

Lethal effects of experimental warming approximating a future climate scenario on southern African quartz-field succulents: a pilot study

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Summary

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- Here we examine the response of succulents in a global biodiversity hot spot to experimental warming consistent with a future African climate scenario.
- Passive daytime warming (averaging 5.5°C above ambient) of the natural vegetation was achieved with 18 transparent hexagonal open-top chamber arrays randomized in three different quartz-field communities.
- After 4-months summer treatment, the specialized-dwarf and shrubby succulents displayed between 2.1 and 4.9 times greater plant and canopy mortalities in the open-top chambers than in the control plots. Those surviving in cooler ventilated areas and shaded refuges in the chambers had lower starch concentrations and water contents; the shrubby succulents also exhibited diminished chlorophyll concentrations.
- It is concluded that current thermal regimes are likely to be closely proximate to tolerable extremes for many endemic succulents in the region, and that anthropogenic warming could significantly exceed their thermal thresholds. Further investigation is required to elucidate the importance of associated moisture deficits in these warming experiments, a potential consequence of supplementary (fog and dew) precipitation interception by open-top chambers and higher evaporation therein, on plant mortalities.

Key words: global warming, mortality, photosynthetic pigments, starches, succulents, sugars.

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Introduction

Changes to the global climate system are anticipated from the accumulation of CO₂ and other greenhouse gases in the atmosphere since preindustrial times. This accumulation has had a discernible influence on global temperature and is predicted to cause further warming in this century (IPCC, 2001). Direct and dramatic ecological responses to global warming are expected (Peters & Lovejoy, 1992; Thomas *et al.*, 2004), as are feedback 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; OIES, 1992). These prospects are supported by long-term monitoring studies, which indicate that recent climatic and atmospheric trends are inconsistent with past climatic variation and are already affecting the phenology, physiology and distribution of plant species (Hughes, 2000; Parmesan & Yohe, 2003). Concerns have been amplified because rates of vegetation change are expected to occur much faster than past successional processes and species dispersal rates (Pastor & Post, 1988; Overpeck *et al.*, 1991).

Various climate futures focusing on regional mean temperature and rainfall changes in different seasons have been predicted for the African continent (Hulme *et al.*, 2001). They draw

upon different draft emission scenarios prepared for the Intergovernmental Panel on Climate Change (IPCC, 2001) and have been incorporated into bioclimatic models to predict ecosystem responses to climate change (Rutherford *et al.*, 1999). The application of these models in vulnerability and adaptation assessments in a South African Country Study on Climate Change predicted future warming and aridity trends sufficient to cause large reductions in species richness in Mediterranean-climate Fynbos and Succulent Karoo biomes (Midgley *et al.*, 2002, 2003). These biodiversity changes accompanied by the displacement of the Succulent Karoo biome southward along the west-coast and interior coastal plain (Hannah *et al.*, 2002), a feature of glacial-interglacial climatic oscillations of the Pleistocene (Midgley *et al.*, 2001). The predictions concur with the purported particular sensitivity of Mediterranean-climate ecosystems globally to changes in biodiversity induced by the five major drivers of biodiversity at the global scale, with climate change rated only second to land use as the driver with the largest effect on biodiversity when all ecosystems are averaged (Sala *et al.*, 2000). They are also supported by local observations, which indicate that the population demographics of some large succulents, such as *Aloe dichotoma*, have already begun responding to anthropogenic induced climate change in a manner projected by bioclimatic models (Foden, 2002). Such changes are of concern for biodiversity conservation in the region, since both the Fynbos and Succulent Karoo biomes are characterized by exceptionally high species richness and endemism (Cowling *et al.*, 1989, 1998; Hilton-Taylor, 1996), the Succulent Karoo biome especially possessing the highest species diversity recorded for an arid vegetation type worldwide (Hilton-Taylor, 1996) and listed among 25 global biodiversity hot spots (Myers *et al.*, 2000). Despite these features, these biomes are not yet represented in a network of 32 ecosystem warming research sites currently representing Forest, Grassland, high and low latitude/altitude Tundra biomes (Rustad *et al.*, 2001).

The ability of bioclimatic models to elucidate biodiversity responses to climate change has been questioned (Woodward & Beerling, 1997), and is certainly limited by a paucity of empirical information from field and laboratory trials. Experimental tests are urgently required to validate and refine bioclimatic model extrapolations, since this remains one of the few methods able to generate predictions of climate impacts on large numbers of individual species (Thomas *et al.*, 2004). In this paper, we report on initial responses of some endemic succulent species in a southern African biodiversity hotspot to experimental warming approximating a future climate scenario (Hulme *et al.*, 2001). For this and logistic and engineering reasons, we focused on specialized dwarf and shrubby leaf succulents occurring on sandy-loam substrates covered by quartz gravel in the Knersvlakte centre of endemism in the Succulent Karoo biome, an area of great ecological significance and conservation value (Schmiedel & Jürgens, 1999; Schmiedel, 2001, 2002).

Materials and Methods

Study sites, treatments and species

Two study sites, roughly 10 km apart, were located on the farms Quagga Kop and Luiper Kop, situated in the Knersvlakte (elevation ± 160 m) north of the town of Vanrhynsdorp ($31^{\circ}36'$ S, $18^{\circ}44'$ E), South Africa. Daytime passive heating of the natural quartz field vegetation at each site was achieved with hexagonal open-top chambers constructed of clear (transmission down to 280 nm) acrylic. The open-top chambers were 46 cm high with distances between parallel sides of 120 cm at their bases and 72 cm at their apices. The efficacy of such open-top chambers as analogues of regional climatic warming has received biotic validation (Hollister & Weber, 2000). Eighteen open-top chamber arrays including controls (demarcated plots equivalent to open-top chamber basal dimensions) were randomized during late spring (November 2002) in three communities (six open-top chamber arrays and six control plots per community). The first community, incorporated in a *Conophytum calculus* (A. Berger) N.E.Br. ssp. *calculus* Community Group (Schmiedel, 2002), was present at the Luiper Kop site and contained *Ruschia burtoniae* L. Bolus as the dominant, in which *Cephalophyllum spissum* H.E.K. Hartmann occurred with a high constancy. The second community, incorporated in a *Salsola* (Chenopodiaceae) spp. – *Argyroderma pearsonii* (N.E.Br.) Schwantes Alliance (Schmiedel, 2002), was also present at the Luiper Kop site and contained *C. spissum* as the dominant in which *Drosanthemum diversifolium* L. Bolus occurred with a high constancy. The third community, also incorporated in the above Alliance, occurred at the Quagga Kop site and contained *A. pearsonii* as the dominant in which *Dactyloopsis digitata* (Aiton) N.E. Brown occurred with a high constancy.

Ambient and open-top chamber microenvironments

Air temperatures at the two study sites were recorded at 30-min intervals by synchronized miniature thermocouple data loggers (Spectrum Technologies Inc., Plainfield, Illinois, USA) installed in ventilated radiation shields positioned 12 cm above the ground at northern, central and southern points within the open-top chambers (Fig. 2a) and control plots (ambient air). These were compared with historical records of ambient air temperatures obtained from two meteorological stations located at similar elevations and degree of longitude proximate to the experimental site (Climate of South Africa, 1986). These included Clanwilliam ($32^{\circ}11'$ S, $18^{\circ}54'$ E) at an elevation of 75 m located c. 56 km south of the experimental site and Garies ($30^{\circ}34'$ S, $18^{\circ}00'$ E) at an elevation of 227 m located c. 99 km north of the experimental site.

Plant and canopy fatalities

In mid-autumn (April) 4 months after placement of open top chambers, the numbers of deceased and live plants of

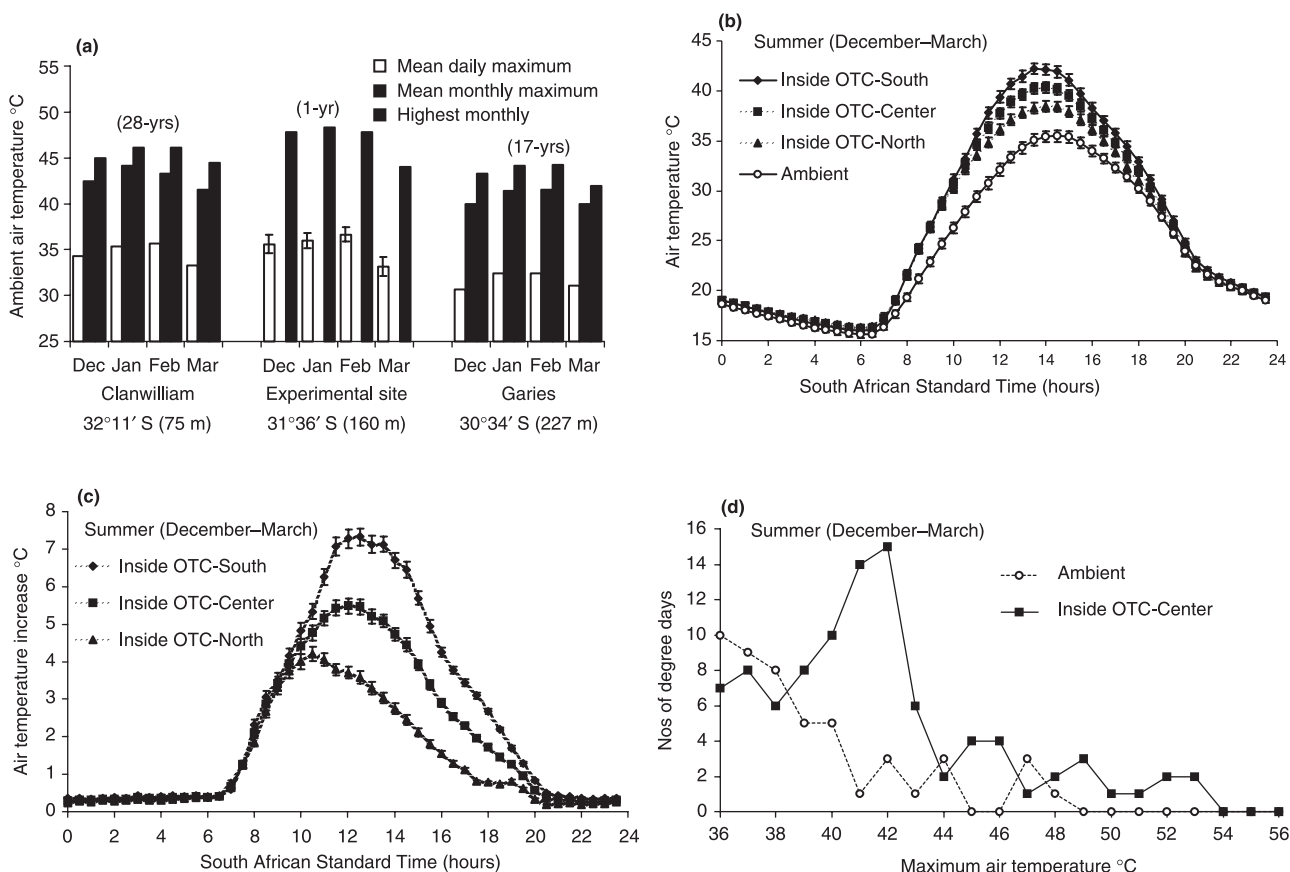


Fig. 1 (a) Historical records of summertime ambient air temperatures from two meteorological stations proximate to the experimental site. (b) Mean diurnal air temperatures (\pm se) in control plots (ambient air) and at different positions inside the open top chambers. (c) Average magnitude (\pm se) of air temperature enhancements at different positions inside the open-top chambers, and (d) duration of diurnal air temperature maxima in control plots and at central positions inside the open-top chambers.

each species, i.e. those with completely and partially lifeless canopies, respectively, present in the open-top chambers and control plots were counted and the fractions of deceased plants expressed as percentages. Also, the numbers of dry lifeless and fresh leaves present in the canopies of live plants in the open-top chambers and control plots were counted and the fractions of lifeless leaves expressed as percentages. Following onset of winter precipitation, deceased plants and canopies were re-examined to confirm their moribund states were irreversible, and plants classified as live were substantiated by their production of new leaves. In *A. pearsonii*, the ages of the deceased and live plants present in the open-top chambers and control plots were also determined from counts of the numbers of residual leaf pairs present on each plant. This species produces a new set of leaves annually, the deceased leaf pairs from previous years remaining permanently attached to the plant.

Leaf physical properties

Fresh intact leaves were randomly excised at midday 4-months after commencement of the study from each surviving succulent species present in the open-top chambers and control plots. In

A. pearsonii, the entire plant comprising a single pair of leaves was removed for analysis.

Fresh leaf samples were weighed, dried in a forced draft oven at 60°C to a constant mass and reweighed. Their water contents were calculated from the differences between their fresh and dry masses and expressed as percentages of their fresh masses.

Leaf chemical properties

Photosynthetic pigments were extracted from fresh leaf samples ground at a low light intensity in 10 ml of 100% methanol at 2°C. Absorbances of centrifuged extracts were measured with a spectrophotometer (Beckman DU 640, Beckman Instruments Inc., Fullerton, USA) at specified wavelengths required for computation of chlorophyll *a*, chlorophyll *b*, and total carotenoid (xanthophylls + β -carotene) concentrations from published formulae (Lichtenthaler, 1987). Leaf pellets remaining after centrifuging were dried at 60°C in a forced draft oven and weighed. Photosynthetic pigment concentrations were expressed as $\mu\text{g mg}^{-1}$ leaf dry mass.

Total soluble sugars (sucrose, glucose and fructose) were extracted from fresh leaf samples ground in two, 10-ml volumes

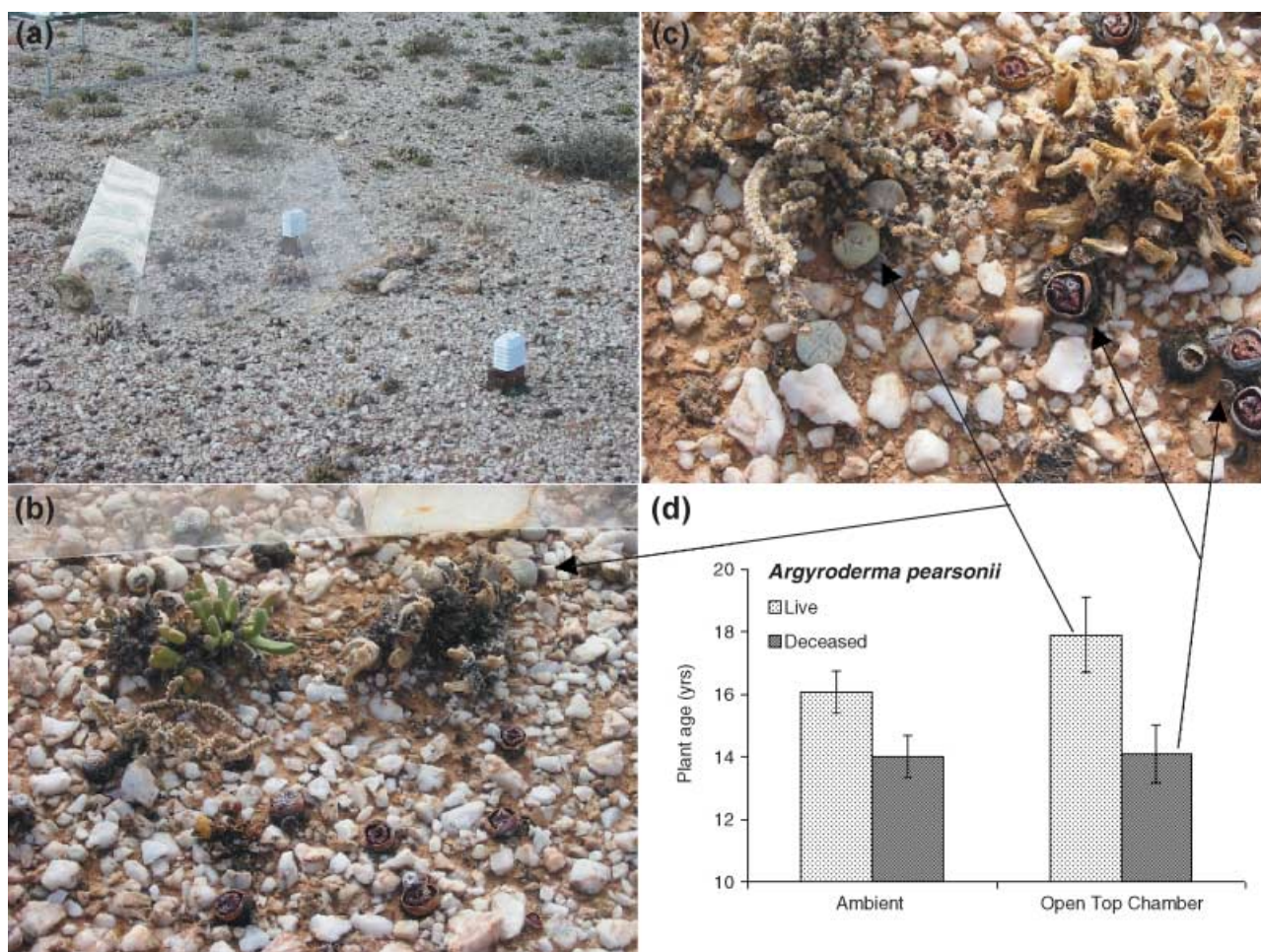


Fig. 2 (a) Hexagonal open top chamber and adjacent control plot each containing miniature thermocouple data loggers installed in ventilated radiation shields. (b,c) Deceased spherical-shaped *Argyroderma pearsonii* and live plants surviving in cooler ventilated areas at the edges of the open-top chamber and shaded refuges beneath the skeleton of a larger succulent *Salsola* spp. (d) Average ages (± SE) of deceased and live *A. pearsonii* in the control plots (Ambient) and open-top chambers.

of 80% ethanol (80 : 20, v : v, ethanol : water). The extracts were centrifuged, and supernatants adjusted to 25 ml in volumetric flasks for spectrophotometric determination of total soluble sugars (Buyse & Merckx, 1993). Residues were dried at 60°C and weighed, before analysis of starch concentrations by hydrolysing for 3 h in 5 ml of 3.6% HCl at 100°C, centrifuging and analysing the resultant sugars in the extracts (Buyse & Merckx, 1993). Soluble sugar and starch (non-structural carbohydrate) concentrations were expressed as $\mu\text{g mg}^{-1}$ leaf dry mass.

Phenylpropanoids (flavonoids and anthocyanins) were extracted from fresh leaf samples ground in 10 ml of acidified methanol (79 : 20 : 1, v : v, methanol : water : HCl). Absorbances (A_b) of appropriately diluted centrifuged extracts were measured with the spectrophotometer at 300 nm, 530 nm and 657 nm. Flavonoid concentrations were computed as A_b at 300 nm g^{-1} dry mass (Mirecki & Teramura, 1984), and anthocyanins as A_b 530 nm $-1/3 A_b$ 657 nm g^{-1} dry mass (Lindoo & Caldwell, 1978).

Statistical analyses

A single-factor nested analysis of variance tested differences in population and canopy mortalities, leaf physical and chemical properties between open-top chambers and control plots. Percentage values were arc-sine transformed to correct non-normality in proportions prior to statistical analysis. A two-factor nested analysis of variance tested differences in ages of deceased and live *A. pearsonii* between open-top chambers and control plot and their interaction.

Results

Ambient and open-top chamber microenvironments

Measured average daily maximum air temperatures at 1400 SAST in the control plots (summertime monthly range: 33.2–35.6°C) were virtually identical ($> 1.3^\circ\text{C}$ difference) to those spanning a 28-yr recording period (summertime monthly range:

Table 1 Impact of diurnal temperature maxima averaging 5.5°C above ambient (Control) in open-top chambers (OTC) over a 4-month summer treatment period on population and canopy mortalities, leaf physical and chemical properties of species of dwarf and shrubby leaf succulents on quartz fields

Parameter	Dwarf succulents						Shrubby succulents					
	Argyroderma pearsonii			Cephalophyllum spissum			Drosanthemum diversifolium			Ruschia burtoniae		
	Control	OTC	$F_{1,10}$	Control	OTC	$F_{1,10}$	Control	OTC	$F_{1,10}$	Control	OTC	$F_{1,10}$
<i>Population and canopy mortalities</i>												
Plants (% deceased)	21.2	74.1	207.9***	6.8	33.0	7.8*	37.5	57.1	0.7	23.5	29.4	0.2
Leaves (% deceased)	–	–	–	9.9	47.3	18.1**	42.9	90.0	5.2*	22.6	27.9	0.2
<i>Leaf physical properties</i>												
Fresh mass (g)	2.202	3.391	10.0**	7.613	7.619	< 0.1	1.481	0.919	22.8***	1.878	1.740	0.9
Dry mass (g)	0.263	0.444	16.3***	0.379	0.362	0.5	0.341	0.221	19.9***	0.272	0.310	2.4
Water content (%)	87.8	86.2	5.6*	95.1	95.3	1.2	76.9	74.7	21.2***	85.0	81.9	5.8*
<i>Leaf chemical properties</i>												
Chlorophyll a ($\mu\text{g g}^{-1}$)	0.067	0.056	1.2	0.045	0.042	0.1	0.096	0.113	2.0	0.077	0.056	4.9*
Chlorophyll b ($\mu\text{g g}^{-1}$)	0.048	0.045	0.1	0.113	0.109	< 0.1	0.076	0.143	10.3**	0.167	0.118	8.6**
Carotenoids x + αC ($\mu\text{g g}^{-1}$)	0.048	0.039	1.8	0.002	0.004	1.1	0.076	0.061	1.5	< 0.001	0.006	0.1
Soluble sugars ($\mu\text{g g}^{-1}$)	83.1	100.6	3.7	27.8	29.4	0.7	13.7	13.0	0.3	11.2	13.3	9.8**
Starch ($\mu\text{g g}^{-1}$)	177.7	162.2	4.1*	87.4	75.6	2.5	70.8	57.6	8.5**	79.6	72.8	2.3
Flavonoids (Abs g^{-1})	11.8	12.2	0.1	11.6	11.1	< 0.1	11.9	10.5	2.2	5.7	5.1	1.9
Anthocyanins (Abs g^{-1})	0.123	0.111	0.2	0.087	0.102	0.5	0.064	0.153	7.0*	0.152	0.103	6.0*

Significantly different at: *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

33.3–35.4°C) at the closest meteorological station (Clanwilliam) to our experimental sites (Fig. 1a). Noteworthy, was that the highest monthly air temperature of 46.1°C recorded at Clanwilliam was exceeded in our control plots on 3 d over the 4-month summer treatment period (Fig. 1d), 1 d of which comprised temperatures in excess of 2°C and 2 d in excess of 1°C of the highest recorded over a 28-yr span at Clanwilliam (Fig. 1a).

Inside the open-top chambers, there was strong diurnal air temperature fluctuation with most of the heating above ambient occurring during the daytime period (Fig. 1b). However, there was considerable day-to-day variation with temperature increases of the largest magnitude evident on clear-sky days with high solar radiation, and those of the smallest magnitude evident on overcast days. Notable, was that the scale of temperature increases and the timing of diurnal temperature maxima displayed gradients along north-to-south diagonals inside the open-top chambers (Fig. 1c). Temperature increases of smallest magnitude were measured at northern points inside the open-top chambers, with diurnal temperature maxima also occurring earlier in the day than those at southern points inside the open-top chambers (Fig. 1c). These temperature gradients inside the open-top chambers concurred with similar trends, but of opposing direction, reported for open-top chambers sited in the northern hemisphere where multiple regression analyses revealed that the scale of temperature increases were signifi-

cantly linked to both wind speed and global radiation intensity (Marion *et al.*, 1997). In the centres of the open-top chambers daily maximum air temperatures over the 4-month treatment period (summertime monthly range: 38.3–41.6°C) averaged 5.5°C above those in the control plots (Fig. 1c). These were still 1.0–4.0°C below corresponding mean monthly maxima recorded over a 28-yr span at the Clanwilliam meteorological station (Fig. 1a), though the highest daily temperature of 53°C measured in the centres of the open-top chambers (Fig. 1d) did exceed that recorded at Clanwilliam by 7°C. Noteworthy, was a close correspondence between ratios of highest recorded monthly temperature against corresponding average daily temperature maxima in our open-top chambers (summertime monthly range: 1.279–1.335) control plots (summertime monthly range: 1.303–1.327) and at the Clanwilliam meteorological station (summertime monthly range: 1.291–1.333).

Plant and canopy mortalities

The fractions of *A. pearsonii* and *C. spissum* populations that deceased were significantly ($P \leq 0.05$) greater (3.5–4.9 times) in the open-top chambers than in the control plots (Table 1). Also, the fractions of deceased leaves in the canopies of surviving live *C. spissum* and *D. diversifolium* were significantly ($P \leq 0.05$) greater (2.1–4.8 times) in the open-top chambers than in the control plots.

Leaf physical properties

Leaf fresh and dry masses of live *A. pearsonii* were significantly ($P \leq 0.05$) larger in the open-top chambers than control plots (Table 1). These concurred with the significantly ($F_{1,87} = 10.8$, $P \leq 0.01$) greater ages of live than deceased *A. pearsonii* in both the open-top chambers and control plots (Fig. 2d). There was no significant interaction ($F_{1,87} = 0.8$, $P = 0.05$) between plant age and warming treatment. Significantly ($P \leq 0.001$) smaller leaf fresh and dry masses were measured in the canopies of live *D. diversifolium* in the open-top chambers than in the control plots (Table 1). *D. diversifolium* and *C. spissum* also displayed slightly, yet significantly ($P \leq 0.05$) lower water contents in the open-top chambers than control plots.

Leaf chemical properties

D. diversifolium displayed significantly ($P \leq 0.01$) higher foliar concentrations of chlorophyll *b* and *R. burtoniae* significantly ($P \leq 0.05$) lower foliar concentrations of both chlorophyll *a* and *b* in the open-top chambers than control plots, but foliar carotenoid concentrations in all study species were unaffected by the elevated temperatures in the open-top chambers (Table 1). Noteworthy, were the low carotenoid concentrations, particularly in *C. spissum* and *R. burtoniae*. Slight instrumental deviation from the tabulated wavelengths λ_{\max} for chlorophyll *b* (Lichtenhaler, 1987), and/or carotenoid decomposition during pigment extraction under the influence of high endogenous organic acids in the CAM (crassulacean acid metabolism) succulents might provide an explanation.

Only *A. pearsonii* and *D. diversifolium* exhibited significantly ($P \leq 0.01$) lower starch concentrations in the open-top chambers than control plots, though *C. spissum* and *R. burtoniae* displayed similar but statistically insignificant ($P = 0.05$) tendencies. Also, a slightly, yet significantly ($P \leq 0.01$) higher soluble sugar concentration was measured in *R. burtoniae* leaves in the open-top chambers than control plots, this tendency apparent in *A. pearsonii* and *C. spissum* leaves as well but statistically insignificant ($P = 0.05$).

Foliar flavonoid concentrations in all study species were unaffected by the elevated temperatures in the open-top chambers. However, foliar anthocyanin concentrations were significantly ($P \leq 0.05$) lower in *R. burtoniae* but significantly ($P \leq 0.05$) higher in *D. diversifolium* in the open-top chambers than control plots.

Discussion

Ambient air temperatures at our experimental sites during the 4-month treatment period did essentially represent average conditions for study area. This supported by the similar average daily maximum air temperatures recorded in our control plots and at the closest meteorological station at Clanwilliam. However, there were 3 d with abnormally high ambient temperatures at

our experimental sites in which monthly diurnal air temperature maxima in the control plots did slightly exceed those recorded over a 28-yr span at the Clanwilliam meteorological station.

Daily maximum air temperatures in the centres of our open-top chambers, which averaged 5.5°C above ambient over the 4-month treatment period (Fig. 1c), approximated temperature increases of between 4.5 and 5.0°C (means of 7-GCM experiments) predicted (SRES A2-high climate sensitivity scenario) for the geographic coordinates 30° S to 31° S, 19° E to 20° E in the year 2080 (Hulme *et al.*, 2001). The observed close correspondence between ratios of highest recorded monthly temperature against corresponding average daily temperature maxima in our open-top chambers, control plots and at the Clanwilliam meteorological station indicated that the temperature extremes accompanying the average daily maxima in our open-top chambers also provided a rational analogue of the predicted climate change.

The elevated temperatures in our open top chambers were associated with a 3.5- to 4.9-fold increase in plant and canopy mortality among the specialized dwarf succulents *A. pearsonii* and *C. spissum*, and a 2.1-fold increase in canopy mortality in the shrubby succulent *D. diversifolium* (Table 1). These substantial reductions in live standing succulent biomass seemingly contrasted with results of 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 (Rustad *et al.*, 2001). The meta-analysis found a 19% productivity increase in response to an average 2.4°C of experimental warming among the 20 sites distributed in cooler regions at latitudes above 35° N (Rustad *et al.*, 2001). However, relative productivity responses to experimental warming declined with increasing site mean annual temperature (Rustad *et al.*, 2001) implying that productivity could be expected to decrease with experimental warming at lower latitude subtropical and tropical sites not included in the meta-analysis. Noteworthy, was the abrupt rather than gradual temperature increase in our open top chambers on commencement of the study, which may have precluded natural plant acclimation to the increased heat stress, thereby contributing to the extraordinarily high mortalities observed. Indeed, an analysis of the age and size distribution of surviving and deceased *A. pearsonii* in the control plots and open-top chambers revealed that the live plants were significantly older (Fig. 2d) and larger than the deceased plants (Table 1); possibly indicative of past selection for heat resistant ecotypes.

An examination of the distribution patterns of surviving dwarf succulents in our open-top chambers revealed that live *C. spissum* and *A. pearsonii* individuals particularly were restricted to cooler microhabitats in more ventilated areas at the edges of the chambers (Fig. 2b) and shaded refuges beneath the skeletons of larger succulents such as *Salsola* spp. (Fig. 2c). These distribution patterns supported our perception that lethal temperature thresholds were exceeded in the open-top

chambers, though ostensibly less severely in the cooler microhabitats. Indeed, diurnal temperature extremes in our open-top chambers were closely proximate to the upper temperature limit of 55°C considered tolerable by most vascular plants (Larcher, 1980; Kappen, 1981). However, there are reports of much higher lethal temperature thresholds in a diverse array of dwarf succulents. These, based on the ability of chlorenchyma cells to uptake a vital stain (Onwueme, 1979), ranging from 66.4°C to 66.9°C in rosette leafed *Haworthia* species (*H. retusa* and *H. turgida*), 68.3°C to 68.7°C in spherical leafed *Lithops* species (*L. leslie* and *L. turbiniformis*), and 69°C to 70°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). Nevertheless, lethal temperature thresholds in the majority of southern African dwarf succulent taxa may be lower, since they occur at high densities virtually exclusively on quartz-fields with milder thermal regimes (Schmiedel & Jürgens, 2002, 2004). Indeed, maximum daily soil temperatures during summer have been measured up to 10°C lower on highly reflective quartz substrates than on adjacent brown shales, and up to 3°C lower leaf temperatures have been measured in *A. pearsonii* growing inside quartz fields compared with the same species growing on neighbouring soils without quartz cover (Schmiedel & Jürgens, 2004). Similarly, another earlier study reported that leaf surface temperatures in a dwarf *Argyroderma* species on a quartz-covered substrate remained close to an ambient air temperature of 35°C whereas those of a shrubby *Ruschia* species on adjacent brown shale exceeded 45°C (von Willert *et al.*, 1992).

Common physiological responses to experimental warming observed among the surviving dwarf and shrubby succulents in the open-top chambers included diminished foliar water contents and starch concentrations, the shrubby succulents also exhibiting altered foliar chlorophyll levels. Relocation of carbon reserves to secondary phenylpropanoid compounds was apparent in *D. diversifolium* where reduced foliar starch concentrations corresponded with increased anthocyanin levels. Nevertheless, the physiological changes observed in the surviving succulents did imply moisture limitations in the open-top chambers. Moisture deficits modify leaf conductance, transpiration and carbon assimilation rates (Ni & Pallardy, 1992) resulting in a degradation of stored non-structural carbohydrate reserves (Dunn *et al.*, 1987), with small stature species with limited root extension and carbon reserves particularly sensitive to low soil water potentials (Donovan & Ehleringer, 1991; Flanagan *et al.*, 1992). Indeed, a higher fraction of small leaves with a lower mass leaves were observed in the canopy of live *D. diversifolium* (Table 1), suggesting an acclimation to reduce transpiration loss under the warmer conditions in the open-top chambers. In this regard, it is known that shallow rooted dwarf succulents of the Mesembryanthemaceae require frequent though small amounts of water for survival, and the role of supplementary precipitation

by fog and dew, estimated at as much as 38% of annual hydrological input (Dawson, 1998), is an important factor in ameliorating summer water deficits in semiarid and arid Mediterranean-climate ecosystems and preventing thermoregulation problems due to reduced transpiration (von Willert *et al.*, 1992; Turner & Picker, 1993). This supplementary precipitation accrued on leaf surfaces drips, or is funnelled via stem-flow, onto the soil (Hutley *et al.*, 1997) where it can be absorbed by plant root systems or directly by leaves from their wetted surfaces (Yates & Hutley, 1995; Martin & von Willert, 2000) or from the vapour-saturated atmosphere (Breazeale *et al.*, 1950). Indeed, the interception of such supplementary precipitation by the open-top chambers and its channelling to the chamber edges could also partly explain the observed prevalence of surviving dwarf succulents in these locale.

In conclusion, it does seem likely that current thermal regimes are closely proximate to tolerable extremes for many of the 1563 almost all endemic succulent species included in the subfamily Ruschioideae which diversified rapidly in the region during the cool Pleistocene (Klak *et al.*, 2004). Anthropogenic warming could therefore significantly exceed their thermal thresholds resulting in localized extinctions of particularly those specialized species range-restricted to specific habitats. However, further investigation is required to elucidate the importance of associated moisture deficits in these passive warming experiments, a potential consequence of supplementary precipitation interception by open-top chambers and higher evaporation therein, to allow reliable assessment of potential extinction losses under a range of climate change scenarios, and to match these with the predictions on the increasingly useful bioclimatic modelling approach.

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