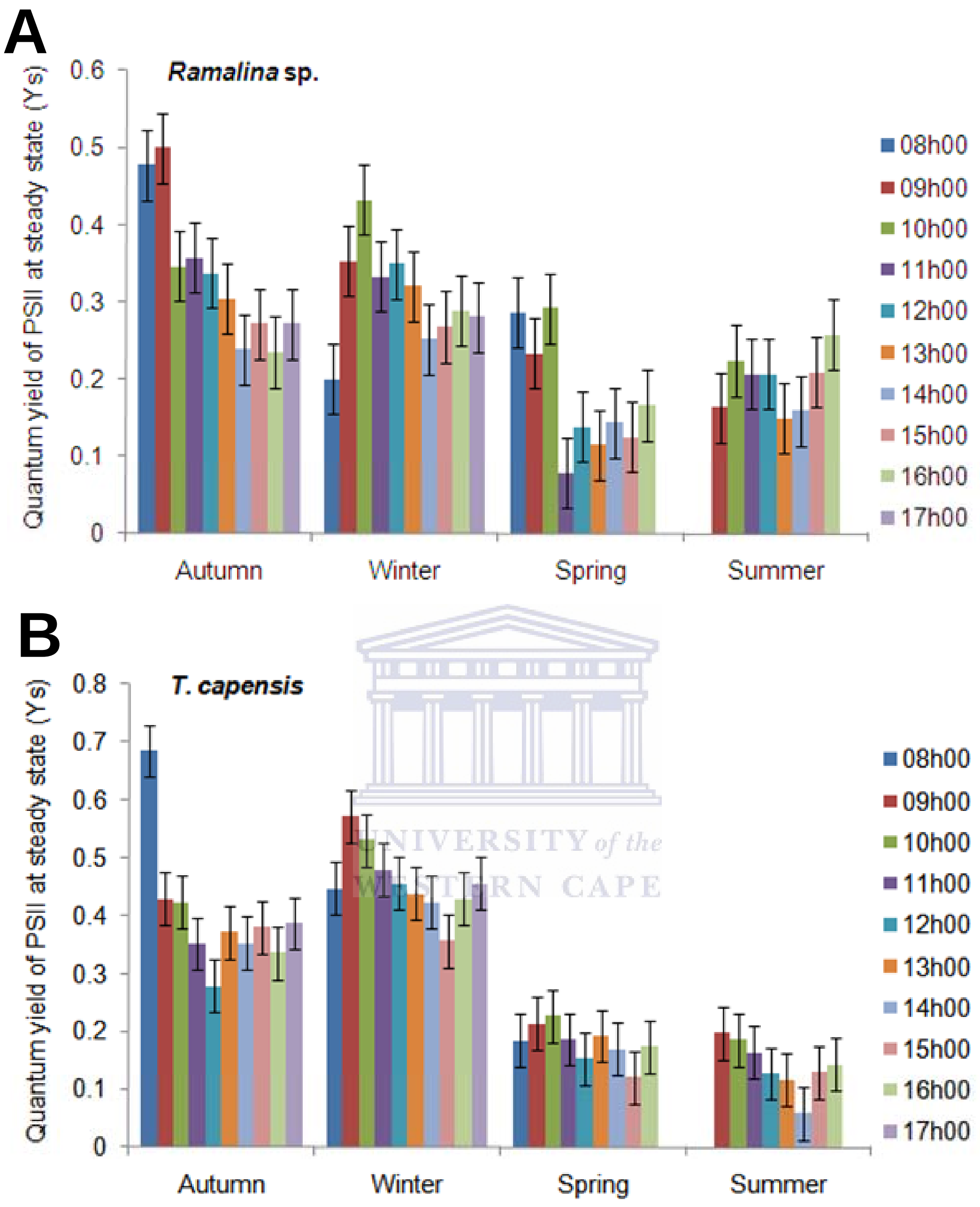

Figure 3.5. Diurnal effective quantum yields of PSII (seasonal averages) for 2 lichen species at a warm coastal site. Average standard error of differences shown by bars.

Despite the similar laboratory and field derive lethal temperatures for lichen maximum quantum yield of PSII, effective temperatures limiting lichen effective quantum yield of PSII under natural conditions (range: 21.7°C to 26.7°C) were up to 20°C lower than those limiting lichen maximum quantum yield of PSII under laboratory conditions (range: 32°C to 44°C). The field exposure temperature of 21.7°C limiting for *Ramalina* sp. maximum quantum yield of PSII in this study only slightly lower than the 25°C exposure temperature reported to cause irreversible depression of CO_2 assimilation in the closely related *Ramalina farinaceae* (Stålfelt, 1939). Measured wintertime lichen quantum yields of PSII (range: 0.2680 to 0.4445) in this study were indicative of moderately stressed lichens (Nayaka *et al*., 2009) and corresponded with a daily maximum temperature range of 23.0°C to 25.7°C. The even lower measured summertime lichen quantum yields of PSII (range: 0.1063 to 0.2045), indicative of severely stressed lichens (Nayaka *et al*., 2009), corresponding with a higher daily maximum temperature range of 26.2°C to 38.2°C. The depressed summertime quantum yields of PSII due not only elevated temperatures but possibly also to increased daylight intensities which are a significant stress factor that not only promote rapid desiccation in lichens, but also induce severe and extensive photo inhibition (Gauslaa & Solhaug, 1996, 2000).

It is concluded that the exceptionally low temperatures limiting lichen quantum yield of PSII under natural conditions suggest that even small increases in temperature especially during early morning periods of peak photosynthetic activity during wintertime could negatively affect the carbon balance of lichens (Zotz *et al*., 2003) already living close to the edge of their physiological abilities.

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Chapter 4

Effects of experimental climate warming on lichen photosynthesis and growth

Abstract

Elevated temperatures accompanying climate warming are expected to have adverse effects on sensitive lichen species which may serve as indicators of environmental change. This premise was examined by artificially elevating temperatures and reducing fog and dew precipitation amounts with transparent hexagonal open-top chambers around natural populations of 6 lichen species at a hot arid site (3.8°C increase; 46.1% precipitation decrease) and warm coastal site (2.1°C increase; 31.9% precipitation decrease). Demarcated plots of equivalent open-top chamber dimensions constructed from 5 cm diameter mesh steel fencing comprised the controls and represented ambient conditions. Lichen populations were photographed with a high resolution digital camera at the commencement and termination of the 12-month artificial warming period and their changes in cover precisely measured with the aid of image analysis software. Also, at monthly intervals quantum yields of PSII of hydrated lichens were measured in the warming chambers and control plots hourly throughout the day. The artificially elevated temperatures and precipitation reductions resulted in slight yet statistically insignificant reductions in growth of lichen thalli but substantial declines in lichen quantum yields of PSII which were of generally much greater magnitude at the hot arid site than at the warm coastal site and most prominent during the cool wet winter season of peak photosynthetic activity. Diurnal responses of the lichens to experimental warming were site, season and species specific with reductions in lichen photosynthetic quantum yield in the open top warming chambers usually evident throughout the day during the cool wet winter season but confined mostly to the early morning and/or late afternoon periods of elevated photosynthetic activity during the hot dry summer season. It is concluded that diminished fog and dew frequencies and elevated lichen respiration rates associated with climate warming as well as a potential climatic shift from a winter to summer rainfall pattern could negatively affect lichen carbon balances leading to a greater incidence of mortality and localized extinction especially among lichens in arid areas.

Key words: Lichens, climate warming, photosynthetic quantum yield, diurnal measurements

4.1. Introduction

The unprecedented accumulation of CO_2 and other greenhouse gases in the atmosphere since pre-industrial times has already had a discernible influence on global temperature and is forecast to cause further warming this century (IPCC, 2001). Direct and dramatic biotic responses to global warming are anticipated (Thomas *et al.*, 2004) as are feed back effects whereby ecological responses generate additional climatic impacts by modifying transfer rates of energy, water, and trace greenhouse gases at the planetary surface (Rosenberg *et al.,* 1983). Progressive migration of plants to more congenial thermal climates will be difficult, since altitudinal and latitudinal movements of isotherms in response to global warming are predicted to be more rapid than the rate at which plants can migrate (Callaghan & Jonasson, 1995; Grabherr *et al*., 1995).

It is presumed that global warming will have the greatest impact on climatic conditions and terrestrial ecosystems in the arctic tundra and high mountain regions (Grabherr *et al.*, 1994; Oechel & Vourlitis, 1994). Diminished cover of mosses and lichens and increased cover and heights of deciduous shrubs and graminoids have been reported from standardized warming experiments at 11 locations across the tundra biome, these findings confirming that recently observed increases in shrub cover in many tundra regions are indeed a response to climate warming (Cornelissen *et al*., 2001; Walker *et al.*, 2006). In contrast to the intensive studies conducted in the sub-arctic and arctic tundra, there are few data on other biomes. A meta-analysis of plant productivity responses to experimental warming in 20 of 32 global sites representing Forest, Grassland, high and low latitude/altitude Tundra biomes revealed a diminished relative productivity response to experimental warming with increasing site mean annual temperature (Rustad *et al.*, 2001) implying that plant productivity could be expected to decrease further with experimental warming at lower latitude, subtropical and tropical sites.

Biological activity of lichens in subtropical arid and semi-arid ecosystems is determined primarily by the size, frequency, and timing of precipitation pulses (Noy_Meir, 1973) because lichens are metabolically active only when wet and their physiological functions are highly responsive to temperature (Lange *et al*., 1999; Lange, 2003). Even moist tropical lowland lichens are considered living close to the edge of their physiological abilities with slight increase in temperature likely to make their current habitats unsuitable (Zotz & Bader, 2009). High air temperature is a major environmental stressor for lichens as it contributes also to thallus dehydration resulting in an inhibition of photosynthetic processes which manifest as a decrease in the efficiency of absorbed energy transfer through Photosystem II (PS II) and net CO_2 fixation (Hájek *et al*., 2006). As a consequence, it is not surprising that lichens and other non-vascular epiphytes have already been affected by global warming. This evident from the new and increased occurrences of sub-tropical epiphytic lichen species in the Netherlands between 1980 and 2001 (van Herk *et al*., 2002; Aptroot & van Herk, 2007), by northward and eastward range extensions of Atlantic and Mediterranean bryophyte species in Central Europe over the same period (Frahm, 2001), and reported changes in the lichen flora from other parts of Europe (Aptroot & van Herk, 2007). In the Netherlands warm-temperate lichen species have significantly increased and species characteristic of cold environments have either decreased or disappeared (van Herk *et al*., 2002). One example is that of *Flavoparmelia soredians* a drought resistant, warm-temperate lichen species presently common in the Netherlands but rare before 1900 with its northern most limit until recently in southern England (Seaward & Coppins, 2004). In Denmark, growth rates of the drought resistant, warm temperate lichen *Flavoparmelia caperata*, have increased over the last 100 years, this seemingly linked to increased temperatures during the last 20 years (Søchting, 2004). Also, several new warm temperate epiphytic lichen species have recently been documented in the Netherlands (Aptroot *et al*., 1997, 1998; Aptroot & van Herk, 1999a, 1999b; van Herk & Aptroot, 1999; Sparrius & Aptroot, 2000, 2003) with lichen species preferring colder environments having declined in numbers (Aproot & van Herk, 2007; Hauck, 2009).

In arid subtropical ecosystems, global warming could potentially exceed native species thermal thresholds. A recent population census of the Namib Desert tree *Aloe dichotoma* over its entire geographic range revealed enhanced mortalities and declines in equatorial populations, this attributed to the surpassing since 1960 of critical climate thresholds at the equatorial sites due to recent climate warming (Foden *et al.*, 2007). In another study of endemic succulent species in the arid southern African Succulent Karoo biome, massively reduced leaf densities and canopy covers were observed, especially among small sparsely branched species comprising single leaf pairs, following one year's exposure to daytime air temperature increases consistent with a future global warming scenario (Musil *et al*., 2005). This and a subsequent study showed that even mild anthropogenic warming could exceed the thermal thresholds of many southern African quartz field succulents leading to increased plant mortalities and metabolic impairment. This impairment attributed to a loss in the catalytic efficiency of Rubisco which was preceded by a decrease in PSII electron transport commencing at temperatures much lower than the threshold for Rubisco de-activatio (Musil *et al*., 2009).

Consequently, it seems likely that increased temperatures and diminished precipitation frequencies and air humidity's associated with climate warming could cause a reduction in lichen species richness. Especially those morphological types most sensitive to aridity are threatened in the southern African Succulent Karoo biome, which is characterized by an extraordinary and peculiar diversity of lichen taxa. A consequence of climatic changes could be the colonization of widespread cyanolichens and the loss of endemic species (Zedda & Rambold, 2009). Such changes could have many profound effects on ecosystem function (Belnap & Eldridge, 2003). In view of these findings, this study's objective was to test the effects of experimental climate warming approximating a future climate scenario on the photosynthesis and growth of lichens from habitats of different aridity in the southern African Succulent Karoo biome.

4.2. Materials and Methods

4.2.1. Study sites, species and warming treatments

There were two study sites. The first hot arid site was the farm Quaggaskop (31^o 24.6' S, 18^o 37.8' E) situated at an elevation ±160 m in the Knersvlakte, a semi-arid winter rainfall region within the South African Succulent Karoo Biome (Rutherford & Westfall, 1986) listed among 34 global biodiversity hot spots (Myers *et al.,* 2000; Mittermeier *et al.,* 2004), with a mean annual precipitation and daily maximum air temperature recorded at the nearby Vredendal weather station between 1957 and 1984 of 145 mm and 25.7°C respectively (Climate of South Africa, 1986). The second warm coastal site comprised a large lichen field (28^o 37'S, 16^o 30'E) situated a few kilometers South East of the mining city of Alexander Bay, 3.2 km distant from the Atlantic coast. The site has a mean annual temperature of 17.2^{o}C and an erratic low rainfall of 39 mm per annum (1951 – 1984 average) occurring predominately in winter, this supplemented by high frequencies of fog averaging 61 days per year and most common in May late autumn (Climate of South Africa, 1986).

Daytime passive heating of the lichen populations at each site was achieved with clear acrylic (transmission down to 280 nm) hexagonal open-top chambers (basal diameters: 120 cm between parallel sides) of 50 cm height (Figure 4.1). Such open-top chambers have been applied extensively in the International Tundra Experiment (ITEX) organized to investigate how vegetation in arctic tundra and high alpine regions may be affected by global warming (Henry & Molau, 1997), and their efficacy as analogues of climate warming has received biotic validation (Hollister & Weber, 2000). Demarcated plots of equivalent open-top chamber basal dimensions enclosed by 40cm high steel fencing with a 5 cm diameter mesh comprised the controls which represented ambient conditions (Figure 4.1). Twelve open-top chambers and 12 control plots were installed over four different lichen species (*X. anthoparmelia austroafricana, X. hyporhytida, Xanthoparmelia* sp.*, Xanthomaculina hottentotta)* occurring on quartz gravel substrates at the Quaggaskop site and 3 open top chambers and 3 control plots installed over the two dominant lichen species (*Teloschistes capensis* and *Ramalina* sp.*)* on gypsum-rich topsoil at the Alexander Bay site. Placement of the open-top chambers and control plots during early winter (June) allowed gradual acclimation of the lichens within each chamber to the artificially elevated temperatures.

4.2.2. Ambient and open-top chamber microenvironments

Miniature Watchdog Model 450 data loggers (Spectrum Technologies Inc., Plainfield, Illinois, USA) set to record at hourly intervals connected to radiation shielded thermocouples and leaf wetness resistance sensors were installed in randomly selected control plots and open-top chambers at the Quaggaskop and Alexander Bay sites. Thermocouples were positioned at ground level at the centers of the open top chambers as a slight temperature gradient was previously reported between the southern and northern sides of these open-top chambers (Musil *et al*., 2005). Leaf wetness resistance sensors were positioned 50mm above ground level at the centers of the open top chambers. The volume of fog and dew moisture present on the active surface of the leaf wetness sensor was derived from measured leaf wetness resistance readings using a published formula (Musil *et al*., 2009). Measured hourly fog and dew moisture volumes were summed for each day to provide the total daily apparent fog and dew precipitation amounts from which monthly and seasonal means were calculated. Those that coincided with rainfall measurements recorded concurrently with a tipping gauge rain sensor interfaced with a Watchdog 450 data logger at the study sites were excluded.

4.2.3. Lichen growth

Lichen populations present in the open-top warming chambers and control plots at each site were photographed on their installation in June 2008 (early winter) and again in May 2009 (late autumn) of the following year using a high resolution 3.4 effective mega pixel (Sigma SD10) digital camera with a three-band Foveon X3 sensor (3 sensor photo detectors per pixel location). The camera was fitted with semi-wide angle lenses (24-70mm zoom, 20 mm fixed) and suspended 1.5m above ground surface on a tripod whose precise orientation was enabled by numbered aluminium tags affixed to the open-top chambers and control plots. A graduated ruler and compass placed on the ground provided indicators of scale and direction. In each digital image, the precise locations of individual thalli of the common crustose lichen *X. austro-africana* and the foliose lichen *X. hottentotta* in the control plots and open top chambers were labeled and their areas measured at the commencement and termination of the warming treatments with the aid of image analysis software (Image-J ver.1.34I, National Institute of Health, USA - http://rsb.info.nih.gov/ij/). The changes in areas of individual thalli of each lichen species measured in the control plots and open top warming chambers over the one year treatment period were expressed as percentages.

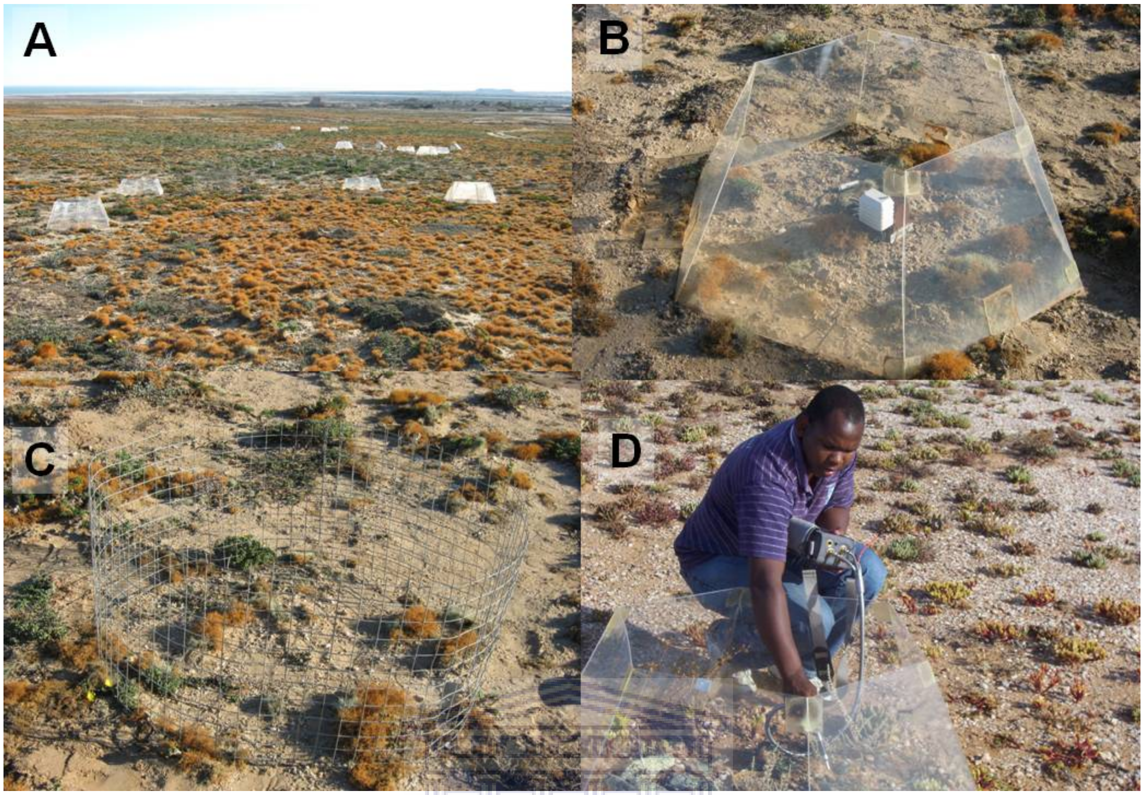

Figure 4.1. A. Alexander Bay lichen field experimental site. B. open-top warming chamber with automated environmental monitoring sensors and logger, C. control plot, D. measuring steady-state fluorescence of lichens in open top-warming chamber at Quaggaskop site.

4.2.4. Lichen effective quantum yield of PSII

Chlorophyll a fluorescence is a particularly useful tool for vitality screening of lichen photosynthetic responses to extreme temperatures (Bilger *et al*., 1989; Baruffo & Tretiach, 2007) and provides a sensitive indicator of photosystem II (PS II) efficiency (Golding & Johnson, 2003). In this study, chlorophyll fluorescence measurements were conducted with a portable modulated fluorometer (OSI-F1, Opti-Sciences Inc., Hudson, USA). In both early morning and diurnal hourly measurements (details presented below), lichen thalli were first hydrated with a fine distilled water mist spray. After a one hour period, randomly selected thalli of each lichen species in the warming chambers and control plots were exposed to an 0.8s saturating light pulse of 15 000 μE and their effective quantum yields of PSII at a steady state (Ys = Fms-Fs/Fms = ΔF/Fm’) determined.

4.2.4.1. Early morning measurements

The first set of fluorescence measurements conducted monthly over a 12-month period were confined to the early morning period between 08h00 and 10h00 when the lichens exhibited the highest effective quantum yields of PSII. Five replicated fluorescence measurements were taken monthly on 12 randomly selected thalli of each lichen species in the warming chambers and control plots (60 measurements per species per treatment per month).

4.2.4.2. Diurnal measurements

The second subsequent set of diurnal fluorescence measurements taken at hourly intervals from 09h00 to 16h00 were also conducted monthly, but only over an 8-month period extending from July (mid winter) through to February (late summer). Five replicated fluorescence measurements were taken hourly on four randomly selected thalli of each lichen species in the warming chambers and control plots (20 measurements per species per hour per treatment per month).

4.2.5 Data synthesis and statistical analysis

4.2.5.1. Ambient and open-top chamber microenvironments

Daily maximum and minimum temperatures and maximum fog and dew precipitation amounts in the open top warming chambers and control plots were extracted for each 24 hour period. An analysis of variance tested for differences in maximum and minimum temperatures and fog and dew precipitation amounts between the open top warming chambers and control plots in the different seasons.

4.2.5.2. Lichen growth

Measured percentage changes in lichen species thalli areas were arcsine transformed to correct for non normality in proportions. Since the experimental design was not fully balanced due to missing measurements, a residual maximum likelihood variance component analysis (REML - linear mixed model) was used to test for differences in the magnitude of change in lichen species thalli areas between the control plots and warming chambers using the Wald X^2 statistic generated by REML (GENSTAT, Discovery Edition 3, VSL Lty, UK). Warming treatments and lichen species were fitted in the fixed model and treatment and species replications in the random model.

4.2.5.3. Lichen effective quantum yield of PSII

Measured effective quantum yields of PSII at a steady state were normally distributed. However, the experimental design was also not fully balanced due to missing measurements, and consequently a REML (residual maximum likehood) variance components analysis (repeated measures mixed model) was used to test for differences in effective quantum yield of PSII between the control plots and warming chambers using the Wald χ^2 statistic generated by the REML (GENSTAT Discovery Edition 3, VSL Lty, UK). In the first set of early morning fluorescence measurements, the REML was conducted separately on the groups of lichen species from the hot arid and warm coastal sites. Here, warming treatments and lichen species were fitted in the fixed model and monthly replications grouped into seasons in the random model. In the second set of diurnal fluorescence measurements, the REML was conducted separately on each lichen species. Here warming treatments and time of the day were fitted in the fixed model and monthly replications grouped into seasons in the random model. Differences exceeding twice the average standard error of differences were used to separate significantly different treatment means at $P \leq 0.05$. This based on the fact that for a normal distribution from REML estimates, the 5% two-sided critical value is two.

4.3. Results

4.3.1. Ambient and open-top chamber microenvironments

Average minimum daily air temperatures were not significantly ($P \geq 0.05$) different in the open top warming chambers and control plots in all seasons (Table 4.1). However, maximum daily air temperatures were significantly ($P \leq 0.05$) higher and apparent fog and dew precipitation amounts were significantly ($P \leq 0.05$) lower in the open top warming chambers and control plots at both the hot arid and warm coastal sites. Moreover, at the hot arid site the magnitude of maximum daily air temperature increases (seasonal range: 2.6^{o}C to 4.9^{o}C) and fog and dew precipitation decreases (seasonal range: 46.5% to 52.2%) in the open top chambers were greater than the temperature increases (seasonal range: 1.9^{o}C to 2.4^{o}C) and fog and dew precipitation decreases (seasonal range: 14.5% to 39.4%) in the open top chambers at the warm coastal site (Table 4.1).

4.3.2. Lichen growth

Both *Xanthoparmelia austro-africana* and *Xanthomaculina hottentotta* did not display significantly ($P \geq 0.05$) greater changes in thalli area in the artificially warmed than ambient environments and no significant ($P \geq 0.05$) interaction between species and warming (Table 4.1). Despite the latter, a larger ($P \geq 0.05$) decrease in lichen thallus area (Figure 4.2) was displayed by *X. hottentotta* in the artificially warmed (-32.5%) than ambient environment (-22.3%).

4.3.3. Lichen effective quantum yield of PSII

4.3.3.1. Early morning measurements

Lichen effective quantum yields of PSII at the hot arid and warm coastal sites differed significantly ($P \leq 0.001$) between seasons, ambient and warming treatments and species (Table 4.2).

The highest quantum yields of PSII at the hot arid site were observed in winter (range: 0.4874 to 0.5528) followed by autumn and spring with lowest quantum yields of PSII (range: 0.1269 to 0.2254) observed in summer.

At the warm coastal site, the highest quantum yields of PSII were observed in autumn (range: 0.5369 to 0.6163) followed by winter and summer with lowest quantum yields of PSII (range: 0.2450 to 0.3578) observed in spring.

There were significant ($P \leq 0.001$) three way interactions between season, warming treatment and species on effective quantum yield of PSII at both sites (Table 4.2). At the hot arid site, effective quantum yields of PSII of all four lichen species displayed significantly ($P \leq 0.05$) lower values in the open-top warming chambers than in the ambient environment in all four seasons with the largest reductions in effective quantum yields of PSII (range: 59% to 73.5%) in the warming chambers apparent during summer (Figure 4.3A). Average annual reductions in effective quantum yield of PSII in the open-top warming chambers ranged from 40.1% to 47.5% in *X. austro-africana*, *X. hyporhytida* and *Xanthoparmelia* sp. with a 34.2% reduction in effective quantum yield of PSII observed in *X. hottentotta* the most resilient of the four lichen species.

At the warm coastal site, where the temperature increases in the warming chambers were not as large as at the hot arid site, both *Ramalina* sp. and *Teloschistes capensis* displayed insignificantly ($P \geq 0.05$) different effective quantum yields of PSII in the open-top warming chambers and ambient environment during autumn (Figure 4.3B). *T. capensis* exhibited significantly ($P \leq 0.05$) lower effective quantum yields of PSII in the open-top warming chambers than in the ambient environment in summer and winter with *Ramalina* sp. only exhibiting significantly ($P \leq 0.05$) lower effective quantum yields of PSII in the open-top warming chambers in spring. Average annual reductions in effective quantum yield of PSII in the open-top warming chambers ranged from only 7.0% in *Ramalina* sp. to 9.3% in *T. capensis.*

Table 4.1. Seasonal temperature and moisture statistics for controls (ambient environment) and open top chambers and (warmed environment) at a hot arid and warm coastal site. Treatment means within each season with dissimilar letters significantly different at * $P \leq 0.05$.

Season	Treatment	Apparent fog/dew precipitation mm d^{-1}				Maximum air temperature °C				Minimum air temperature °C			
		Hot arid site		Warm coastal site		Hot arid site		Warm coastal site		Hot arid site		Warm coastal site	
		Mean	Change %	Mean	Change %	Mean	Change °C	Mean	Change °C	Mean	Change °C	Mean	Change °C
Winter	Control	0.1070a		31.9a		25.7a		23.0a		6.7a		9.6a	
	Warm	0.0572b	-46.5	19.9b	-37.6	28.3b	2.6	24.9b	1.9	7.2a	0.5	10.0a	0.4
Spring	Control	0.0479a		38.5a		33.8a		23.8a		11.5a		10.8a	
	Warm	0.0233b	-51.4	23.5b	-38.9	38.5b	4.7	26.2b	2.4	12.3a	0.8	11.2a	0.4
Summer	Control	0.0225a		38.6a		38.2a		26.2a		16.4a		14.0a	
	Warm	0.0108b	-52.2	33.0b	-14.5	43.1b	4.9	27.6b	1.4	17.2a	0.8	14.1a	0.1
Autumn	Control	0.0778a		41.6a		30.7a		24.5a		12.8a		11.0a	
	Warm	0.0439b	-43.5	25.2b	-39.4	33.9b	3.2	27.2b	2.7	13.4a	0.6	11.4a	0.4
Annual	Control	64.0a		37.3a		32.1a		24.3a		11.8a		11.4a	
	Warm	34.0b	-46.9	25.4b	-31.9	35.9b	3.8	26.4b	2.1	12.5a	0.7	11.7a	0.3

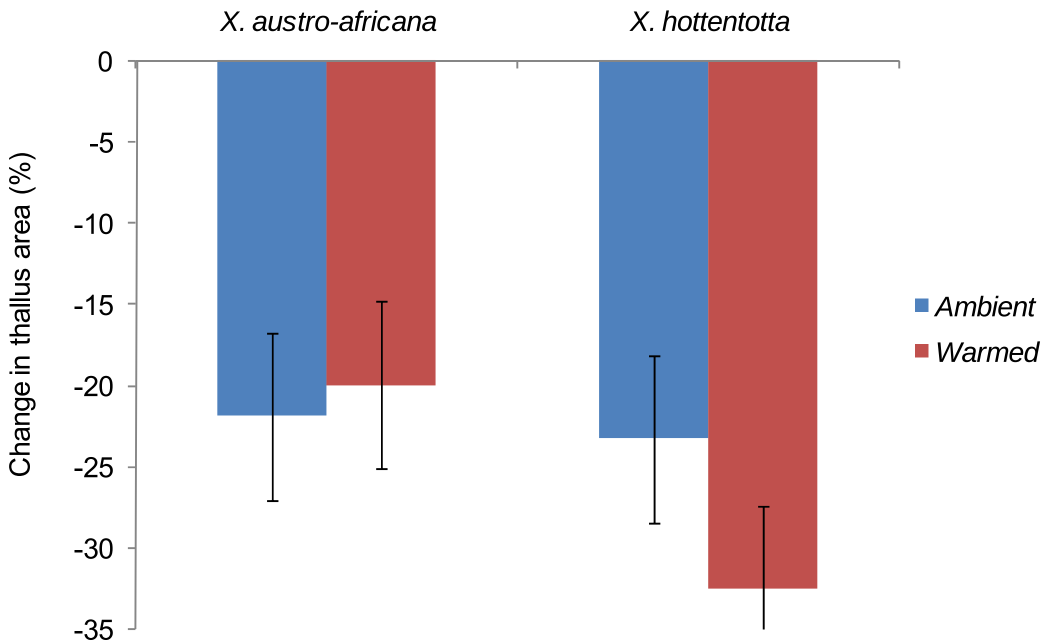

Figure 4.2. Changes in thalli areas (arcsine transformed percentages) of two lichen species after one year's growth in ambient and artificially warmed environments. Average standard errors of differences shown by bars.

4.3.3.2. Diurnal measurements

Effective quantum yields of PSII of all 6 lichen species differed significantly (P ≤ 0.001) with season, time of the day and experimental warming, except in *X. austro-africana* (Table 4.2). The highest quantum yields of PSII in lichen species from both the hot arid and warm were observed in the early morning period between 09h00 and 10h00, with second phases of elevated quantum yields of PSII also apparent in the late afternoon after 16h00 (Figure 4.4A to D and 4.5A & B). The greatest reductions in lichen effective quantum yield of PSII in response to experimental warming were observed in winter, followed by spring and summer. However, the lichen species differed in the magnitude of their effective quantum yield of PSII reductions to experimental warming at different times of the day in the different seasons with no distinct common patterns apparent.

At the hot arid site, for example, *Xanthoparmelia* sp. effective quantum yields of PSII were significantly (P ≤ 0.05) reduced in the warming chambers throughout the day in winter and spring but only between 09h00 and 12h00 in summer, the largest declines in summer apparent during early morning peak periods of peak photosynthetic activity (Figure 4.4D). In contrast, in *X. austro-africana* effective quantum yields of PSII were significantly reduced in the warming chambers only at 16h00 in winter and at 14h00 in spring but not at any time of the day in summer (Figure 4.4A). These discrepancies supported by the significant (P ≤ 0.05) three way interactions between season, warming treatment and time of the day (Table 4.3). At the warm coastal site, where the temperature increases in the warming chambers were not as large as at the hot arid site the observed significant (P ≤ 0.001) reductions in effective quantum yield of PSII in *Ramalina* sp. and *T. capensis* were confined mostly to the afternoon between 12h00 and 16h00 (Figure 4.5A & B).

Table 4.2. REML statistics for tests of experimental warming on lichen growth and Effective quantum yield of PSII at two sites. Significantly different at *P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001.

REML	Hot arid site				Warm coastal site	
	Thallus area		Effective quantum yield of PSII		Effective quantum yield of PSII	
	df	Wald χ^2 statistic	df	Wald χ^2 statistic	df	Wald χ^2 statistic
Main effects						
Season	-	-	3	4447.1***	3	416.8***
Species	1	2.14	3	87.2***	1	42.1**8
Warming	1	2.02	1	1216.5***	1	12.0***
2-way interactions						
Season x Species	-	-	9	93.1***	3	12.6**
Season x Warming	-	-	3	207.7***	3	5.5
Species x Warming	1	2.85	3	62.6***	1	0.5
3-way interactions						
Season x Species x Warming	-	-	9	52.4***	3	26.9***

Table 4.3. REML statistics for tests of experimental warming on effective quantum yield of PSII different times of the day at two sites. Significantly different at *P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001.

REML		Wald χ^2 statistic					
		Hot arid site				Warm coastal site	
	df	*X. austro-africana*	*X. hottentotta*	*X. hyporhytida*	*Xanthoparmelia* sp.	*Ramalina* sp.	*T. capensis*
Main effects							
Season	2	1352.9***	417.4***	534.2***	1189.7***	673.8***	1165.2***
Warming	1	1.4	86.9***	87.4***	372.9***	29.2***	63.1***
Time	7	126.4***	33.1***	56.3***	70.7***	63.8***	116.***
2-way interactions							
Season x Warming	2	0.1	1.4	52.4***	13.5***	105.2***	11.2**
Warming x Time	14	42.6***	100.4***	40.1***	53.5***	24.4*	23
Species x Warming	7	26.7***	54.9***	29.3**	8.7	19.7**	11.1
3-way interactions							
Season x Warming x Time	14	34.6**	29.3*	30.8**	31.5**	36.8***	13.8

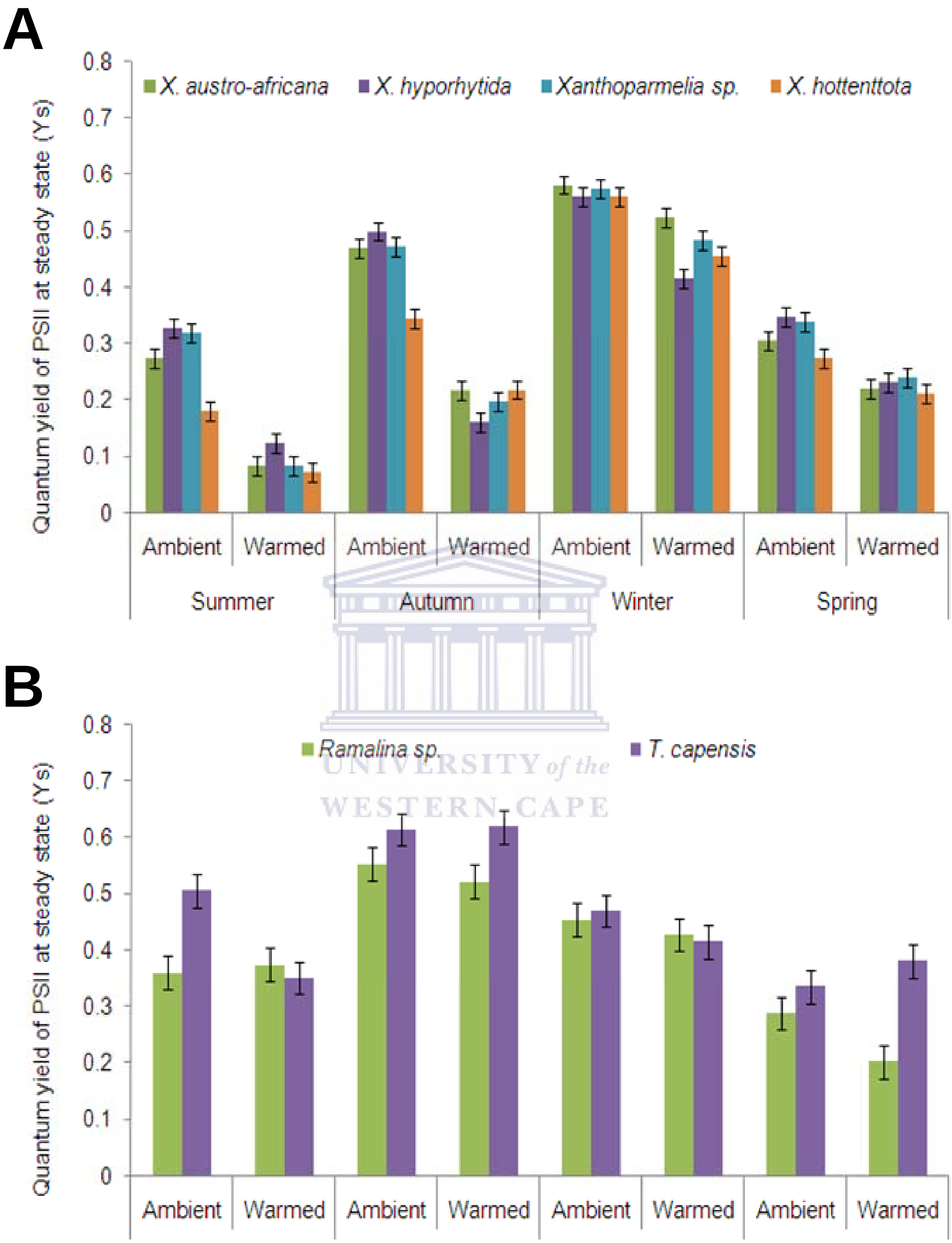

Figure 4.3. Effective quantum yields of PSII (seasonal averages) under ambient and artificially warmed conditions for A. 4 lichen species at a hot arid site and B. 2 lichen species at a warm coastal site. Average standard error of differences shown by bars.

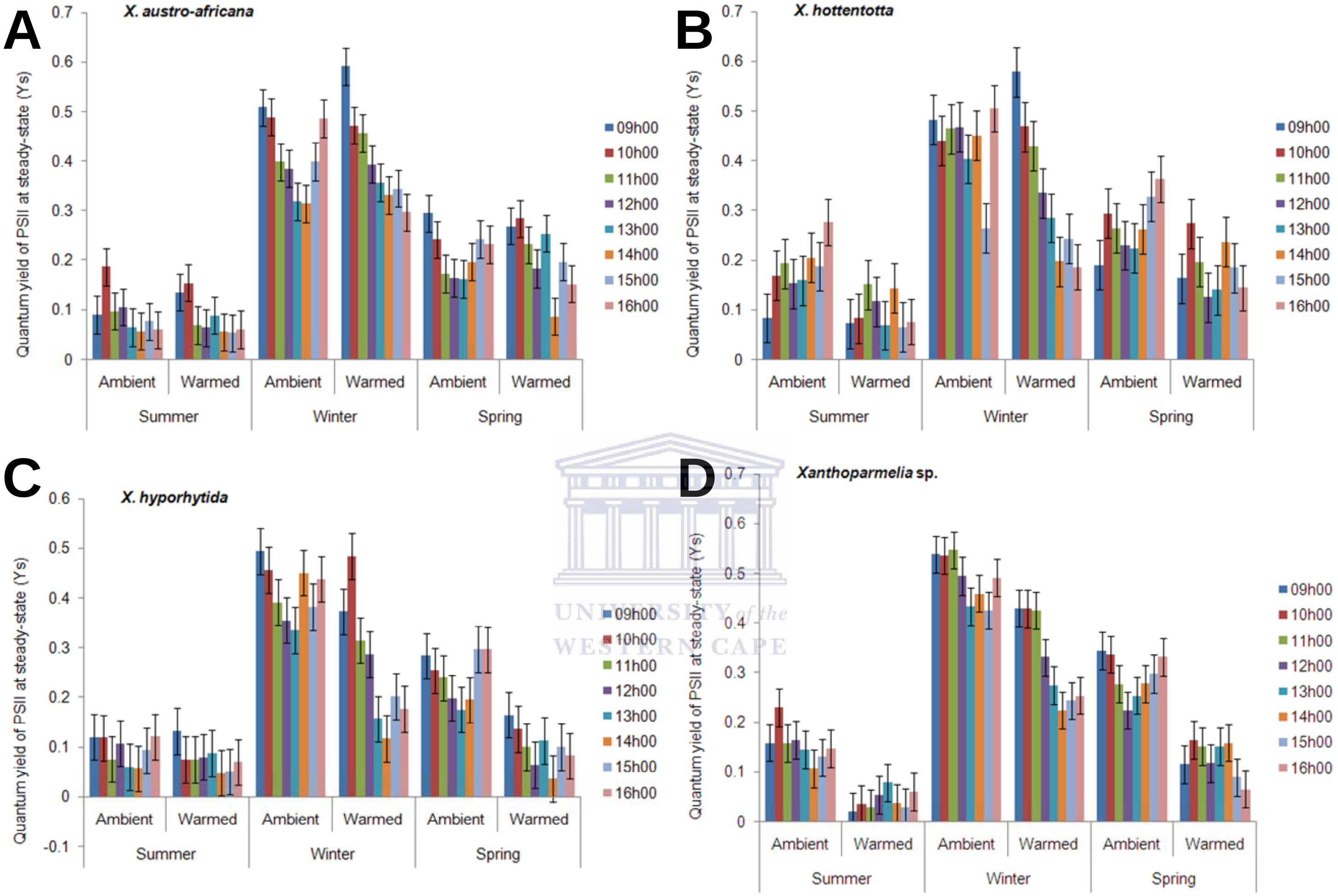

Figure 4.4. Diurnal effective quantum yields of PSII (seasonal averages) under ambient and artificially warmed conditions for 4 lichen species at the hot arid site. Average standard error of differences shown by bars.

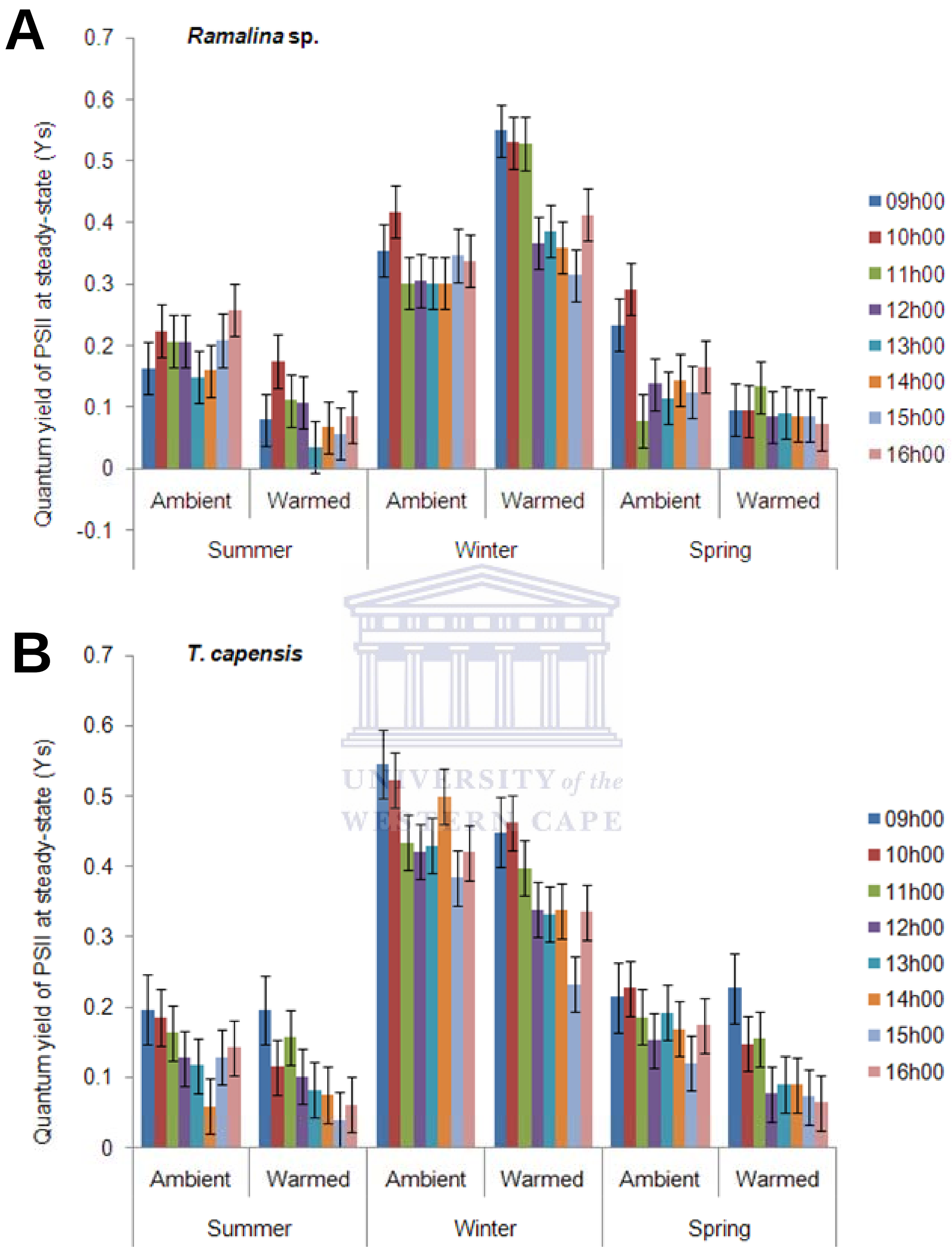

Figure 4.5. Diurnal effective quantum yields of PSII (seasonal averages) under ambient and artificially warmed conditions for 2 lichen species at a warm coastal site. Average standard error of differences shown by bars.

4.4. Discussion

Larson (1980) reported that lichens exhibit seasonal changes in their photosynthetic capacity which could, at least partly, be interpreted as an acclimation to prevailing weather conditions. This is in agreement with the results of this study where hydrated lichens from both the hot arid and warm coastal sites displayed the highest quantum yields of PSII during winter which is usually regarded as the period of greatest metabolic activity for lichens in temperate climates (Nash, 1996) and the lowest during summer season. The winter quantum yields of PSII (range: 0.3978 to 0.4915) indicative of healthy to moderately stressed lichens and summer quantum yields of PSII (range: 0.0919 to 0.1782) indicative of severely stressed lichens (Nayaka *et al*., 2009).

Lange *et al*. (2006) concluded that nocturnal moistening by fog and/or dew drives a subsequent short phase of peak lichen photosynthetic activity in the early morning hours which is almost the only diurnal pattern for lichen productivity throughout the year. In the Namib desert, peaks in photosynthetic activity observed in *Ramalina maciformis* and *Teloschistes lacunosus* in the 3 hour period after sunrise are complemented by short second phases of enhanced photosynthetic activity driven by increased humidity in the late afternoon (Lange *et al.*, 1991) with crustose and foliose lichens from the Negev desert displaying similar characteristics (Lange, 1970). These typical response patterns for lichens in arid and semiarid desert climates (Kappen, 1988) are also found in lichens in Mediterranean (Lange *et al*., 1985) and temperate climates (Lange, 2003). Similarly, in this study, peak quantum yields of PSII in the lichens from both the hot arid and warm coastal sites were observed in the early morning period between 09h00 and 10h00 with second phases of elevated effective quantum yields of PSII also apparent in the late afternoon after 16h00.

The diminished effective quantum yields of PSII observed in the hydrated lichen species around the solar noon in this study were attributed to the elevated midday temperatures though photo inhibition of photosynthesis by the high light intensities (photosynthetic photon flux densities) around solar noon may also have been a factor. Although, the amount of light received by the photobiont during periods of thallus hydration may determine lichen growth (Dahlman & Palmqvist, 2003), it also represents a significant stress factor in that a high light intensity not only promotes rapid desiccation in lichens, but also induces severe and long-lasting photoinhibition (Gauslaa & Solhaug, 1996, 2000). However under natural conditions, lichens experience considerably longer periods of high solar radiation in the desiccated than hydrated state (Lange *et al*., 1999) with a functional disconnection of photosynthetic components (Sigfridsson, 1980; Bilger *et al*., 1989) and diminished transmittance of solar radiation through the protective upper cortex apparent in desiccated lichens (Ertl, 1951; Gauslaa & Solhaug, 2001). Despite this, extended high light intensities have been reported to cause more damage in air-dry than hydrated forest lichens (Gauslaa & Solhaug, 1999, 2004), a possible consequence of switched off repair mechanisms during desiccation.

The elevated air temperatures of 2.1°C and 3.8°C and reduced precipitation amounts of 31.9% and 46.1% measured in the open-top chambers at the warm coastal and hot arid sites respectively approximated mean annual air temperature increases of 1.5°C to 5.0°C and precipitation reductions of about 30% predicted (means of 7 GCM models) by the SRES B1-low and A2-high climate sensitivity scenarios respectively for the Succulent Karoo biome towards the end of the century (Hulme *et al.,* 2001). These temperature increases and precipitation reductions in the open top warming were accompanied by slight yet statistically insignificant reductions in growth of lichen thalli but substantial declines in lichen effective quantum yield of PSII. Kershaw & Alvin (1963) reported radial growth increments for lichen thalli in general of about 1 mm to 10 mm per year and Hawksworth & Rose (1976) reported radial growth increments for British crustose and foliose lichens in the order of 0.5 mm to 5.0 mm year. These small growth increments made it difficult to detect statistically significant changes in lichen thalli areas in response to artificial climate warming over the short one year treatment period in this study. However, over longer treatment periods of 8 years, statistically significant reductions in lichen cover and diversity have been reported in open top warming chambers in the Alaskan arctic tundra (Wahren *et al*., 2005), these changes qualitatively similar to standardized warming experiments at several other locations across the arctic tundra (Walker *et al*., 2006)

In contrast to lichen growth, significant reductions in lichen effective quantum yield of PSII were observed in the open top warming chambers. The reductions in lichen effective quantum yields of PSII at the hot arid site were of generally much greater magnitude that those at the warm coastal site and most prominent during the cool wet winter season of peak photosynthetic activity. Diurnal responses of the lichens to experimental warming were site, season and species specific with reductions in lichen effective quantum yield of PSII in the open top warming chambers usually evident throughout the day during the cool wet winter season but confined mostly to the early morning and/or late afternoon periods of elevated photosynthetic activity during the hot dry summer season. Since the lichens were hydrated prior to each set of fluorescence measurements, the observed reductions in effective quantum yield of PSII reflected their acclimation mainly to the prevailing temperature conditions in the warming chambers.

It has been proposed that a combination of high night temperatures that enhance carbon loss due to elevated respiration rates and high day temperatures that promote more rapid dehydration of lichen thalli restrict the time available for carbon gain by photosynthesis

(Zotz, 1999). Studies on cyanobacterial lichens in a Panamanian lower montane rain forest have revealed that nocturnal respiration losses are often higher than carbon gains during the day (Lange *et al*., 2000, 2004). The lichens *Parmotrema endosulphureum* and *Leptogium azureum,* for example, respiring their entire day time carbon gain at night (Zotz & Winter, 1994; Zotz *et al*., 2003) with their virtual absence from lowland forests explained by negative carbon balances resulting from the higher nighttime temperatures (Lange *et al*., 1994; Zotz & Winter, 1994; Zotz *et al.*, 2003). In *P. endosulphureum,* CO_2 fixation at maximum rates must persist, for at least 40% of the light period to balance a 12-h nocturnal respiration (Zotz & Winter 1994; Zotz *et al*., 2003). Consequently, photosynthesis needs to persist at maximum rates for more than 90% of the day to achieve a positive carbon balance for a temperature increase of 3°C, this clearly not feasible naturally where photosynthesis persists for only 30–80% of the light period, and at mostly suboptimal rates (Lange *et al*., 2004). Such negative effects of warming on lichen carbon balance may at least be partly offset by increases in atmospheric CO_2 levels. However, the inability of lichens to regulate water loss limits their potential responses to atmospheric CO_2 compared to vascular plants.

In terrestrial bryophytes, it has been proposed that the stimulating effect of higher atmospheric CO_2 levels may be limited, because their close proximity to the respiring soil already exposes them to increased CO_2 levels (DeLucia *et al*., 2003). This may also apply to those epiphytic lichens that grow closely attached to canopy soil or directly on living branches. For such species, increased respiration of the substrate due to higher temperatures may provide more additional CO_2 than increased atmospheric levels (Sveinbjörnsson & Oechel, 1992; Tuba *et al*., 1999). However, generally, such epiphytes are much better coupled to the atmosphere than terrestrial species, so that global atmospheric CO_2 levels can certainly be of influence. An additional advantage of higher CO_2 levels under a warming scenario is that the temperature optimum for net photosynthesis is shifted to higher temperatures (Sveinbjörnsson & Oechel, 1992). Light compensation points are also lowered, so that species can grow at darker microsites, where they dry out more slowly and stay active for longer. Activity time is also prolonged because net photosynthesis can take place down to lower and up to higher water contents (Tuba *et al*., 1999). This may be particularly beneficial for tropical lowland species, for which it has been proposed that carbon gain may become negative at higher temperatures due to lower net photosynthesis and through shorter activity times. As in vascular plants, acclimation to high CO_2 levels can cause a return to the low-CO_2 photosynthesis rates. However, species differ in their acclimatization potential, the lichen *Cladonia convoluta* for example maintaining its positive response to increased CO_2 (Tuba *et al*., 1999).

It is concluded that diminished fog and dew frequencies and elevated lichen respiration rates associated with climate warming as well as a potential climatic shift from a winter to summer rainfall pattern could negatively affect lichen carbon balances leading to a greater incidence of mortality and localized extinction especially among the investigated lichens in arid areas.

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Chapter 5

Moisture interception and elemental accumulation by lichens in a South African coastal subtropical desert

Abstract

Two dominant fruiticose lichens *Teloschistes capensis and Ramalina* sp. at a coastal site were cultivated on their gypsum substrates in automated weighing micro-lysimeters which precisely measured at hourly intervals their changes in mass due to fog and dew interception and loss from which net daily, monthly and annual amounts were computed over the 12 month monitoring period. The influence of rainfall on net amounts of fog and dew intercepted by the lichens was excluded by omitting those lysimeter records which coincided with incidences of rainfall simultaneously monitored with a tipping bucket rain gauge interfaced with a miniature data logger. Also, canopy areas of the two lichens at the coastal site were determined from overhead digital images of the ground surface using image analysis software and samples on lichen tissue were collected monthly for analysis of 11 different elemental concentrations. *T. capensis* displayed larger daily fluctuations in moisture gain and loss and intercepted greater net amounts of fog and dew annually (502.3 mm a^{-1}) than *Ramalina* sp. (372.4 mm a^{-1}) which may explain its dominance at the coastal site evident from its approximately three times larger canopy cover (961.9 cm^2 m^{-2}) than that of *Ramalina* sp. (286.9 cm^2 m^{-2}). However, net quantities of fog and dew intercepted annually by both lichens were about ten times greater than the rainfall amount of 42.6 mm a^{-1}. Measured elemental concentrations in the two lichens were in the range of background concentrations reported in other lichen species except Fe, Mg and Na concentrations which more closely approximated concentration ranges reported for lichens in other seashore ecosystems. The higher concentrations of all elements, except B and Na, measured in *T. capensis* than *Ramalina* sp. were attributed to subtle morphological and structural differences between the two species particularly *T. capensis* thinner thallus evident from its lower dry mass to canopy surface area (146.1 g m^{-2}) than that of *Ramalina* sp. (154.8 g m^{-2}). Rainfall appeared a more important source of elements than fog and dewfall as it was positively correlated with Ca, N and B concentrations in these lichens compared with fog and dewfall correspondence with only K concentrations. The high Ca concentrations present in both lichens reflected the high calcium content in the gypsum rich soils on which they occur. However, the relative influence of wet and dry atmospheric deposition and substrate on lichen elemental concentrations at the coastal site requires further study.

Key words: Fog and dew, rainfall, moisture uptake, elemental concentrations, lichens

5.1. Introduction

Fog and dew have been reported to constitute a considerable portion of the hydrological input into ecosystems in tropical montane, desert and coastal regions (Burgess & Dawson, 2004; Fischer & Still, 2007). However, the interception and utilization of fog and dew water by plant canopies remains one of the least considered aspects of vegetation studies at any scale (Yates & Hutley, 1995; Andrade, 2003). Only a few studies have examined the role of fog and dew as an ecological factor in southern African natural ecosystems. These include an unpublished study of mist interception by natural vegetation on Table Mountain in Cape Town (Snow, 1985), and several other studies emanating from the Gobabeb Training and Research Centre in the Namib Desert which have investigated fog and dew exploitation by some plants and animals (Henschel & Seely, 2005).

Lichens are known to utilize variety of water sources, such as rain, fog, dew and even elevated water vapour to activate gas exchange. There is an abundance of lichens in coastal deserts where rainfall is minimal and sporadic, but where fog, dew, and elevated night time humidity occur frequently (Kappen, 1988). The utilization of water vapour alone by lichens as a moisture source is remarkable (Butin, 1954; Lange & Bertsch, 1965). This feature and the capacity of lichens to become metabolically active after moistening by fog and dew explains why lichens are successful colonizers of world deserts as they do not rely entirely on infrequent rainfall events (Matthes-Sears & Nash, 1986). This evident from reports that in southern African coastal deserts the lichen *Teloschistes capensis* is able to collect sufficient fog and early morning dewfall to sustain positive net photosynthesis for considerable portion of the day (Lange *et al*., 1990). Dew and fog also favour lichen productivity in other climates such as alpine, Mediterranean and temperate climate regions (Nash, 2008), the captured dew and fog frequently richer in nutrients than rain (Nash, 2008). In interior arid and semi-arid regions, lichens occur commonly as part of the biological crusts that are particularly extensive on undisturbed soils. These crusts not only intercept precipitation, but also facilitate infiltration of water into the soil which, in the absence of these cryptogams, frequently develops an impervious calcium carbonate layer at or near the soil surface (Harper & Marble, 1988).

A variety of techniques have been applied to quantify the amount and frequency of moisture deposited by fog and dew. These include both direct systems such as leaf wetness resistance sensors, weighing lysimeters and indirect systems using stem flow sensors, stem microvariation sensors (dendrometers) and water isotopes (Noffsinger, 1965; Agam & Berliner, 2006). Leaf wetness resistance sensors comprising rectangular epoxy-fiberglass printed circuit boards etched with a grid network of gold-copper lines (Scherm & Van Bruggen, 1993; Kidron, 2000) are widely used. These are relatively simple to install but only provide a means of detecting the frequency and duration of fog and dew and not the total amounts deposited (Agam & Berliner, 2006). More recently, portable weighing micro-lysimeters, originally used for quantification of evapo-transpiration (Allen *et al*., 1991; Johnson & Odin, 1978; Evett, 1995; Marek *et al*., 2004; Starr *et al*., 2004; Yunusa *et al*., 2004), have been developed that allow for automated recording of fog and dew accumulation and evaporation from soil surfaces (Kidron, 1998, 2000; Heusinkveld *et al*., 2006). These have been successfully applied in measuring dew deposition in Negev Desert from which simple physical models simulating the dew deposition and evaporation have been developed (Jacobs *et al*., 1999).

The accumulation of elements by lichens through wet and dry atmospheric deposition and from their substrates (Nash, 1996) mostly exceeds their physiological requirements (Nash, 2008), which makes them useful biomonitors of the environment (Puckett, 1988; Garty, 2001). Wet deposition of elements by fog and dew is often more important than that of intermittent rainfall events as it contains higher undiluted elemental concentrations (Nash, 2008). Dry deposition of elements is by sedimentation, impaction, and gaseous absorption (Knops *et al*., 1991). Elemental accumulation from substrates has been studied extensively in lichens (Nieboer *et al*., 1978; Prussia & Killingbeck, 1991). Soil particles are readily incorporated into intracellular spaces within lichen thalli as their surface characteristics, *i.e.* incidence of cilia, pits and isidia which determine the efficiency of particle entrapment (Puckett & Finegan, 1980), assist in the absorption of high concentrations of Al, Fe, Sc, Ti, and other elements of lithic origin (Nash, 2008). Also, lichen morphological and structural features determine the efficiency of elemental accumulation (Chiarenzelli *et al*., 1977; Clair *et al*., 2002) with several reports of foliose lichens with thin flat thalli, which provide a high ratio of surface area to dry weight (Nieboer *et al*., 1972), being more effective at accumulating elements in airborne particles than fruticose lichens (Lawrey & Hale, 1981; Gough *et al*., 1998; Glenn *et al*., 1995; Garty, 2001). These elemental accumulations play a crucial role in ecosystems by incorporating atmospheric nitrogen fixed by photobionts and other elements into nutrient poor soils (Kallio, 1975; Crittenden, 1983; Nash 1996; Longton, 1997), and by contributing to nutrient cycling (Crittenden, 1983; Crittenden, 1989; Nash, 1996; Kielland, 1997; Longton, 1997), improving seedling establishment (Brown & Mikola, 1974; Kershaw, 1985) and acting as carbon sinks (Nash, 1996; Lange *et al*., 1998).

An astonishing phenomenon of coastal subtropical deserts, especially the hyper arid Atacama and Namib, is their exceptionally high lichen biodiversity. In the Namib Desert, lichens occur so frequently that they dominate the floral landscape. Mattick (1970) defined such areas as “lichen fields”, eight of which occur between the Kuiseb and Ugab rivers (Schieferstein & Loris, 1992). These lichen fields are dominated by the fruticose lichen

Teloschistes capensis which forms orange coloured mats of high biomass (Lalley & Vlies, 2006). The largest of these lichen fields which occurs at Alexander Bay comprises thirty-one lichens species (Jürgens & Niebel-Lohmann, 1995). Two dominant lichen species are clearly visible as a well-developed, striking upslope zonation. The upper parts of the slopes, characterized by gypsum-rich topsoil, are dominated by the above mentioned orange coloured, fruticose lichen *T. capensis* which forms cushion-like tufts, 3-12 cm in height that are loosely attached to the ground (Lange *et al*., 2006). Intermingled with the *T. capensis* cushions is the irregularly branched, pale green *Ramalina* sp. whose classification is still uncertain (Zedda, pers. com.) that forms small solitary tufts that are more common at the bottom of the slopes in deeper gypsum soils (Jürgens & Niebel-Lohmann, 1995; Lange *et al*., 2006). However, there are no data on moisture interception and elemental accumulation by these two dominant lichens in this coastal subtropical desert and consequently formed the basis of this study.

5.2. Materials and methods

5.2.1. Study site and species

The study site comprised a large lichen field (28° 37'S, 16 ° 32'E) situated a few kilometers South East of the mining city of Alexander Bay 3.2 km distant from the Atlantic coast. The site has a mean annual temperature of 17.2°C and an erratic low rainfall of 39 mm per annum (1951 – 1984 average) occurring predominately in winter, this supplemented by high frequencies of fog averaging 61 days per year and most common in May late autumn (Climate of South Africa, 1986). Of the 31 lichens species recorded at this site, two dominant lichen species were selected for study, namely *Teloschistes capensis* common on slope apices, characterized by gypsum-rich topsoil, and *Ramalina* sp. more common at the bases of slope, with deeper gypsum rich soils.

5.2.2. Rainfall, fog and dewfall measurements

Rainfall amounts at the study site were monitored hourly with a tipping bucket rain gauge interfaced with a miniature data logger installed in a radiation shield (Watch Dog 450, Spectrum Technologies Inc., Plainfield, Illinois, USA). These were cross checked with those logged at the South African Weather Services meteorological station at Alexander Bay.

Fog and dew amounts intercepted by soils and *T. capensis* and *Ramalina* sp. thalli were monitored hourly with automated weighing micro-lysimeters (Figure 5.1A & B) modified from a published design (Heusinkveld *et al*., 2006). The lysimeters comprised 240 mm diameter x 35 mm deep weighing pans which straddled load cells (Model 535QD-D20-6Kg, RS485, DSEnet protocol, 0DS-Europe, Milano, Italy), manufactured without a silicon gel filler to reduce hysteresis, one of the most important characteristics of force transducers (Aydemir *et al*., 2006). The load cells were connected to programmable micro-controllers both of which were sealed inside the lysimeter housings and energised by external batteries connected to solar panels. Cylindrical soil cores of similar dimension to that of the weighing pan were carefully excavated at the study site and placed into the pans of three lysimeters. Thalli of *T. capensis* and *Ramalina* sp. of similar volume and fresh mass were placed separately into the soil bearing pans of two lysimeters, the third lysimeter pan comprising only soil. Separate samples of soil and thalli of the two species taken simultaneously were dried in a forced draft oven at 60^{o}C to a constant mass and weighed to determine the dry masses of the excavated soil cores and added lichen thalli in each lysimeter pan. Changes in soil and lichen moisture mass (measured mass minus dry mass) in the lysimeter pans due moisture gain (precipitation) or loss (evaporation and transpiration) were logged hourly by the micro-controller unit. Load cell temperatures obtained from an attached thermocouple were also simultaneously logged by the micro-controller unit. These were used to standardize measured moisture masses at 20^{o}C by applying predetermined calibration functions to correct for temperature deviations in load cell output (Figure 5.1C). The differences between the highest and lowest recorded temperature standardised moisture masses over each 24-h period provided the net masses of moisture intercepted daily exclusively by the soil controls and by the soils with the added lichen populations in the lysimeter pans (Figure 5.1D). The influence of rainfall on measured net moisture masses was excluded by omitting those lysimeter records which coincided with incidences of rainfall. Computed masses of fog and dew moisture intercepted daily by the soil cores without lichens and those gained daily by the soil cores including each of the two lichen species were converted to mm of fog and dew precipitation by dividing them by the lysimeter pan surface area.

5.2.3. Lichen cover

Three transects each comprising 6 x 1m^2 plots spaced 1.5m apart was arranged along topographical elevation gradients at the study site (Figure 5.2A). The lichen populations present in the plots (Figure 5.2B) were photographed with a high resolution 3.4 effective mega pixel (Sigma SD10) digital camera with a three-band Foveon X3 sensor (3 sensor photo detectors per pixel location).

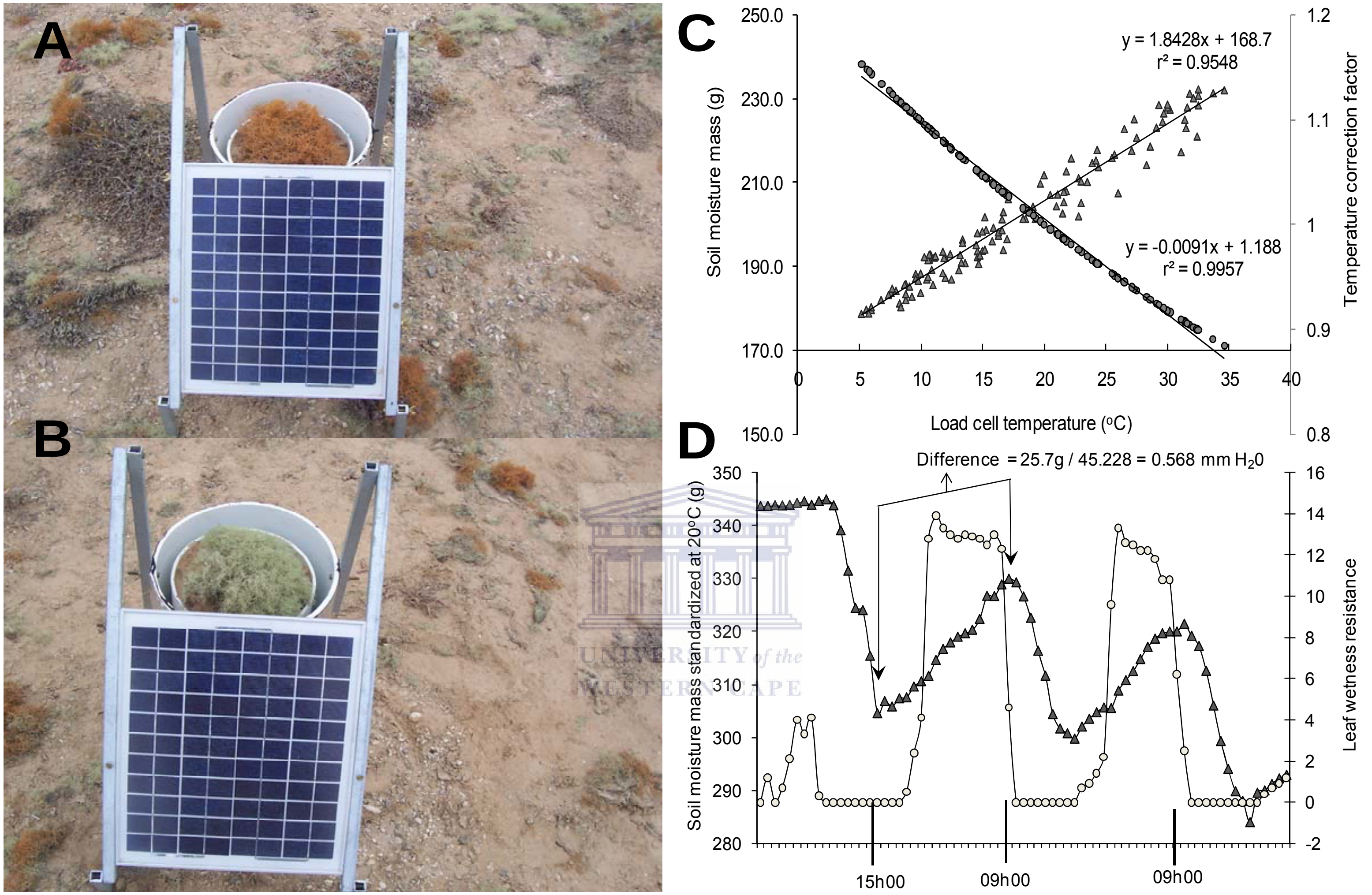

Figure 5.1. Lysimeters containing A. *T. capensis* and B. *Ramalina* sp., C. calibration curves for correction of measured soil moisture masses for temperature and D. calculation of net daily water interception from difference between maximum and minimum temperature corrected soil moisture mass over each 24-h period.

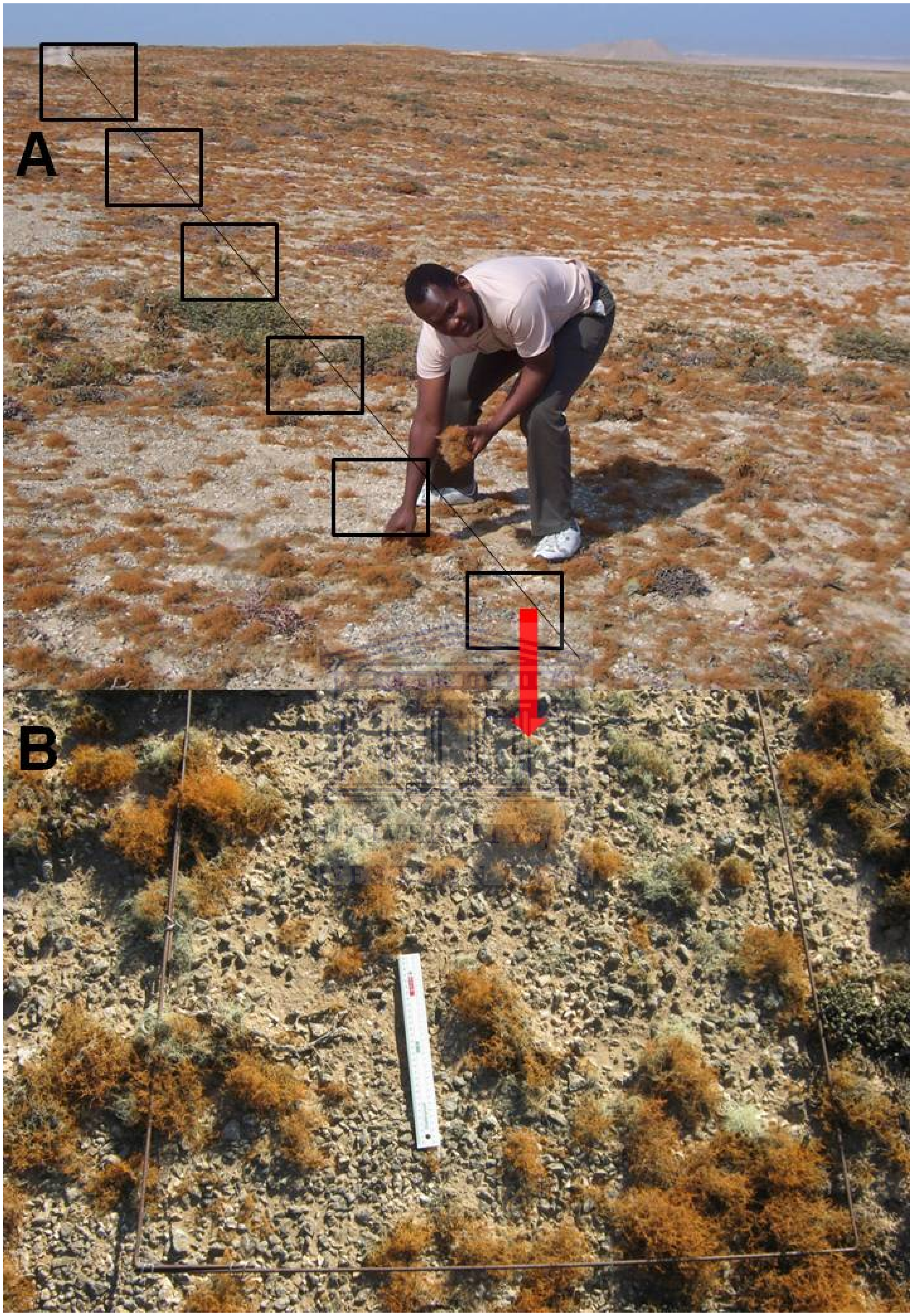

Figure 5.2. A. Transect with plots along topographical elevation gradient in the Alexander Bay lichen field, B. single 1m^2 plot containing orange coloured populations of *T. capensis* and yellowish-green coloured populations of *Ramalina* sp.

The camera was fitted with semi-wide angle lenses (24-70mm zoom, 20 mm fixed) and suspended 1.5m above ground surface on a tripod. A graduated ruler placed on the ground provided an indicator of scale. In each digital image of each plot, the canopy areas of individual thalli of both lichen species were measured with the aid of image analysis software (Image-J ver.1.34I, National Institute of Health, USA - http://rsb.info.nih.gov/ij/) and these summed for each species in each plot. In three randomly selected plots, all *T. capensis* and *Ramalina* sp. were harvested, dried in a forced draft oven at 60°C, weighed, and their total dry masses per m^2 of plot calculated.

5.2.4. Chemical analyses

Three separate batches of lichen thallus tissue were collected at random from *Ramalina* sp. and *T. capensis* populations at monthly intervals at the study site. The tissue samples were dried in a forced draft oven at 65°C to a constant mass and milled to pass a 40µm-mesh screen. One gram sub samples of dry lichen thallus tissue were ashed in a muffle furnace at temperatures not exceeding 480°C to avoid potential volatilization of Al, B, Cu, K and Mn. The ashed sub-samples were extracted in 5ml of HCl and diluted with deionized-distilled water in 50ml volumetric flasks (Campbell & Plank, 1998; Miller, 1998). Elemental concentrations in the extracted sub samples were determined with an Inductive Coupled Plasma Optical 24 Emission Spectrometer (700-ES, Varian Inc. Melbourne, Australia) according the method of Isaac & Johnson (1998). Nitrogen concentrations in 0.15 g sub samples of dry lichen thallus tissue were determined with an elemental analyser (FP-528, LECO Corporation, USA) at a combustion temperature of 900°C (Horneck & Miller, 1998).

5.3. Data synthesis and statistical analysis

Measured canopy areas, net daily fog and dew interception and elemental concentrations in the two lichen species were normally distributed. However, the experimental designs were not fully balanced due to missing or omitted measurements. Consequently a REML (residual maximum likelihood) variance components analysis was used to test for differences in canopy area between lichen species (linear mixed model) and for differences in fog and dew interception and tissue elemental concentrations between lichen species and months (repeated measures mixed model) using the Wald χ^2 statistic generated by the REML (GENSTAT Discovery Edition 3, VSL Lty, UK). In the linear mixed model lichen species were fitted in the fixed model and replicated plots in the random model. In repeated measures mixed model, lichen species were fitted in the fixed model and replicated months in the random model. Differences exceeding twice the average standard error of differences were used to separate significantly different treatment means at $P \leq 0.05$. This based on the fact that for a normal distribution from REML estimates, the 5% two-sided critical value is two.

Pearson correlations and a student's t-test tested for significant correspondence between *Ramalina* sp. and *T. capensis* tissue elemental accumulations, fog and dew precipitation amounts and rainfall amounts.

5.4. Results

5.4.1. Lichen cover and rainfall, fog and dew interception

Lichen canopy cover differed significantly ($P \leq 0.01$) between species (Table 5.3) with that (286.9 $cm^2\ m^{-2}$) of *Ramalina* sp. about three times smaller than that (961.9 $cm^2\ m^{-2}$) of *T. capensis* (Figure 5.3). Dry mass per unit area of *Ramalina* sp. (154.8 g m^{-2}) was slightly greater than that of *T. capensis* (146.1g m^{-2})

Over an entire year, the net quantity of fog and dew intercepted by the soil (507.7 mm a^{-1}) and that intercepted by the soil including the lichen *T. capensis* (502.3 mm a^{-1}) and the lichen *Ramalina* sp. (372.4 mm a^{-1}) were about ten times greater than the rainfall amount of 42.6 mm a^{-1}. The highest fog and dew precipitation amounts were observed during winter between June and July and coincided with a rainfall peak during the same period (Figure 5.3).

On both daily (Figure 5.3) and monthly and annual bases (Figure 5.4), the net quantities of fog and dew precipitation intercepted by the soil including either *Ramalina* sp. or *T. capensis* were generally smaller than that intercepted by the soil only, except during sporadic rainfall events when the net quantities of total precipitation (fog, dew and rainfall) intercepted by the soil including the two lichen species exceeded that intercepted by the soil only by several orders of magnitude (Figure 5.3).

Significant ($P \leq 0.001$) monthly and lichen species differences were observed in the net quantities of fog and dew intercepted (Table 5.1). Also, there was a significant ($P \geq 0.01$) lichen species *versus* month interaction on net quantities of fog and dew intercepted (Table 5.1), the amounts of fog and dew intercepted differing in magnitude between the two lichen species monthly (Figure 5.3).

5.4.2. Lichen elemental concentrations

All 11 elemental concentrations in lichen tissues differed significantly ($P \leq 0.01$) between species and months with exception of N, P and Cu (Table 5.2). Elemental concentrations were significantly ($P \leq 0.05$) higher in *T. capensis* than *Ramalina* sp. tissues, with exception of B and Na where the converse was apparent. Also, there were significant ($P \leq 0.05$) species *versus* month interactions on lichen tissue elemental concentrations, with the exception of Mg, P and Mn, with differences in tissue elemental concentrations between the two lichen species varying in magnitude monthly (Figures 5.5 to 5.7).

Fog and dew precipitation amounts were positively ($P \leq 0.05$) correlated with K concentrations in *Ramalina* sp. and *T. capensis* and negatively ($P \leq 0.05$) correlated with Fe concentrations in *T. capensis* (Table 5.3). Rainfall amounts were positively ($P \leq 0.05$) correlated with Ca concentrations in both *Ramalina* sp. and *T. capensis,* and N and B concentrations in *Ramalina* sp. but negatively ($P \leq 0.05$) correlated with Na and Cu tissue concentrations in *T. capensis* and P concentrations in *Ramalina* sp. (Table 5.3).

Table 5.1. Wald statistics derived from REML which tested for differences in canopy cover (linear mixed model) between lichen species and net fog and dew water interception (repeated measures mixed model) between lichen species in different months and their interaction. Values presented in bold significant at *P <0.05, **P <0.01, ***P <0.001.

		Wald χ^2 statistic	
Factor	df	Canopy cover	Net daily fog and dew interception
Main effects			
Month	11	-	**44.5*** **
Species	1	**8.20** **	**61.9*** **
2-way interactions			
Month x Species	11	-	**29.3** **

Table 5.2. Wald statistics derived from REML (repeated measures mixed model) which tested for differences in elemental concentrations between lichen species and months and their interactions. Values presented in bold significant at *P <0.05, **P <0.01, ***P <0.001.

				Wald χ^2 statistic			
Macro-elements	df	Ca	K	Mg	Na	N	**P**
Main effects							
Month	11	**113.2*** **	**651.3*** **	**142.3*** **	**306.1*** **	**129.1*** **	**71.1*** **
Species	1	**104.7*** **	**68.0*** **	**24.4*** **	**54.5*** **	0.7	0.2
2-way interactions							
Month x Species	11	**57.7*** **	**54.5*** **	18.2	**27.4** **	**20.6* **	15.0
				Wald χ^2 statistic			
Micro-elements	df	Fe	B	Cu	Mn	Zn	-
Main effects							
Month	11	**189.6*** **	**93.1*** **	**149.9*** **	**67.3*** **	**96.8*** **	
Species	1	**79.9*** **	**13.0*** **	0.0	**25.5*** **	**167.4*** **	
2-way interactions							
Month x Species	11	**68.2*** **	**24.5* **	**28.8** **	16.4	**70.8*** **	

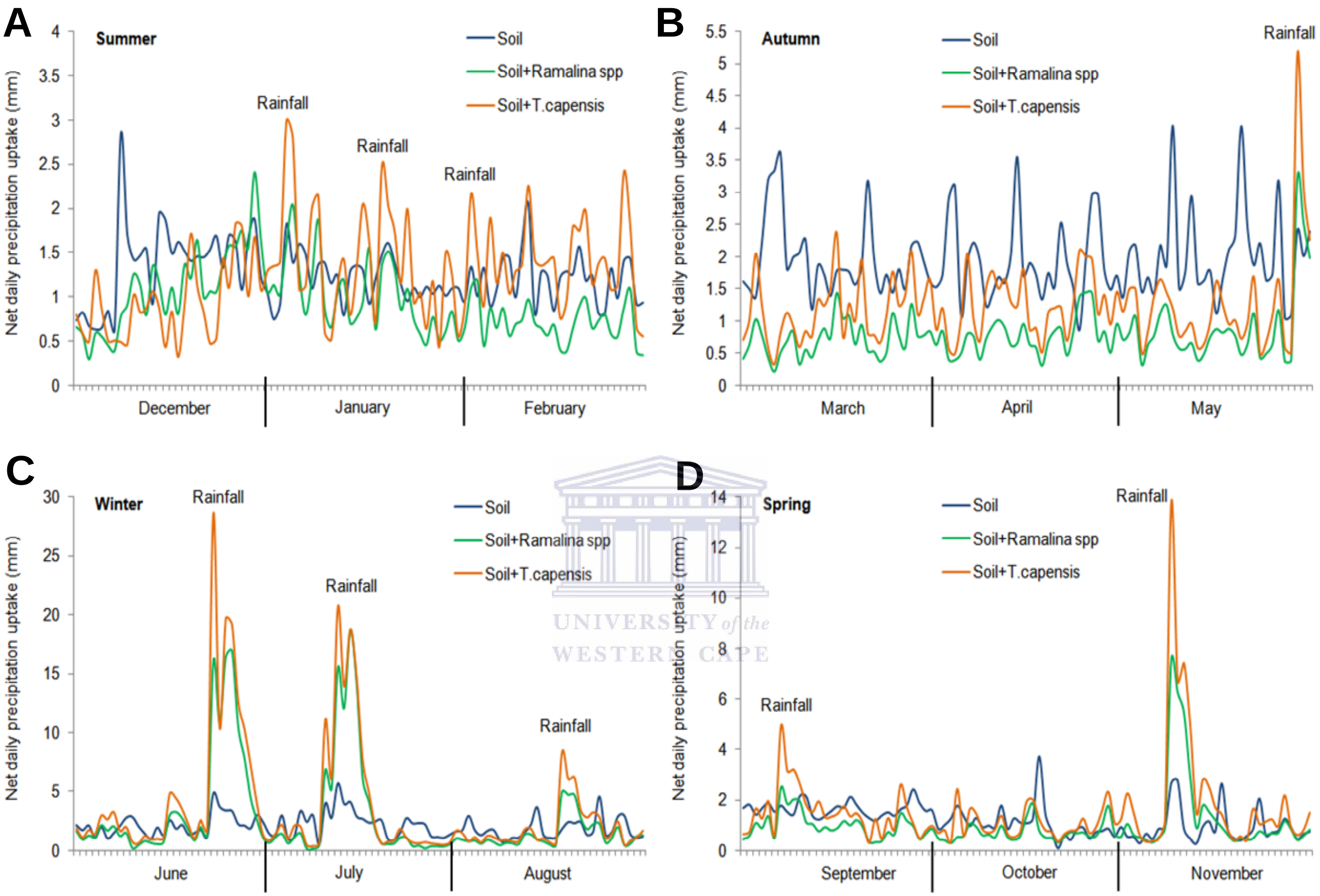

Figure 5.3. Net daily interception of fog and dew precipitation and sporadic rainfall by the soil and by the soil with the lichens *Ramalina* sp. and *T. capensis* at Alexander Bay in A. Summer, B. Autumn, C. Winter and D. Spring.

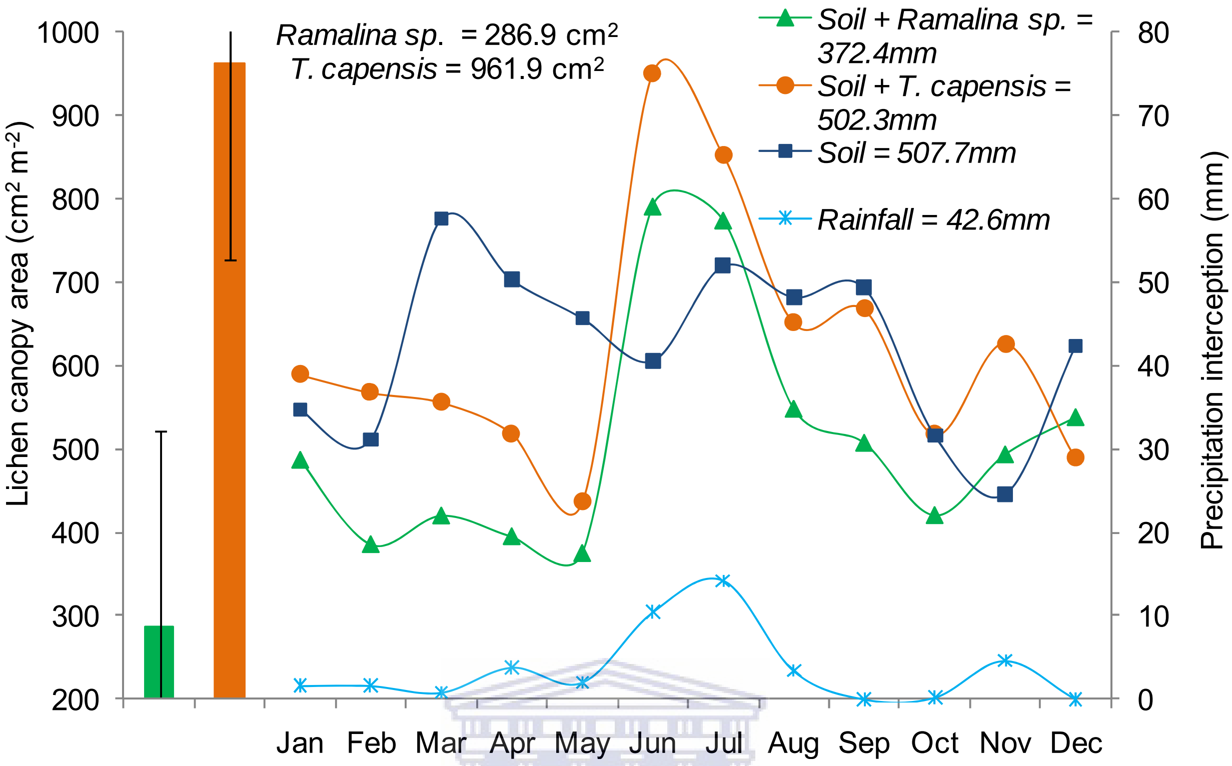

Figure 5.4. Measured canopy areas of the lichens *Ramalina* sp. and *T. capensis*, annual rainfall amounts and annual fog and dew precipitation amounts intercepted by soils and by soils with added lichen species.

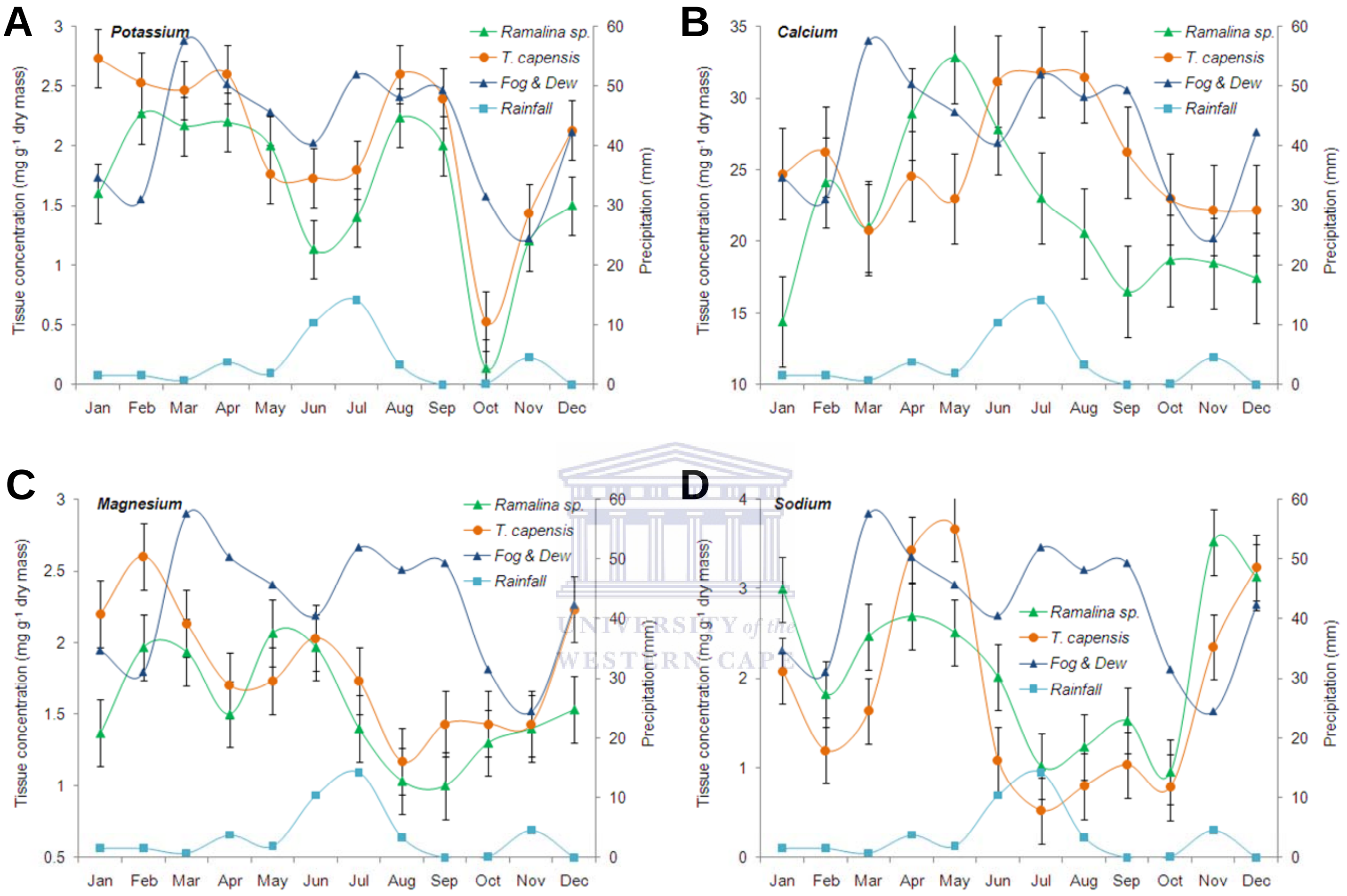

Figure 5.5. Monthly A. potassium, B. calcium, C. magnesium and D. sodium concentrations in *Ramalina* sp. and *T. capensis* thalli and fog/dew and rainfall precipitation amounts. Average standard errors of differences shown by bars.

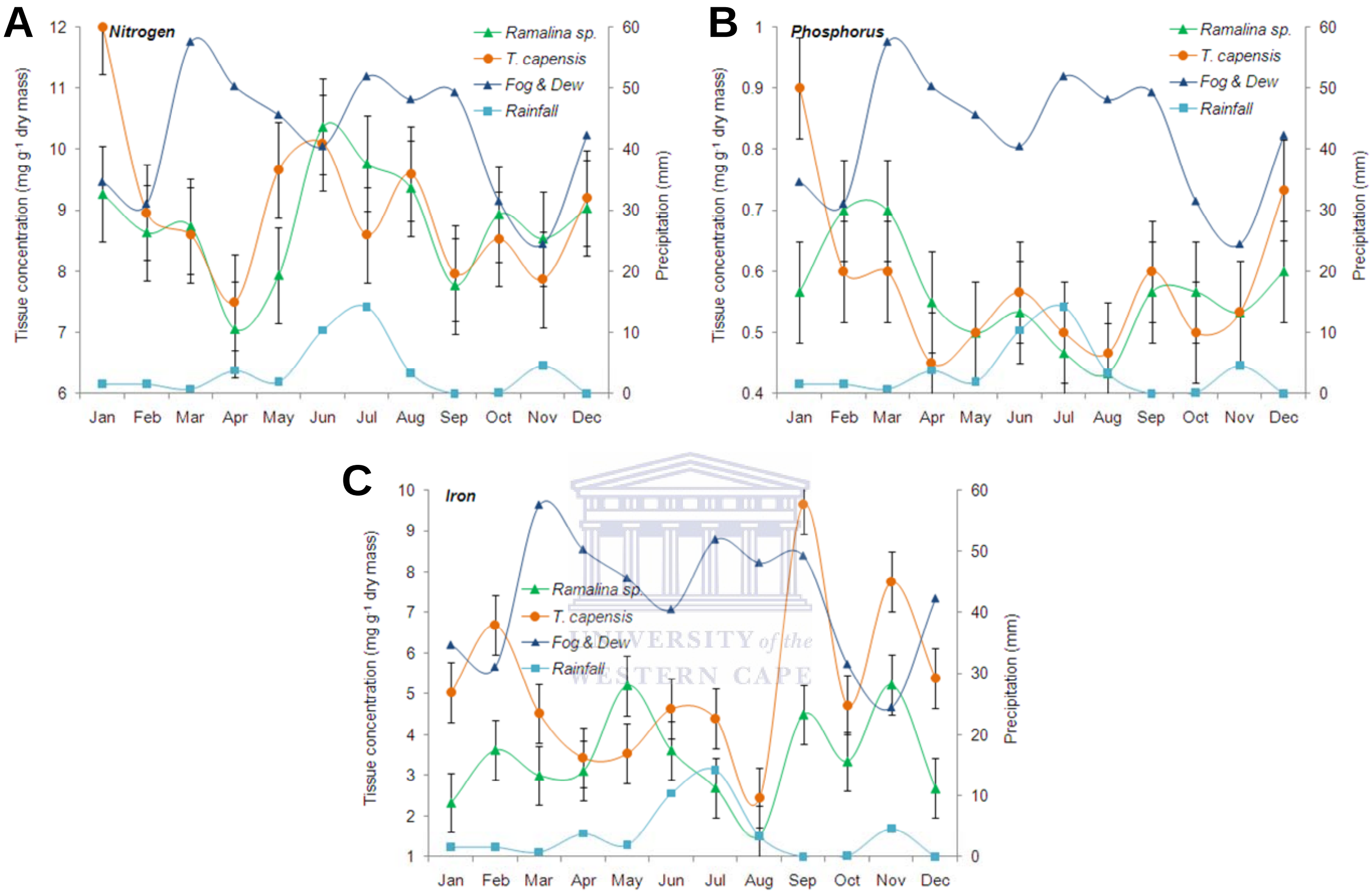

Figure 5.6. Monthly A. nitrogen, B. phosphorus and C. iron concentrations in *Ramalina* sp. and *T. capensis* thalli and fog/dew and rainfall precipitation amounts. Average standard errors of differences shown by bars.

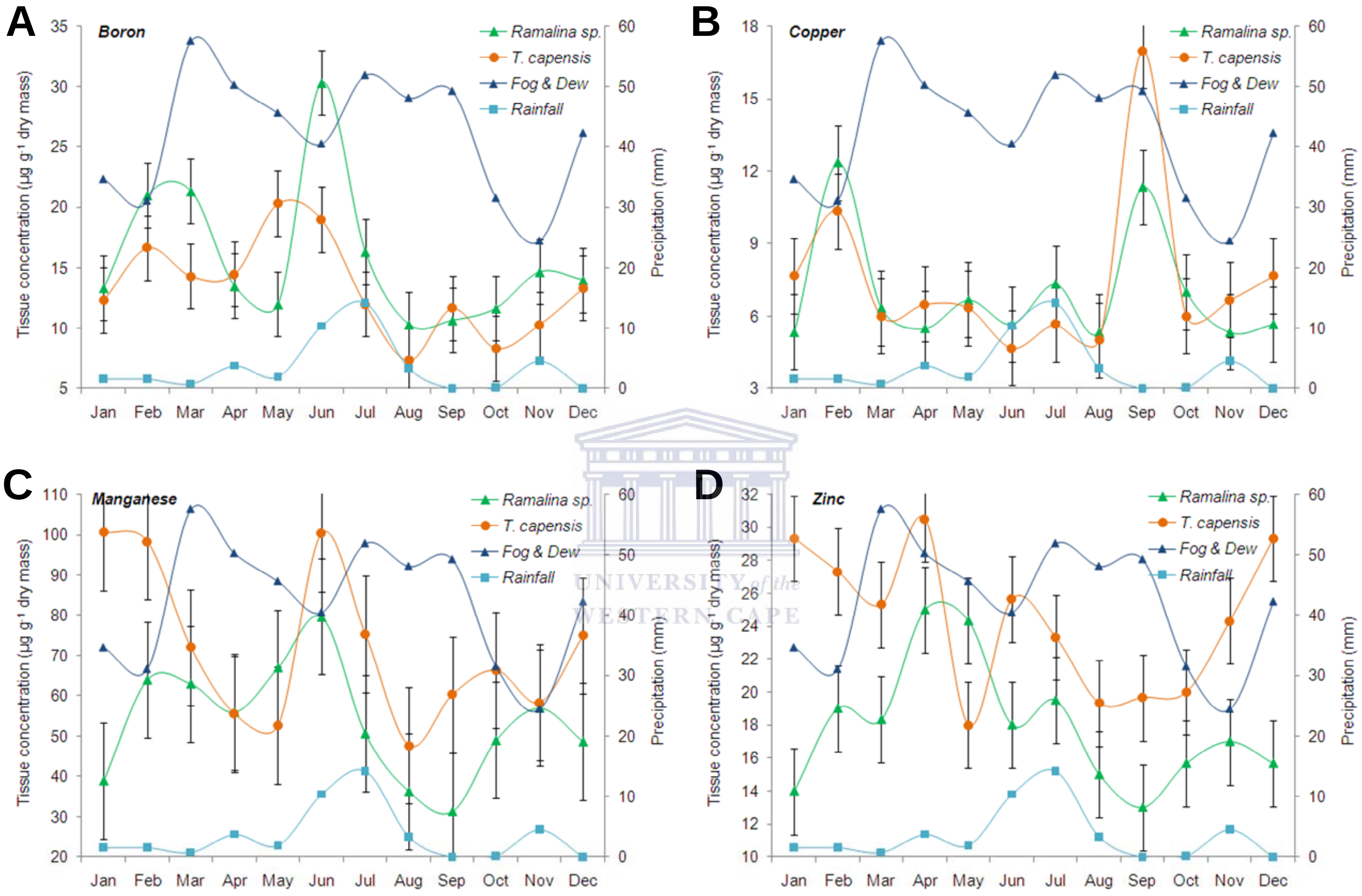

Figure 5.7. Monthly A. boron, B. copper, C. manganese and D. zinc concentrations in *Ramalina* sp. and *T. capensis* thalli and fog/dew and rainfall precipitation amounts. Average standard errors of differences shown by bars.

5.5. Discussion

The lower dry mass to canopy surface area of *T. capensis* (146.1 g m^{-2}) than that of *Ramalina* sp. (154.8 g m^{-2}) implied a thinner thallus. This reflected in the larger daily fluctuations in moisture gain and loss displayed by *T. capensis* than by *Ramalina* sp. and also by the substantially greater net amounts of fog and dew intercepted annually by *T. capensis* (502.3 mm a^{-1}) than *Ramalina* sp. (372.4 mm a^{-1}). These findings concur with reports that highly, branched, fruticose lichens which have a high a surface area to volume ratio display more rapid diurnal drying and wetting patterns than lichens with lower surface area to volume ratios (Nash, 2008).

T. capensis greater capacity to retain intercepted fog and dew may also explain its dominance at the study site, this evident from its approximately three times larger canopy cover (961.9 cm^{2} m^{-2}) than that of *Ramalina* sp. (286.9 cm^{2} m^{-2}). In fact, *T. capensis* structural and morphological characteristics are particularly suitable for survival in fog deserts (Rundel, 1978; Kappen, 1988). Its fruticose growth form exposes large areas of terete, thin branches arranged perpendicular to moisture laden winds with cilia and microscopic hair-like fibrils covering the branches further increasing the thallus surface area to promote water absorption (Kärnefelt, 1989).

Most elemental concentrations measured in *T. capensis* and *Ramalina* sp. were in the range of background concentrations reported in other lichen species (Table 5.4). However, Fe, Mg and Na concentrations in *T. capensis* and *Ramalina* sp. were exceptions as these more closely approximated concentration ranges reported for lichens in other seashore ecosystems (Table 5.4.). The higher concentrations of all elements, except B and Na, measured in *T. capensis* than *Ramalina* sp. concurred with results of other studies which have demonstrated that different lichen species from the same location often contain contrasting elemental concentrations (Garty, 2001).

Trace elemental concentrations in particular have been reported to exhibit high variability between different lichen species growing on similar substrates (Ahmadjian & Hale, 1973). However, this was not clearly apparent in this study, with the possible exception of Mn and Fe whose concentration ranges in *Ramalina* sp. were substantially larger than those in *T. capensis* (Table 5.4). The generally higher elemental concentrations measured in *T. capensis* than *Ramalina* sp. were attributed to subtle morphological and structural differences between these two species (Chiarenzelli *et al*., 1977; Clair *et al*., 2002), particularly *T. capensis* thinner thallus evident from its smaller dry mass to canopy area surface area.

Table 5.3. Pearson correlation coefficients (r) and t-statistics (33 degrees of freedom) which tested for correspondence between *Ramalina* sp. and *T. capensis* tissue elemental concentrations, rainfall and fog and dew water amounts. Significant at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001.

Species	**Ca**	**K**	**Mg**	**Na**	**N**	**P**
Fog and dewfall						
***Ramalina* sp.**						
r	0.2022	**0.4777**	0.0071	-0.2501	-0.0806	-0.0812
t-statistic	t = 1.1863	**t = 3.1232****	t = 0.0406	t = -1.4840	t = -0.4646	t = -0.4683
T. capensis						
r	0.1789	**0.3729**	-0.0822	-0.0325	-0.0971	-0.1415
t-statistic	t = 1.0448	**t = 2.3089***	t = -0.4740	t = -0.1868	t = -0.5602	t = -0.8210
Rainfall						
***Ramalina* sp.**						
r	**0.2901**	-0.1683	0.0822	-0.2404	**0.4812**	**-0.4049**
t-statistic	**t = 1.7413***	t = -0.9809	t = 0.4737	t = -1.4227	**t = 3.1530****	**t = 2.5437****
T. capensis						
r	**0.6128**	-0.1422	-0.0653	**-0.3261**	0.0066	-0.2133
t-statistic	**t = 4.4544*****	t = -0.8254	t = -0.3757	**t = -1.9815***	t = 0.0379	t = -1.2539
	Fe	**B**	**Cu**	**Mn**	**Zn**	
Fog and dewfall						
***Ramalina* sp.**						
r	-0.2746	-0.0053	-0.0293	-0.0732	0.1817	
t-statistics	t = -1.6407	t = -0.0304	t = -0.1683	t = -0.4215	t = 1.0616	
T. capensis						
r	**-0.3130**	0.1029	0.0115	-0.2133	-0.1353	
t-statistics	**t = -1.8928***	t = 0.5942	t = 0.0662	t = -1.2539	t = -0.7847	
Rainfall						
***Ramalina* sp.**						
r	-0.0814	**0.3923**	-0.1407	0.2535	0.2178	
t-statistics	t = -0.4694	**t = 2.4496****	t = -0.8163	t = 1.5052	t = 1.2817	
T. capensis						
r	-0.2168	0.1184	**-0.3665**	0.1494	0.0211	
t-statistics	t = -1.2758	t = 0.6852	**t = -2.2627***	t = 0.8682	t = 0.1215	

Table 5.4. A comparison of published background and seashore elemental concentrations in lichens with those measured in *Ramalina* sp. and *T. capensis* at Alexander Bay.

Element	Background μg g^{-1}	Reference	*T. capensis* μg g^{-1}	*Ramalina* sp. μg g^{-1}
Ca	20 - 40 000	Scotter (1972); Kuziel (1973); Kovás-Láng & Verseghy (1974)	14 400 – 32 830	20 800 – 31 800
Ca seashore	40 000 – 55 000	Fletcher (1976)		
K	500 – 5 000	Scotter & Miltmore (1973); Kuziel (1973); Kovás-Láng & Verseghy (1974)	133 – 2 267	533 – 2 733
K seashore	5 000 – 9 500	Fletcher (1976)		
Mg	100 – 1 000	Tuominen & Jaakkola (1973); Scotter & Miltmore (1973)	1 000 - 2067	1 167 – 2 600
Mg seashore	1000 – 12 000	Fletcher (1976)		
Na	50 – 1 000	Tuominen & Jaakkola (1973)	953 – 3 522	526 – 3 668
Na seashore	1 000 – 6 000	Fletcher (1976)		
N	6 000 – 50 000	Syers & Iskandar (1973); Millbank & Kershaw (1973); Hitch & Millbank (1975)	7 050 – 10 367	7 500 – 12 000
P	200 – 2 000	Scotter (1972); Syers & Iskandar (1973); Lawrey & Rudolf (1975)	433 - 700	450 - 900
Fe	50 – 1 600	Lounamaa (1965); Tomassini *et al*. (1976); Nieboer *et al*. (1977)	1 529 - 5220	2 450 – 9 649
Fe seashore	2 000 – 30 000	Fletcher (1976)		
Cu	≤ 1 - 50	Scotter & Miltmore (1973); Tomassini *et al*. (1976); Fletcher (1976)	5 -12	5 - 17
Mn	10 – 130	Lounamaa (1965); Lawrey & Rudolph (1975)	31 - 80	48 - 101
Mn seashore	300 - 350	Fletcher (1976)		
Zn	30 - 500	Leroy & Koksoy (1962); Lounamaa (1965); Nash (1975)	13 - 25	18 - 31
B	17	Nash & Somerfield (1981)	10 – 30	7 - 20

This premise concurring with reported differences in Pb and Fe concentrations in the Antarctic lichens *Umblilicaria decussate* and *U. aprina,* the higher concentrations measured in *U. decussate* also attributed to its smaller dry weight to canopy area and thinner thallus than that of *U. aprina* (Upreti & Pandey, 1994).

Rainfall appeared a slightly more important source of elements for *T. capensis* and *Ramalina* sp. than fog and dewfall as it was positively correlated with Ca, N and B concentrations in these lichens compared with fog and dewfall's correspondence with only K concentration in these lichens. In fact, rainfall, fog and dewfall are all considered important sources of elements for lichens, since leaching of inorganic solutes such as K, Ca, Mg and Mn from soils occurs by the action of rain, dew and fog (Tukey, 1970; Bosserman & Hagner, 1981). The relatively high Ca concentrations measured in *T. capensis* and *Ramalina* sp. seemingly reflected the high calcium content of the gypsum rich soils on which they occurred. This feature was also reported in the lichen *Acarospora clauzadeana* on gypsum substrates (Nash, 2008). The relatively high N concentrations measured in *T. capensis* and *Ramalina* sp. concurred with reports that in desert ecosystems lichens accumulate high levels of nitrogenous compounds (Shields *et al*., 1957). However, it was unclear whether this accumulation of N by *T. capensis* and *Ramalina* sp. was a consequence of atmospheric uptake ammonium ions dissolved in rainfall, fog or dewfall or a consequence of N fixation by algal photobionts (Pike, 1978), a significant component of the nitrogen economy of ecosystems (Kallio, 1973; Alexander & Schell, 1973; Nieboer *et al*., 1978). Indeed atmospheric uptake is considered the dominant source of elements for many lichens (Brodo, 1973; Touminen & Jaakkola, 1973), especially epiphytic lichens whose mycobionts possess higher cation exchange capacities than epilithic lichens allowing them to obtain nourishment from nutrient-poor environments with sporadic precipitation (Clymo, 1963; Touminen & Jaakkola, 1973). In fact, epiphytic lichens, such as *Usnea* which are capable of rapid water uptake receive significant quantities of elements from pulses of rainfall and dewfall (Brodo, 1973; Kappen, 1973; Bosserman & Hagner, 1981), this due to the ion exchange characteristics of fungal and algal cell walls which allow effective and rapid uptake of elements from rainfall and dewfall (Brown, 1976; Puckett, 1976). In this study, Na concentrations measured in *T. capensis* and *Ramalina* sp. were in the mid range of those reported for lichens in other seashore ecosystems (Fletcher, 1976). This feature, and the high Na concentrations reported in southern African west coast fog (Oliver, 2002) pointed to oceanic origins of precipitation of which Na is the dominant cation (Rykiel, 1977). Other major wet fall elements are K and Ca, but their measured concentrations in both *T. capensis* and *Ramalina* sp. were below the concentration ranges reported for lichens in other seashore ecosystems and seemingly did not reflect oceanic origins of precipitation. The positive correspondence found between K concentrations in *T. capensis* and *Ramalina* sp. and fog and dew precipitation amounts, and the elevated K concentrations reported in lichens from high elevation sites that receive large amounts fog (Bennett & Benson, 2005), implied that fog and dew was the predominant source of this element for lichens at the study site.

Other potential sources of elements for lichens at the study site were dry atmospheric deposition of dust and other materials suspended in intermittent strong offshore berg winds and substrate mineralization by the lichens (Bosserman & Hagner, 1981) through secretion of extracellular enzymes (Nieboer *et al*., 1978). A close correspondence has been reported between elemental amounts in the lichens *Lecanora gangaloides* and *Parmelia omphalodes* and materials deposited from the atmosphere (Jenkins & Davies, 1966). Also, the higher P, Si, K, Fe, Al, Zn concentrations measured in *Parmelia* and *Usnea* than their substrates (Bosserman & Hagner, 1981) and the reported absence of any linear correlation between Al, Fe and Ti concentrations in *Parmelia sulcata* and those in their substrates (Conti & Cecchetti, 2001) do point to dry atmospheric deposition as a supplemental source of these elements. In fact, soil and dust particles are readily incorporated into intracellular spaces of lichen thalii that result in the accumulation of Al, Fe, Sc, Ti, and other elements of lithic origin (Nash, 2008). However further studies are required to determine the relative influence of wet and dry atmospheric deposition and substrate on lichen elemental concentrations at the study site.

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Chapter 6

Conclusions and recommendations

Temperatures limiting for lichen photosynthesis in this study were lower than those limiting for lichen respiration which is in agreement with several other published reports of a greater sensitivity of lichen photosynthesis than respiration to heat stress (Macfarlane & Kershaw, 1978). Consequently future studies should concentrate on determing photosynthetic sensitivities of lichens from a wide range of different environments so species highly sensitive to elevated temperatures can be identified as early warning indicators of climate warming.

Laboratory derived temperatures limiting for lichen photosynthesis in this study were much higher than those determined under natural conditions. Consequently future studies should concentrate on determing photosynthetic sensitivities of lichens in their natural environments.

Photosynthetic quantum yields of lichens from hot arid sites sites were more sensitive to temperature increases than those from cool motane. Consequently, future studies should concentrate on monitoring changes in distribution, photosynthesis and growth of lichens from high elevation sites as early warning indicators of climate warming. In this regard, more extensive lichen distribution records are required so changes in lichen diversity and distribution can be linked to changes in climate as reported in several European lichen species (Aptroot & van Herk, 2007). Also, future studies should concentrate in measuring changes in carbon balance of lichens from high elevation sites. The reason being that higher night temperatures associated with climate warming enhance carbon loss due to elevated respiration rates and high day temperatures promote more rapid dehydration of lichen thalli restricting the time available for carbon gain by photosynthesis (Zotz, 1999) leading to increased incidences of mortality in lichens already living close to the edge of their physiological abilities. Futhermore, changes in lichen growth as an indicator of climate warming should also be consistently monitored in lichens from high elevation sites, at least over the long term, since over the short term changes in lichen growth in response to elevated temperatures are difficult to detect as observed in this study. The reason being that lichens grow very slowly, with reported radial growth increments for lichen thalli in general of between 1 mm to 10 mm per year (Kershaw & Alvin, 1963) with even smaller reported radial growth increments of 0.5mm to 5.0 mm per year reported for British crustose and foliose lichens (Hawksworth & Rose, 1976). However, over the long term, statistically significant reductions in lichen cover and diversity have been reported in the Alaskan arctic tundra lichens exposed to experimentally elevated temperatures for 8 years (Wahren *et al*., 2005).

Depite larger quantities of moisture contributed by fog and dew than rainfall and reports that wet deposition by fog and dew is a more important source of elements than that of rainfall in coastal fog deserts, rainfall appeared a slightly more important source of elements for *T*. *capensis* and *Ramalina* sp in this study than other sources of precipitation. However, it is unclear whether the elements present in these two lichens were absorbed directly from rainfall or indirectly from rain wetted substrates. Consequently, the relative influence of wet and dry atmospheric deposition and substrate on lichen elemental concentrations in coastal fog dererts requires further study.

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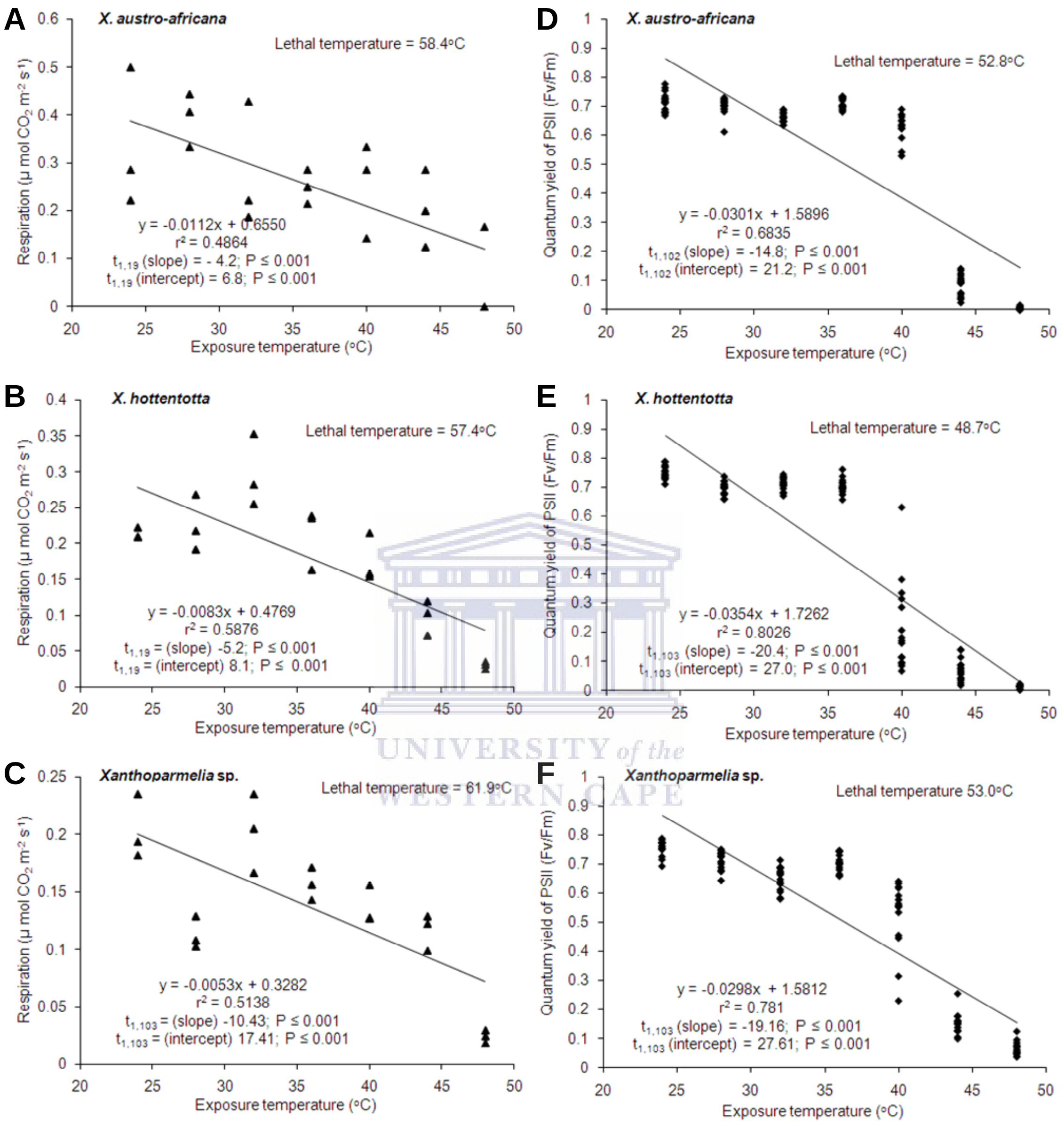
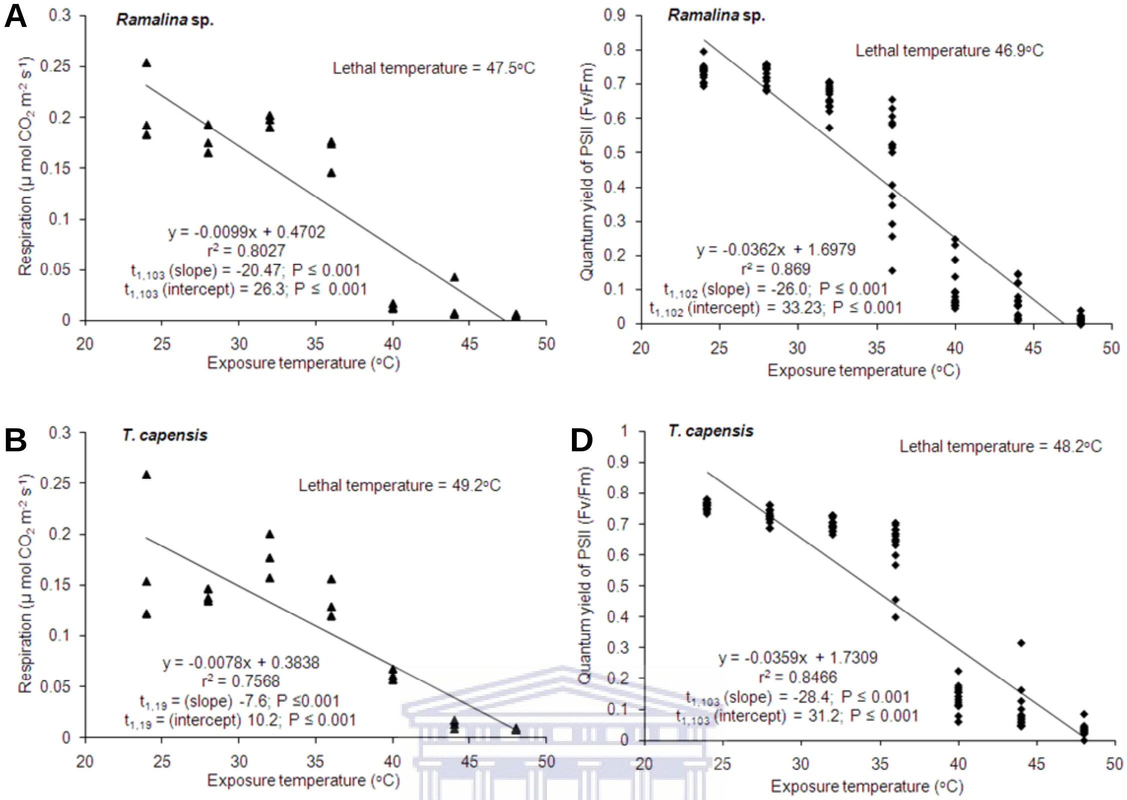
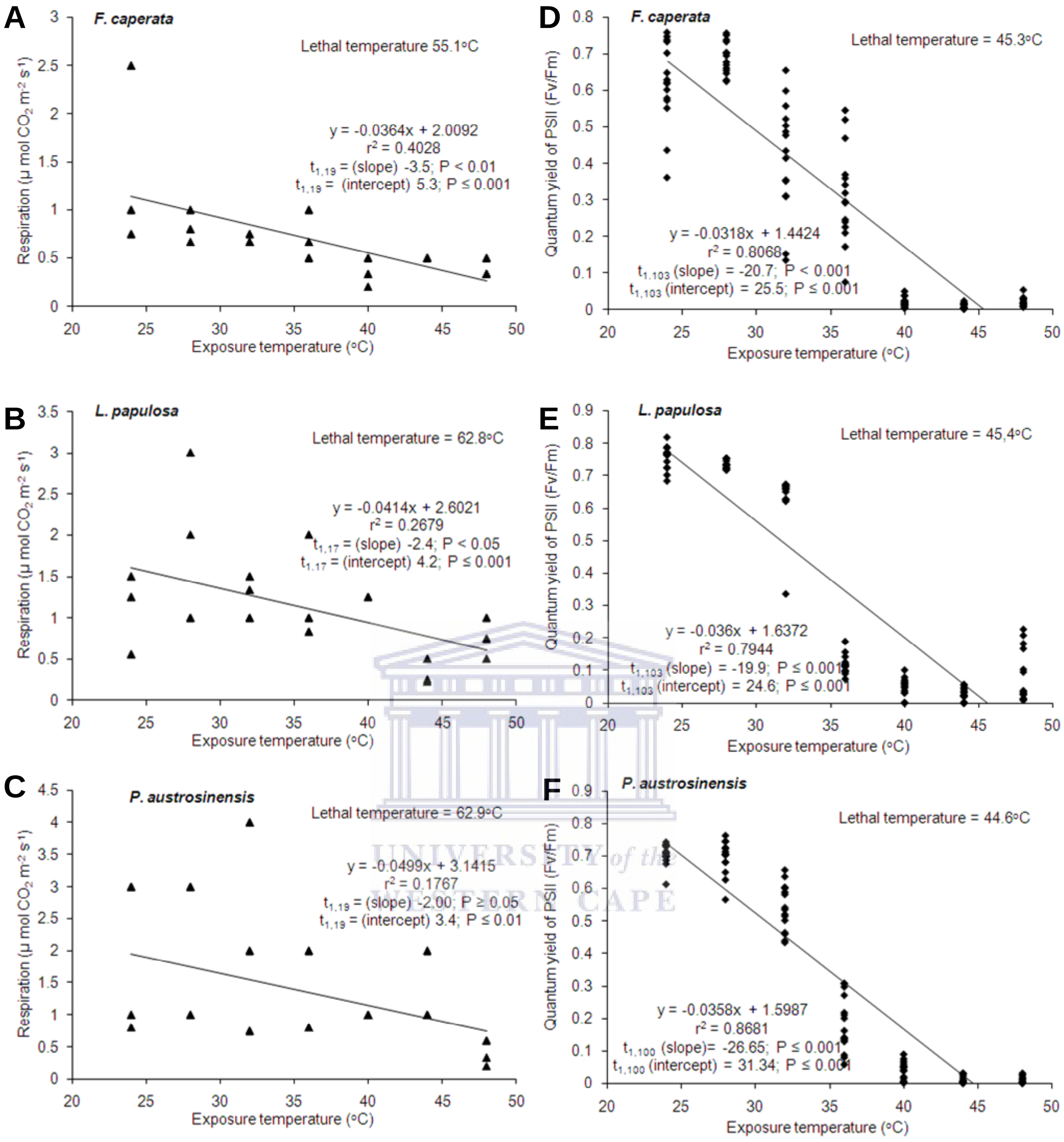
Appendices to Chapter 3



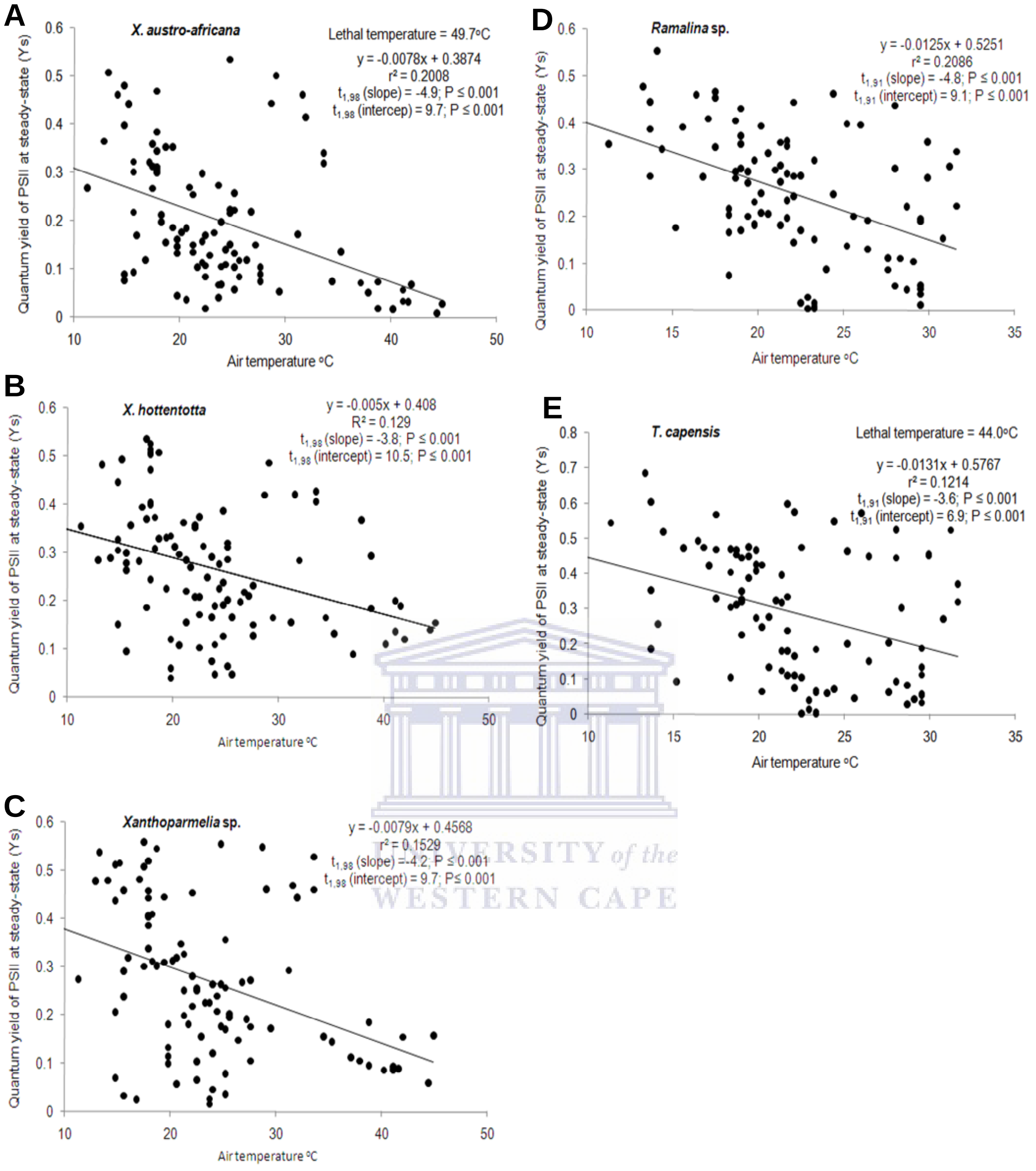
Appendix 3.1. Least square regressions of laboratory exposure temperature against respiration (A to C) and maximum quantum yield of PSII (D to F) for 4 lichen species from the hot arid site



Appendix 3.2. Least square regressions of laboratory exposure temperature against respiration (A & B) and maximum quantum yield of PSII (C & D) for 2 lichen species from the warm coastal site



Appendix 3.3. Least square regressions of laboratory exposure temperature against respiration (A to C) and maximum quantum yield of PSII (D to F) for 3 lichen species from the cool montane site



Appendix 3.4. Least square regressions of field exposure temperature against effective quantum yield of PSII at a steady state for 6 lichen species from the hot arid site (A to C) and the warm coastal site (D & E)