2017-04

Complexity confers stability: Climate variability, vegetation response and sand transport on longitudinal sand dunes in Australia's deserts

Hesse, PP

http://hdl.handle.net/10026.1/8568

10.1016/j.aeolia.2017.02.003
Aeolian Research
Elsevier BV

Manuscript Details

Manuscript number	AEOLIA_2016_131
Title	Complexity confers stability: Climate variability, vegetation response and sand transport on longitudinal sand dunes in Australia's deserts
Article type	Full Length Article

Abstract

The relationship between antecedent precipitation, vegetation cover and sand movement on sand dunes in the Simpson and Strzelecki Deserts was investigated by repeated (up to four) surveys of dune crest plots (≈25x25 m) over a drought cycle (2002-2012) in both winter (low wind) and spring (high wind). Vegetation varied dramatically between surveys on vegetated dune and active crests. Indices of sand movement had significant correlations with vegetation cover: the depth of loose sand has a strong inverse relationship with crust (cyanobacterial and/or physical) while the area covered by ripples has a strong inverse relationship with the areal cover of vascular plants. However, the relationship between antecedent rainfall and vegetation cover was found to be complex. We tentatively identify two thresholds; (1) >10 mm of rainfall in the preceding 90 days leads to rapid and near total cover of crust and/or small plants <50 cm tall, and (2) >400 mm of rainfall in the preceding three years leads to higher cover of persistent and longer-lived plants >50 cm tall. These thresholds were used to predict days of low vegetation cover on dune crests. The combination of seasonality of predicted bare-crest days, potential sand drift and resultant sand drift direction explains observed patterns of sand drift on these dunes. The complex vegetation and highly variable rainfall regime confer meta-stability on the dunes through the range of responses to different intervals of antecedent rainfall and non-linear growth responses. This suggests that the geomorphic response of dunes to climate variation is complex and non-linear.

Keywords	Simpson Desert; Strzelecki Desert; climate change; aeolian

Corresponding Author	Paul Hesse
Corresponding Author's Institution	Macquarie University
Order of Authors	Paul Hesse, Matt Telfer, Will Farebrother

Suggested reviewers	Matthew Baddock, Giles Wiggs, Alan Halfen, Joel Roskin

Submission Files Included in this PDF

File Name [File Type]

1609 Hesse cover letter.docx [Author Agreement]

1701 Comments from the editors and reviewers.docx [Response to Reviewers]

1701 Complexity confers stability revision changes accepted.docx [Manuscript (without Author Details)]

Fig 1 1701_Strz_Simpson_map.tif [Figure]

Fig 2 1701 Moomba AP monthly and annual DP and Precip.tif [Figure]

Fig 3 1701 Birdsville AP monthly and annual DP and Precip.tif [Figure]

4a Mayan Crest 2004.jpg [Figure]

4b Mayan Crest 2012.JPG [Figure]

4c Mayan Right flank 02 v2.jpg [Figure]

4d Mayan Right Flank 2012.JPG [Figure]

4e Aztec North 2004.jpg [Figure]

4f Aztec North 2012.JPG [Figure]

4g Della Crest 05.jpg [Figure]

4h Della Crest 2012.JPG [Figure]

4i Bosca North 2004.jpg [Figure]

4j Bosca North 2012.JPG [Figure]

Fig 5 1701 Veg distn plots Mayan Della Bosca.tif [Figure]

Fig 6 1701 veg % v H.tif [Figure]

Fig 7 1701 sand depth and ripples v veg.tif [Figure]

Fig 8 1701 summary rainfall v veg.tif [Figure]

Fig 9 1701 Moomba AP storms BW.tif [Figure]

Fig 10 1701 Birdsville daily P dry periods BW.tif [Figure]

Fig 11 1701 annual and seasonal distribution of risky days.tif [Figure]

Fig 12 1701 Birdsville at risk days v month and RDD and DP.tif [Figure]

Tables.docx [Table]

Supplementary Material.pdf [e-Component]

1609 Highlights.docx [Highlights]

1609 Hesse et al title page.docx [Title Page (with Author Details)]

To view all the submission files, including those not included in the PDF, click on the manuscript title on your EVISE Homepage, then click 'Download zip file'.

DEPARTMENT OF ENVIRONMENTAL SCIENCES
Faculty of Science and Engineering

Macquarie University
NSW 2109 Australia

Dr Paul Hesse

T: +61 (2) 9850 8384
F: +61 (2) 9850 8420

MACQUARIE University SYDNEY·AUSTRALIA

22nd September 2016

Dear Editors

We would like to submit the paper 'Complexity confers stability: Climate variability, vegetation response and sand transport on longitudinal sand dunes in Australia's deserts' to Aeolian Research for consideration.

The paper documents a study quantifying the relationship between antecedent precipitation, vegetation cover and sand movement on sand dunes in the Simpson and Strzelecki Deserts. The study uses detailed surveys plots on dune crests to monitor vegetation cover and composition periodically over 10 years during a complete drought cycle. We documented the influence of soil crusts on sand availability and plant cover on sand movement showing a simple inverse relationship. Vegetation cover and composition show complex and non-linear responses to antecedent rainfall. Threshold responses appear to govern the abundance of crust, small plants and large plants on different timescales. We have used those empirically identified thresholds to model the periods of low cover over the last century, confirming broadly to deep drought periods. This model helps to explain aspects of the observed behaviour of dunes, such as their migration direction and level of activity. The novelty of the paper lies in its unique data set of observations covering a decadal drought cycle and the extremes of the modern climate regime. We believe it has significance beyond Australia, to understanding how complex vegetation and complex, highly variable, rainfall combine to affect sand dune behaviour in meta-stable subtropical dunefields.

All diagrams can be printed in black and white/greyscale, including those provided here in colour.

The paper is an original piece of research which has not been submitted elsewhere for review. There are no financial or personal conflicts of interest or external funding bodies requiring acknowledgment (funding was entirely in-kind through Macquarie University). All co-authors have participated in conduct of the study and writing of the paper and agree to its submission.

Potential referees include:

Joel Roskin Email: yoelr@post.bgu.ac.il; Department of Maritime Civilizations, Charney School of Marine Studies and the Leon Recanati Institute for Maritime Studies (RIMS), University of Haifa, Mt. Carmel Haifa, 31905 Israel

Alan Halfen afhalfen@ku.edu, Department of Geography and Atmospheric Science, University of Kansas.

**DEPARTMENT OF
ENVIRONMENTAL SCIENCES**
Faculty of Science and Engineering

Macquarie University
NSW 2109 Australia

Dr Paul Hesse

T: +61 (2) 9850 8384
F: +61 (2) 9850 8420

MACQUARIE University
SYDNEY · AUSTRALIA

Giles Wiggs, School of Geography and the Environment, University of Oxford, UK
giles.wiggs@ouce.ox.ac.uk

Matt Baddock, m.c.baddock@lboro.ac.uk; Department of Geography, Loughborough University, UK.

Yours sincerely

Paul Hesse on behalf of all authors.

We have added our responses to the editor's and reviewers' comments in red (for clarity).

Comments from the editors and reviewers:
-Editor

- Hesse et al present an analysis of vegetation and sand transport responses to drought and rainfall in the Australian Simpson and Strzelecki Deserts. The manuscript has now been examined by two reviewers who are in agreement that the manuscript is worthy of publication in Aeolian Research, but requires some revision to provide more depth to the work as well as some clarification. I encourage the authors to address the reviewers' comments, giving particular consideration to those of reviewer #2 who provides a number of suggestions to strengthen the scientific basis of the research.

My sense is that this manuscript perhaps raises many more questions about the drivers of dune activity in the Simpson and Strzelecki Deserts than it answers. In addressing the reviewers' comments, I would therefore encourage the authors to openly identify the limitations of their research approach, but also what the important ongoing questions are and how they might be tackled in the future. Aeolian processes in the authors' study area more generally have linkages and feedbacks to ecological dynamics, including the effects of fire, that would be of interest to readers outside Aeolian Research. Drawing the research findings into the more general discussion about eco-geomorphic processes in the dune systems may broaden both the readership and impact of the work. The references below (and others by the listed authors) may provide some of this context:

AC Greenville, CR Dickman, GM Wardle, M Letnic, 2009. The fire history of an arid grassland: the influence of antecedent rainfall and ENSO. International Journal of Wildland Fire 18 (6), 631-639.

GM Wardle, CR Pavey, CR Dickman, 2013. Greening of arid Australia: new insights from extreme years. Austral Ecology 38 (7), 731-740

Throughout the paper we have reviewed and added comments about the limitations of this study. We have indicated ongoing questions in several places, particularly in the discussion. Also in response to the reviewers' comments we have added new references and comments to our discussion of the ecology and some comments on the possible role of fire.
We refrained from entering into a discussion about fire because we did not observe burning on these sites. We are very aware that it is a presence in the landscape and know of several papers which have covered the role of fire in rangeland ecology, but none have actually dealt with the effects on sand movement, only on cover and vegetation recovery. To the extent that this is relevant, we have added some comments to the introduction and at the end of the discussion. We have cited the Greenville paper.

We have drawn on the paper by Nano and Pavey (2013) in the same special issue as the editorial paper as Wardle et al. We have added a citation to Wardle because it does contain useful documentation of the 2010-21011 La Nina event, but it also draws on Nano and Pavey, the only paper dealing with dunefield vegetation dynamics in the special issue. Later, in response to suggestions from the reviewers we have also added discussion of and reference to other papers dealing with arid zone ecology and vegetation.

-Reviewer 1

-

Line 9: By itself, the claim that "Indices of sand movement had significant correlations with veg cover" is not very helpful…this should be rephrased to be in conjunction with the following lines where you describe these unique indices.
We had split the sentences to avoid a long sentence. We have now joined them with a colon.
21: provide >> confer ??
thanks for pointing out the opportunity – done.
23: I don't think you can make this non-linearity claim, and especially not in the executive summary of the abstract. Non-linearity is not explicitly mentioned or discussed in any of the discussion part of the paper. Either remove, rephrase, or address.
Threshold responses are a form of non-linearity. The bistability of dune vegetation – forcing relationships (discussed in the paper) is another. We have made the language more explicit in the discussion.
40: I agree. Is it worth also adding "and direction" to wind strength in this case of linear dunes? The seasonally variable nature of bimodal formative winds for linear/longitudinal dunes does often complicate aspects of their study, just as you suggest.
Done
43: Can you consider adding Lancaster and Helm here as well. I feel this is an often neglected 'companion' paper to the classic Lancaster (1988) as it provides measured Q flux to support M values, which would fit with your work, and relate better to your argument of sand mobility (not just dune activity state).
Lancaster and Helm (2000) A test of a climatic index of dune mobility using measurements from the SW US. Earth Surface Processes & Landforms, 25, 197-207.
Done – thanks for pointing out this paper.
46: Perhaps rein in the general nature of this point a touch by specifying Bullard et al.'s work was focussed on the Kalahari.
Qualified as suggested
50: Moller takes a slashed o (Ø).
Done
48-58: Paragraph should be improved as it steps from drought as a disturbance, to overgrazing (…you don't actually link your review of Tsoar to drought). Then back to drought.
Restructured as suggested

Also, in above paragraph, by considering multiple disturbance mechanisms in this Introduction (i.e. drought, overgrazing), do you deliberately not include fire? This is relevant for vegetation removal from dunes in the Simpson Desert. Could a line or two be added to recognise this, if you are featuring other disturbances such as grazing?
Added. We have added some coverage and relevant references.
59: Relative importance of veg for/in what? Please specify this as you craft your paper's position.
The sentence has been reworded.
82: >> sand transport & "range of Australian climate variability"
done
95-110: The position of this paragraph here, dipping back as it does into literature review mode seems to weaken the prominence of your current study. I realise the current work links strongly to Hesse and Simpson, but, having stated the aims and established a nice niche for the current study in 79-94, switching to providing specifics of Hesse and Simpson at this point seems to reduce the clarity of the current paper's objectives, and furthermore, its significance. Can this be restructured?
This paragraph was moved to the discussion and considerably rewritten.
120-122: It is not clear what is meant by this sentence. "monitor the less common patches of mobile sand"??
This sentence has been modified to clarify the meaning.
133-134: reword for clarity to "…but wind speeds and direction are only available for 9 a.m. and 3 p.m., with a daily maximum gust also recorded."
This sentence (and the method) have been superseded by new analysis of a 3-hourly observation record.
137: Readers would like to see more information on the derivation of threshold value. The footnote where values are stated at the bottom of Table 2 is insufficient.
A sentence has been added to the text. The value is based on Fryberger and Dean (1979) and assumes an average sand size of 0.3 mm diameter.
144-147: Later on (149), you state that your results are not comparable with other studies because you do not bin the direction and windspeed data. It would be straightforward to additionally provide a binned version of your measurements as you describe, which would allow wider, international comparison with other studies that use DP. This would increase the appeal of your study. Having high resolution data is not enough of a reason to not make your work more relatable.
It's not particularly straightforward and we question how relevant it is. To quote Bullard (1997, J Sed Res) 'Because values of DP are usually recognized as being relative to one another, the actual magnitude of the value is unimportant provided that the data have been standardized to the same specific units. However, the values are important if they are to be interpreted using Fryberger's classification of wind-energy environments…'. In the paper we only ever make internal comparisons but we infer that what the reviewer is driving at is the broader comparison. We have added a citation to a paper (Ashkenazy et al., 2012, Climatic Change) which has calculated DP for Australia (from observational and re-analysis data). The only other instrumental study we know of for Australia (Kalma and Wasson, 1988. J

Climatology) followed the Fryberger method but used velocities in ms^{-1} (not knots), using only 3pm wind speeds and only 4 months (Jan, Apr, July, Oct) to characterize the seasonal cycle and annual wind environment.

Furthermore, Fryberger and Dean (1979) stated that degradation of the record (by observer bias etc) was undesirable and that they used a mixture of 3 hourly and 6 hourly observations, depending on availability. We chose to use an approach which takes maximum advantage of the high quality automatic weather station data (which is not inherently binned, as observer data is). We have improved the quality of the analysis by using 3-hourly recordings (in response to Reviewer 2) and weighted the values according to the frequency of the observations but they are still not comparable with the Fryberger method (in either knots or ms^{-1}).

Quite unsolicited, a colleague sent this (to PH) recently:

"Almost every recent application of DP modifies the original method in some way, including the use of hourly (or more often two to six per day) measurements, somewhat different threshold velocities, use of original data rounded to even or fractional knots or m/s, binning of wind directions, use of the original "Vector Units" or conversion to metric units, etc. Many of these make a difference in the kind of bias introduced and certainly in comparing with other studies. The key details can be stated concisely,…"

So, in summary, we are happy to provide a value from a paper which characterizes the wind environment broadly but for this analysis our objectives are best served by generating the highest accuracy index of potential sand transport that we can and we believe that our approach does that.

170: Aggregates would be a preferable soils/sediment term to "clumps".

Changed.

170-172: Perhaps another useful reference here in support of the nature of crusts you describe in your dune study environments would be Strong et al. (2010) Impact of wildfire on interdune ecology and sediments: an example from the Simpson Desert, Australia. Journal of Arid Environments, 74: 1577-1581. doi:10.1016/j.jaridenv.2010.05.032

Citation added.

190 & 205: It is an interesting dataset to cross drought/wet cycles, but recent climate literature would suggest the Millennium Drought began earlier than the 2001 you state here. Can you clarify this? See

Timbal, B., and R. Fawcett (2013), A Historical Perspective on Southeastern Australian Rainfall since 1865 Using the Instrumental Record. J. Climate, 26, 1112-1129. doi: 10.1175/JCLI-D-12-00082.1

That study was restricted to southeastern Australia, south of our field areas. The record from Birdsville and Moomba (figures 2 and 3, and older data for Birdsville) show that rainfall was average until 2001/02. The citation was added to the introduction.

Verdon-Kidd, D. C., A. S. Kiem, and R. Moran (2014), Links between the Big Dry in Australia and hemispheric multi-decadal climate variability - implications for water resource management. Hydrol. Earth Syst. Sc., 10, 13539-13593. doi:10.5194/hess-18-2235-2014

This paper further complicates the picture (last point) by finding that decadal scale regime shifts have occurred at many met stations across Australia but there is no clear geographic pattern. Their inference that IPO is an important factor but not solely responsible for these shifts, is consistent with our findings and the citation was added to the discussion.

243: Include "bind" to link back to 'effect on sand' as mentioned in Table 3?

Thankyou. Done.

248: Again, it is not clear to me what your patch unit is (as 120 and line 299). A landscape-scale absence of vegetation?.... The meaning of this sentence should be clearer, with regard to ripples but no transport?

Perhaps there is some confusion because of the appropriation of the word 'patch' by ecologists as a technical word. We have replaced it with 'area', a generic (plain English) term which does not have a fixed size or size limits. In two of the three uses mentioned, the 'area' is defined by the presence of slip faces. At line 248 it refers to vegetation and we have added a practical (but approximate) lower limit to guide the reader.

315: What are these changes? Please specify.

added

339: In the manuscript, there seems to be a few cases of crossover between results and Discussion. The statement here, that "Both observations suggest that there is quite a high level of inertia for each morphodynamic state and that large perturbations are required to achieve a change of state." is a major argument and seems out of place as a somewhat throwaway remark in the results. This ought to be a specific piece of Discussion, a case/position argued from the data that is offered, not presented as a result.

We removed this sentence to the Discussion.

356: I found it misleading to read "sand movement" here. You are really only presenting evidence or proxies of sand movement or activity. Likewise, on 357, I recommend you replace "mobile sand" with the term you use later, "loose sand", so your meaning is clearer.

The sentence was changed to read 'Two proxy measures of sand movement were made: the coverage of ripples … and the coverage of loose sand …".

L367: change to "…but the expanded dataset here, although…"

Done

L365-373: Given the paper is structured as Results and Discussion separately, this portion again reads rather too Discussional to me, with the significance of the data being discussed in light of other research, not, merely its presentation. Discussion should come later in the way your paper is set up.

While these paragraphs are entirely descriptive, rather than interpretive, we have moved all comparisons with previous work to the discussion.

L376: What threshold value are you referring to? I assume veg cover, but this is rather vague.

The sentence has been modified to more specifically describe the relationship.

L383: "behave" in what terms? And, "earlier observations" as in Hesse and Simpson (2006), or not? All a bit unclear.

Behave as in increase or decrease (added to sentence). Earlier observations as in section 3.3 (added to sentence).

L430: What do you mean by "lag on possible responsiveness."? Do you mean a (dune) morphological response?

We simply meant a lag in the response of measures of vegetation growth (cover) to environmental drivers. This has been added to the sentence.

427-436: If you re-read this paragraph, it appears to be stepping out of Results. This paragraph offers explanations of patterns presented. I think there is another case of 'mission creep' from the Results here. The crossover of Results/Discussion reduces the clarity and quality of the manuscript at present, and just requires a simple re-think/re-organisation.

We have moved it to the Discussion. It was intended that inclusion of this relatively procedural/technical issue in the results section would free the Discussion for bigger issues.

L444-447: I appreciate this is referring to work carried out in earlier Hesse and Simpson earlier work, but for a first point to your discussion, having read these two sentences, I do not understand the approach, and this undermines the larger point you are making. What could "cumulative sand thickness" be?

Furthermore, please define what you mean by 'equivalent sand thickness' for the purpose of this study. Most aeolian geomorphologists will understand it on a dune system scale, with regard to a control on dune type, but your work would benefit from more clarity in terms of the small scale that you mean it for here (e.g. sand above the crust layer?)

We restructured and rewrote much of this section, eliminating this sentence.

L462: a bit overloaded with complexity/complex…

The repetition was intended to create emphasis. We have considered alternatives but cannot think of anything that does not sound contrived or obscure.

481: "gibber" (desert pavement)

done

470-490: In this paragraph, please make it clearer which is reflecting on Nano And Pavey's work, and when the current study is being referred to. (L475 "the findings", their's or yours? It's actually not very clear..)

The paragraph has been modified to make it clearer.

487: ", and that in some cases,"

done

491: >> Analysis…supports

done

508-509: "but high scatter between sites and dune position reflecting the long term relationship." Does not make sense.

corrected

514-515: "Our analysis…" Please refer back specifically to your results (e.g. the Figure) that show this, to better link your Discussion with Results portion.

Reference to figure 8 was added.

541 and onward: Having read the paper, I have to object to the term "at risk" or "risk" that is introduced here and is now used from here onwards. "Risk" is not a suitably geomorphological term, and personally, I think a different way of discussing

the concept you are referring to ought to be found. There is no “risk” inherent in bare crests developing on Simpson dunes. In this paper, I find “risk” to be an unmeaningful and frankly unhelpful term which doesn’t contribute to the Discussion. In response, the author/s might justify their use of the word, but I felt strongly enough to raise the objection.
Risk is a widely used term in the study of natural hazards, including geological and geomorphological ones. Nevertheless, after consulting some dictionaries (which all agreed that (to summarise) risk is the probability of a negative event) we concede that we only meant to indicate probability and not the negative connotation. We have removed the word and used alternative phrasing throughout.
583: Please use east/west etc., not left/right.
Because the dunes change orientation (in fact they make a full 360 degree whorl over the continent), using compass directions is not always simple and makes comparison between sites more confused. Hesse and Simpson introduced the terminology of left and right, borrowing from the convention applied to rivers. We have added a note to this effect.
599: Where on the dune was the stake? Crest, flank?
“on the crest” added.
619: Please elaborate on ”the model of bi-stable hysteric behaviour”, and the importance you are attaching to it. Other than the citation, this is a rather throwaway contribution at present.
Discussion was added in section 4.1.
621. New sentence needs to start around “inherent”.
Done
617-624: While their paper focuses primarily on influences of land use, are some of the ideas about stability and resilience of vegetated dunes (in the Kalahari) put forward by Bhattachan et al. of any value to your arguments here? (Resilience and recovery potential of duneland vegetation in the southern Kalahari. Ecosphere, 5, http://dx.doi.org/10.1890/ES13-00268.1)
A very interesting paper but (removing the differences between the sites - especially grazing pressure) the Bhattachan study found very high resilience of the vegetation (or its recovery potential). It is of interest in the broader topic of vegetation on dunes but does not seem to be of value in this discussion.
628: change of >> change from
Done
638: Consider rephrasing “scale and style” to “magnitude and frequency”? If that’s what you mean. I’m not convinced by style of sand movement.
Done. We intended ‘style’ to refer to the form (i.e. slip-faces etc) but the next clause makes the point.
651-652: Please summarise dates in your conclusion.
Done
673: It is much preferable here that right/left sides of the dune are not used. Please see my earlier note about how east/west etc. is more intuitive for a reader.
The use of ‘NE’ here is deliberately to be concordant with the description of the wind direction.

678-680: I am not sure your manuscript has done enough to extend the claim you are making here so widely to "other deserts". I feel this closing mark needs to be toned down, more in line with what your paper has found regarding Simpson/Strzelecki. Perhaps a remark suggesting your approach and ideas should be applied to other vegetated/stabilized dunefields would be appropriate.
Fair comment. Changed as suggested.
707: Craddock reference is incomplete.
The DOI has now been added. (there are no page numbers for this journal)
Table 2: Looking at the site details (I was interested in the height of windspeed measurement), I gather the Birdsville Airport record began in the end of June 2000? Is your data start correct?
http://www.bom.gov.au/clim_data/cdio/metadata/pdf/siteinfo/IDCJMD0040.038026.SiteInfo.pdf
The reviewer is correct: although the station (as at Moomba AP) began operation in the last days of June, the first data we have used is from July, the first complete month. The table has now been substantially revised.
Figure 1: What is the source of your dunefield basemap? And, can the Australia map not be made a inset of the main Simpson-Strzelecki figure. Two maps like this looks irregular, especially when the Aus map is merely a context one.
The origin of the map of the dunefield areas (original) and dune crests (Geoscience Australia) is added to the caption. The map of Australia was added as an inset.
Figure 4: A very nicely presented figure. Legend should be "Bosca North"?
Done
Throughout, Bosca/Bosca North seems to vary as a field site.
We reviewed all instances of use of 'Bosca'. Bosca North refers to a specific quadrat. Bosca refers to the dune as a whole, on which three quadrats were located.
Figure 6: Please use east/west/north/south flanks, not right and left.
Hesse and Simpson already used the site names with left and right. As a result, it is not feasible to change the site names at this stage.
Figure 11: y-axis of middle plot should not be Julian Day. These are not technically Julian Days (which is often incorrectly used), it is are Day of Year.
Done.

-Reviewer 2

-
Summary and recommendation:

The authors report 3-4 surveys they performed between 2002-2012 in a few locations in the Simpson and Strzelecki Deserts, Australia. The surveys focused on the vegetated on active crests of sand dunes. During the research period, the research area experienced prolonged drought and recovery as a result of 2010-2012 La-Nina event. The authors study the variability in dune mobility/activity as a result of the variability in crust and vegetation cover, and as a results of the variability of precipitation. They found that accumulated precipitation in the past 90 days drastically affect crust and low vegetation cover while accumulated precipitation in the past three years affect higher vegetation. Based on their observations and analysis, the authors estimated the number of "at-risk" days, i.e., the days at risk of vegetation low cover.

To my opinion the study is certainly important and worth publication in Aeolian Research. Field surveys of sand dunes are very important for the understanding of dune dynamics and the impact of climate variability on dune variability. Yet, unfortunately, the number of surveys is very limited (only 3-4) and the timing of the surveys is, to some degree, problematic. More specifically, only one cite (Della Crest) was examined four times at July 2002, Sep. 2004, Sep. 2005, and Jun. 2012 where all the other sites where surveyed less frequently. In addition, the authors by themselves recognized that dune activity is concentrated during the spring (SON) while the timing of the surveys is just before this season of activity. While I realize that there is nothing that can be done to improve this situation, I think that the conclusions drawn by the authors should be weaken significantly. In addition, there are other issues that the authors may find helpful to improve their manuscript. In summary I recommend publication in AR after major revision, i.e., after considering the comments listed below.
We accept that the number of surveys is small (because it is a severe logistical undertaking to do this fieldwork). We have reviewed the paper to make sure all the findings are suitably qualified (in addition to those we already had included). The reviewer is only partly correct about the timing of the surveys: the 2012 Simpson survey was in September, making the majority of observations in that month, rather than the quieter winter months. In addition, the re-analysis of the higher resolution wind data we undertook at the recommendation of Reviewer 2 strengthened the finding that September is one of the windiest months and that the transition from low DP to high DP conditions occurs between July and August in most years (modified figures 2 and 3).

Major comments:
----

1) To evaluate the study and its findings please specify clearly in the abstract that only up to four surveys were performed during the research period and that these were performed just before the dune activity period.
Modified, but the comments on seasonal windiness have been modified, consistent with the findings described above.
2) In many places the authors refer to (biological) crust as "vegetation". In addition, they distinguish between "low" and "high" vegetation. I believe that there is a fundamental difference between biogenic crust and low level vegetation. In addition, a more reasonable vegetation classification is between "annual" plants and "perennial" plants instead of low and short living vegetation and high and long living plants--the latter is known to affect the long term stability of sand dunes. Thus, I would suggest to classify the vegetation into three classes: biogenic crust, annual plants, and perennial plants. Trees can be another class if needed.

We reviewed all usage of the term 'crust' and found 3 cases where it was necessary to disambiguate the sentence. We clearly explained our inclusion of both cyano-bacterial and physical crust under the term 'crust' in section 3.2 and repeated it in the conclusion as well as the abstract. Where we have treated crust and low plants together it was only after identifying that they independently share a common (tentative) antecedent rainfall threshold but we always described them as being separate components.

We firmly disagree that the terms 'annual' and 'perennial' are sufficient to describe the vegetation on these dunes. We followed previous Australian studies (Clarke et al., 2005; Nano and Pavey, 2013) in using a terminology combining both form and longevity (Table 3). None of the plants we encountered can be adequately described as annual. In this subtropical desert, temperature is rarely limiting and plants are observed to germinate and grow during winter if the conditions (including rainfall) are suitable. These plants can be described as ephemeral but we follow Clarke et al., and Nano and Pavey in using the term 'short-lived'. Likewise, we also included the third group of 'longer-lived' because it is highly appropriate to a group of larger plants whose life-cycle lasts only 1-3 years.

3) Throughout the paper I did not see estimation for the significance of the results. More specifically, what is the variability between the different research plots? Can the authors average the different measures between the different research plots of the same location? Alternatively, it is possible to divide each research plot into, e.g., four quarters and calculate the mean and the maximal minus the minimal values as error bars. This will provide some measure of dispersion of the results and will hint about the confidence of the results.

We are very aware of the lack of replicates in this study. We have shown significance for the regressions in figure 7 but do not believe that it is appropriate to apply either regressions or measure significance in any other cases. We believe that in these figures (7 and 8) we have combined enough independent observations to make meaningful (if restricted) statements about the response of sand movement and vegetation to climate variability.

While the climate is similar between the two sites, they are different enough to prevent a legitimate averaging between them (which, in any case, would only really increase the sample size from 1 to 2). We believe that the proposed sub-division of the plots would be pseudo-replication and not valid.

4) Lines 131-152: the calculation of DP and RDP. There are several issues here. First, explain how exactly (using formula) you calculated the DP and RDP. Second, the calculation of the DP is based only on two daily values. Since the DP is basically proportional to cube of the wind speed, such calculation can lead to large deviation from the real DP. Third, the authors average the DP in non-conventional way. I suggest to use the conventional averaging procedure of Fryberger (1979), to allow easier interpretation of the results, and to be able to compare the results to previous studies. The values reported by the authors are much larger than the conventional values, which, according to previous studies, should be around DP~100 in the study region. Forth, I suggest to also use (6-hourly and high resolution) reanalysis data to estimate the DP and RDP in the research area; see comment 10 below.

We have already commented on this issue in response to reviewer 1 (above). Firstly, the study by Ashkenazy et al. (2012) shows the limitations of the reanalysis data. They derived DP (using Fryberger's method) from observational records (from NCDC), NCEP reanalysis and ECMWF reanalysis data. For the Simpson/Strzelecki area they used no observational records (the closest being Alice Springs) and consequently much of the area of interest is blank. The area to the SW showed DP values >250 and areas to the NE values <200. The NCEP-derived DP values for the area of interest were around 400, while the ECMWF values were <50. We have cited Ashkenazy for the instrumental values but we believe that the reanalysis data are not suitable for this task.
We reiterate that we have only used our derived DP values for internal comparison. We have referred the reader to Ashkenazy for a global view (with its limitations). The only other specifically Australian study (Kalma et al., 1988. J Climatology) used only 3pm wind speeds, in ms-1, and only 4 months (January, April, July, October) to characterize the seasonal cycle and annual values. None of these are comparable with the original Fryberger values.
We believe it is preferable to use the best and closest observational records - being Birdsville and Moomba. Both these sites have high quality automatic weather station records (since 2000 and 1995 respectively). While the peripheral task of providing some international comparison may be served by using Fryberger and Dean's original method, we believe that taking maximum advantage of the high quality data best serves the central goals of this study. To that end, rather than bin data into velocity and direction classes, we have modified the Fryberger method by calculating $(V-V_t)V^2$ for each observation and weighting each observation (according to the number of above-threshold observations each day, the number of observations each day and the number of days each year). To derive the RDP and RDD, we added the vectors for each observation (weighted). These details are now added to the methods section.
In response to suggestions from both reviewers we did obtain new records of 3-hourly observations from both sites and analysed those records for this revision. We believe this has overcome one of the problems which we flagged with the original analysis – absence of wind measurements from the windiest time of day. The Australian Bureau of Meteorology does not supply hourly observations. We noted that Fryberger and Dean (1979) used a combination of 3 hourly and 6 hourly observations in their study.

Other comments:
----

1) There are several studies that discussed the variability of vegetation and biogenic crust on vegetated linear dunes but not cited by the authors. These are closely related to the present study and probably the authors will benefit from reading them.
Some additional citations have been added, where appropriate.

2) Abstract: A) Include briefly the size if the research plots (e.g., "~25x25 m"). B) Mention that dune's activity exhibits seasonal variations and that you measure this variability during the summer period. C) Line 9: "negative" correlations?

We added the plot size and the seasonality (winter and spring) of the measurements. It is an inference, not an observation, that there is more sand transport ('dune activity') in spring. We change negative correlation to inverse relationship.

3) line 44: elaborate briefly on the mobility index M.

done

4) line 64: "to be proportional to vegetation cover". This statement is valid only up to a certain threshold as several studies reported that the sand is masked from the wind when the vegetation cover reach a certain value (e.g., Wolfe and Nickling, 1993; Bullard, 1997; Wiggs et al., 1995; Wiggs, 2008; Ash and Wasson, 1983). See comment 23 below.

We referred to all of these papers (except Bullard - which does not derive a vegetation threshold) later in the paper when discussing the results, the limiting role of vegetation and threshold responses. We could not locate any relevant paper authored by Wiggs in 2008 or around then.

5) lines 63-65: wind suppresses the growth of vegetation in two ways: the wind exerts stress on vegetation and thus suppresses the growth of vegetation and sand movement limit growth of vegetation(though root exposure and plants burial. Please elaborate on this if relevant.

This topic is not the focus of this study. We added an extra citation (Bel and Ashkenazy) relevant to controls on plant growth in modeling studies (including precipitation) but it is too far off topic to go into empirical studies as suggested.

6) line 91: I guess that by vegetation the authors refer also to crust. Following my comment above, I would suggest to explicitly mention "crust and vegetation" to avoid any possible misunderstanding.

Modified as suggested.

7) line 104: mention crust explicitly.

Added

8) line 115: please describe briefly the research sites either here on in an appendix, to make the paper more "readable".

We added a paragraph giving a physical description of the dunes.

9) line 123: why only the crests were surveyed? Please explain. Also mention that the surveys were conducted during the months June, July and Sep.

Season was added. We have rewritten the earlier sentences in this paragraph and, together with the new site description, believe that it is clear that the dune crests are the most dynamic parts of the dune and of interest because they show (by the distribution of patches) the transition from active to inactive states.

10) Fig. 1: it will be useful to add to this figure maps (as the lower panel of the figure) of mean precipitation and wind power (DP), to give a general idea regarding the climate in the area. These can be constructed based on reanalysis data (like the 6-hourly high resolution ERA-Interim or NCEP reanalysis). Also mention in the caption that the meteorological data was collected from Birdsville and Moomba stations.

For the reasons stated above, regarding DP, we do not believe that the reanalysis data is reliable or suitable. There are very few meteorological stations in these areas (as the reviewer shows below). There are no meteorological stations within the Simpson Desert and very few within the Strzelecki Desert. As a result, combined with the high variability of the climate, the actual pattern of climate within the dunefields is unknown and must be extrapolated and this cannot be done well. Generally, even BoM maps of annual average precipitation over Australia do not show contours below 200 mm because the data is sparse and the patterns are not reliable. We have summarized the relevant climatic statistics for Birdsville and Moomba in Table 2 and believe this is sufficient to inform the reader of the nature of the climate.

11) The NCDC hourly database contains some stations in the study region. The authors may find better (hourly) data from this database. The stations includes:

Station no.	Station name	Lat.	Lon.
943340	BEDOURIE POLICE STA	-24.367	+139.467
944800	MARREE	-29.650	+138.067
944810	MOOMBA (PRIVATE)	-28.117	+140.217
944820	BIRDSVILLE POLICE S	-25.900	+139.350
944850	TIBOOBURRA POST OFF	-29.433	+142.000
954800	MARREE AERO	-29.667	+138.067
954810	MOOMBA AIRPORT	-28.100	+140.200
954820	BIRDSVILLE AIRPORT	-25.900	+139.350
954870	BALLERA GAS FIELD	-27.417	+141.817

We could not locate the data on the NCDC website. We already have daily data for some of these sites (incl 9am and 3 pm wind speeds) from the BoM. All are further from our field sites than Birdsville and Moomba. Generally, other sites have lower quality (more gaps, for example) and lower frequency observations. We obtained new 3 hourly wind observation data from Moomba AP and Birdsville AP and made new analyses based on that data.

12) Table 2: A) please present the mean value of 2002-2012 as this is the period that you focus on. B) How come the error bars (std?) of the median precipitation are as large as the mean value itself? Please recheck.

a) Done. We added long-term average precipitation figures to give a larger context.

b) The rainfall is highly variable, reflected in the standard deviations. Inclusion of the 2010-2011 precipitation, particularly, increases the scatter of measurements (see figures 2 and 3). The distribution is, as a result, highly skewed. The distribution of differences from the median precipitation is log-normal and so a simple SD is not strictly a good measure of the variability. To this end we added standard error values for annual precipitation.

13) lines 169-172: please specify more clearly how did you determined the presence of crust and its level of development. Visual inspection is crude.

We have described the method which identified very effectively the relevant physical property: the binding or cohesion of the sand grains, even if our method is very simple. This is why we also stated that we did not/could not distinguish between biological crust and physical crust. To confirm the presence of a cyanobacterial crust in each of our thousands of observations would indeed require much more sophisticated analysis, time and cost.

14) lines 177: according to previous studies, skimming flow can occur even under partial cover of vegetation.

We added the clause 'or closely spaced'.

15) line 184 and Fig 2a,b: it will be useful to present also the mean seasonal cycle with the seasonal standard deviation as error bars, to clearly visualize the existence or absence of the seasonality.

The figure was redrafted (with new wind data) as box plots. These more clearly show the central tendency.

16) lines 196-197: you can mention here that, in general, the wind over vegetated linear dunes is bi-directional.

The sentence was changed to include this idea.

17) lines 208 and 209: are the years should be 2001 instead of 2002 and 2011 instead of 2012?

The sentence has been modified. The intention was to compare the years of field survey, not the highest or lowest on record.

18) Fig. 2 and 3: I suggest to be consistent and to cover the same time interval in these figures.

We understand the motivation for the comment. However high quality AWS wind observations began at Moomba in 1995 and Birdsville in 2000. It would not be reliable to combine these records with the older observational records (different locations, different methods). However, we feel it is useful to show the additional 'average' years (1995-2000) at Moomba to give a greater context for the drought and following wet period. In table 2 we have given climatic averages for the decade 2002-2012.

19) Table 3: I suggest to also include in this table the type of vegetation, annual or perennial.

The form and longevity (= type) have already been included. We have discussed, above, our preference for categories other than 'annual' and 'perennial'.

20) The figures seem not to be in order. For example, in line 197 you mention Fig. 12, before mentioning Figs. 4-11. Another example is Fig. 6 that is mentioned in lines 271-272, before discussing Fig. 4. Please check.

In the case of the reference to figure 12, we thought it would be helpful to direct the reader to this graph of RDD because RDD is mentioned in the description of the wind climate here. However the figure attempts to illustrate a different point only covered in the Discussion and including data which only makes sense after reading the Discussion. Therefore we do not believe it would be helpful to the reader to move the figure. The reference to the figure at this point seems to us to be the lesser of two evils. The issue is less important for figure 6 and we have re-ordered figures 4, 5 and 6.

21) lines 290-292: what was the crust cover at that time?

Added to the paragraph
22) Fig. 5: please provide details regarding this figure. What is "H" of title of the x-axis and what is its value?
H refers to height (in cm) – the y-axis values. The figure caption has been modified.
23) Fig. 7: explain in more details what is the frontal area index. In addition, the panel showing the ripples area versus plant cover seems to indicate the existence of critical cover. I.e., when excluding the the full circle at the upper top corner, one can fit a step function like function to the observation, thus suggesting a critical vegetation cover at ~50% above which no ripple are observed. This will be consistence with previous studies (e.g., Ash and Wasson, 1983).
A definition of the FAI derivation was added to the methods section.
Thankyou for pointing out this possibility. However, we are not so sure that such a definite conclusion is valid. The relationship between vegetation cover and ripple coverage (recently mobilized sand) found here (Fig. 7) can be modeled by a simple linear regression ($r^2 = 0.77$). However, the distribution of residuals is not uniform and another model may be more suitable. Visually, it is possible to infer a break or change in the relationship at around 50% vegetation cover. Consequently, the data above and below 50% vegetation cover were split and linear regressions were fitted to each set of data (Fig. 7). The correlation coefficients (r^2) are 0.6 for quadrats with high cover but only 0.19 below 50% cover. An alternative non-linear model is suggested by the higher Spearman $\rho = -0.90$. A cubic regression model has the highest $r^2 = 0.86$ (compared with linear or quadratic), is significant, but has unusually high residuals and predicts a physically unrealistic reversal of ripple cover at low vegetation cover levels, a product of the small number of measurements. A further alternative is a simple clustering of points above and below 50% cover. We retain the linear model as having high explanatory power but acknowledge that alternative models are possible. The evidence here for a threshold response of sand movement (ripple cover) to vegetation cover, as has previously been proposed (e.g. 40% - Ash and Wasson, 1983; 16% - Lancaster and Baas, 1998; 14% - Wiggs et al., 1995; 16% - 40% Wolfe and Nickling, 1993), is therefore ambiguous and requires further data to be adequately tested.
24) line 370: please add citation here.
It would be unusual to repeat the same citation in the same sentence.
25) line 377: see comment 23 above. In fact it seems that your data indicates the existence of a threshold value.
See comments above. We do not believe it is possible to be so definite.
26) lines 400-402: the authors do aware to the fact that their observations are not sufficient to asses statistical confidence. I would thus suggestion to refrain from concluding regarding the threshold.
We used the word ‘suggest’ twice in these three lines to indicate the tentative nature of this interpretation. We have added the word ‘tentatively’ to further declare this.
27) lines 404-405: it is known that crust can withstand prolonged droughts and strong winds. I would thus suggest to exclude the statement included in the brackets.
A mention of crust durability in other parts of the world has been added to the Discussion section. It is worth noting that we cannot be sure of the comparability of

those findings to our study because we have included both biological and physical crusts under this category. A new study (Kidron et al., 2017) documents a mechanism for weakening and erosion of cyanobacterial crust beneath patches of mobile sand.

28) Fig. 8: in all panels the measurements are scattered, indicating low statistical confidence. This was acknowledged by the authors but yet questioning the conclusions of the study.

The word 'scattered' does not describe the nature of the data. The problem (specifically in figure 8) is the poor distribution of antecedent rainfall values, concentrated in the low range with only one set of observations with high antecedent rainfall and no intermediate values. We have been very open about the limitations and specifically reviewed the language of the conclusions (Conclusions section and abstract) to be sure that we do not misrepresent the data and the inferences drawn from them.

29) lines 476-477: this, of course, depends on the intensity of the rain--intense rain (that often occurs in arid areas) can result in runoff on the crust and thus to lower infiltration compare to more gentle rain.

A comment to this effect has been added to the Discussion. We note that figure 9 shows that the frequency of low intensity 'storms' is higher than high intensity storms and the frequency of low intensity sorms is similar in both dry and wet years.

30) Fig. 12: I suggest to include also the seasonal mean and seasonal standard deviation.

Box plots of DP have been used in the revised figure and mean values of RDD have been shown in addition to the scatter of monthly values.

31) line 598: do you mean "crust cover"?

The sentence has been reworded to make it clear that we are referring to ripple cover (i.e. recently transported sand).

32) lines 639-640: maybe your results can shed some light on the question of the role of annual plants on the stabilization of sand dunes.

We're not entirely sure of the nature of the question. We have spelled out the roles of both vegetation elements on these dune crests.

33) line 653: is this statement valid also for crust cover?

We specifically mean vegetation because of the relationship we found between ripple cover (as a proxy of sand transport) and vegetation cover (not including crust) (Figure 7). We make the distinction with the effect of crust in the next sentence.

Complexity confers stability: Climate variability, vegetation response and sand transport on longitudinal sand dunes in Australia's deserts

Abstract

The relationship between antecedent precipitation, vegetation cover and sand movement on sand dunes in the Simpson and Strzelecki Deserts was investigated by repeated (up to four) surveys of dune crest plots (≈25x25 m) over a drought cycle (2002-2012) in both winter (low wind) and spring (high wind). Vegetation varied dramatically between surveys on vegetated dune and active crests. Indices of sand movement had significant correlations with vegetation cover: the depth of loose sand has a strong inverse relationship with crust (cyanobacterial and/or physical) while the area covered by ripples has a strong inverse relationship with the areal cover of vascular plants. However, the relationship between antecedent rainfall and vegetation cover was found to be complex. We tentatively identify two thresholds; (1) >10 mm of rainfall in the preceding 90 days leads to rapid and near total cover of crust and/or small plants <50 cm tall, and (2) >400 mm of rainfall in the preceding three years leads to higher cover of persistent and longer-lived plants >50 cm tall. These thresholds were used to predict days of low vegetation cover on dune crests. The combination of seasonality of predicted bare-crest days, potential sand drift and resultant sand drift direction explains observed patterns of sand drift on these dunes. The complex vegetation and highly variable rainfall regime confer meta-stability on the dunes through the range of responses to different intervals of antecedent rainfall and non-linear growth responses. This suggests that the geomorphic response of dunes to climate variation is complex and non-linear.

Keywords: Simpson Desert; Strzelecki Desert; climate change; aeolian

1. Introduction

Vegetated sand dunes are widespread in the deserts and desert margins of all continents except Antarctica. They are often the foundation of commercial or subsistence grazing economies in drylands. The response of vegetated dunes to future climate change has been investigated using model scenarios of future climate state and empirical relationships between average climate, dune vegetation and sand transport (Knight et al., 2004; Thomas et al., 2005; Yizhaq et al., 2009). However, the response of arid land vegetation to climate on both climatic (seasonal – multi-decadal) timescales, and timescales of sand transport events (seconds – days), is poorly described (Nano and Pavey, 2013) and the effect of vegetation on sand transport rates is based on a limited body of empirical data (e.g. Kuriyama et al., 2005; Lancaster and Baas, 1998).

Longitudinal sand dunes present an additional complex set of conditions, with variable wind strength (Wiggs et al., 1996), wind direction and vegetation cover over the dune surface. Wiggs et al. (1995) found an exponential relationship between dune surface mobility and exposed (non-vegetated) surface area as well as a complex distribution of sand mobility over the dune surfaces. This is consistent with observations of the climate parameter M (the ratio of frequency of strong winds to the effective precipitation at a site) (Lancaster, 1988), describing dune mobility, driving variations in sand transport, modified by lags in vegetation response (Lancaster and Helm, 2000). Bullard et al. (1997) also found that M is variable on inter-annual to decadal timescales and proposed that this variability results in fluctuations in dune activity in the Kalahari Desert.

Drought has been proposed as a disturbance which may result in activation of dunes (Forman et al., 2006; Mangan et al., 2004) by reducing protective plant cover. A recent study of the impacts of the prolonged drought in the Israeli dunes (Siegal et al., 2013) concluded that although vegetation cover had been reduced dramatically, following a lag of some years, the dunes were unlikely to become active because of the persistent biological crust. By contrast, a further study (Kidron et al., 2017) found that biological crust was degraded and ruptured during drought by complex interactions with mobile sand areas. These results highlight the importance of both the degree and duration of drought (Mangan et al., 2004), as well as the complexity added by diverse flora (Nield and Baas, 2008).

There are other important drivers of vegetation change on sand dunes. Tsoar and others (Thomas and Tsoar, 1990; Tsoar and Møller, 1986) have described how the removal of vegetation by over-grazing has led to widespread activity of Sinai dunes, separated by a national border from well-vegetated and largely stable dunes where grazing is currently restricted in Israel. Fire is also another vegetation disturbance factor which has been proposed as a driver of sand dune activation (Barchyn and Hugenholtz, 2013). Fires in Australian desert dunefields have been documented to reduce covering vegetation for years (Levin et al., 2012; Strong et al., 2010). In the eastern Simpson Desert, fire area has been shown to have a complex relationship with antecedent rainfall and drivers of rainfall variability (Greenville et al., 2009). However, none of these studies have documented sand transport or dune activity following fires and the effectiveness of fire in driving dune activation has been questioned because of this lack of evidence (Barchyn and Hugenholtz, 2013).

However, the role of vegetation as a driver of dune activity or passive response is disputed. For example, a recent model of dune activation (Yizhaq et al., 2007; 2013) proposes that the transition from dunefield activity to stability and back, is dependent on wind strength, and that dune stabilization occurs through wind velocity relaxation. Certainly, wind strength has long been linked to sand transport rates (Bagnold, 1941) and sand transport has also been shown to be proportional to vegetation cover (Kuriyama et al., 2005; Lancaster and Baas, 1998), however the extent to which wind limits plant growth is not well known. Models of dune evolution which incorporate vegetation (Duran and Herrmann, 2006; Nield and Baas, 2008) utilise growth functions partly dependent on wind-driven sand transport rates but also with growth 'vigour' manipulated to achieve the effects of dry or wet periods (Nield and Baas, 2008; Bel and Ashkenazy, 2014).

The actual impacts of drought on vegetation can be very severe at ecosystem scales (Ponce Campos et al., 2013) and landscape scales (Nano and Pavey, 2013). However, this response has been found to be complex and non-linear (Reynolds et al., 2004). Rainfall frequency and amount are important in determining plant growth response (Schwinning and Sala, 2004). The pulse-reserve model (PRM) suggests that a pulse of resources (precipitation) will produce a growth response (reserve) if there is sufficient rainfall to increase soil moisture and sustain growth for each plant functional type. Some rainfall events are ineffective if they are either too small or not followed by further rain (Fernandez, 2007; Nano and Pavey, 2013).

Around 2000, much of eastern Australia entered a long drought (the 'Millennium Drought') which lasted until it was broken by a strong La Niña event in 2010 (Gergis et al., 2012; Timbal and Fawcett, 2013; Wardle et al., 2013). The extreme 'Millennium Drought' provides an opportunity to test the response of vegetation and sand transport over the most extreme range of climate variability in Australia in the modern era. In this study, we present the first analysis of dune vegetation response over an entire decadal drought cycle.

Together with data from Hesse and Simpson (2006), additional surveys from Simpson and Strzelecki sites in 2005 and 2012 are used to analyse (1) the response of sand mobility to vegetation cover, and (2) the response of vegetation on dunes to precipitation, to better understand how dunes respond to climatic variability, (3) over both the drying and wetting phases of a drought cycle. This study aims to better understand the responsiveness of desert dunes to climate forcing, specifically the role of vegetation cover and crust in limiting the availability of transportable sand. Assumptions regarding the response of vegetation cover to climate change underlie the interpretation of sand dunes as proxy indicators of past climate where alternative sources of palaeoclimate proxy data are limited (Thomas and Burrough, 2012).

2. Field Sites and Methods

In this study, sand dunes within the Strzelecki Desert dunefield (Della, Bosca and Teilta dunes) and Simpson Desert dunefield (Mayan and Aztec dunes) were investigated (Fig. 1; Table 1). The sites have been described previously (Hesse and Simpson, 2006). Dunes in each area are longitudinal, tending to dendritic in the Strzelecki, and are composed of medium red sand with very low clay content, in contrast to some source-bordering dunes in the same dunefields (Wasson, 1983). The Simpson Desert dunes (Mayan and Aztec) are around 20 m high, spaced around 1 km apart separated by broad flat interdunes with exposed cay-rich sediment and some pans. Both dunes and interdunes are well vegetated, generally, but there is a strong zonation of vegetation according to substrate and elevation on the dunes so that the dune crests are usually the least well-vegetated parts of the landscape and with a distinctive species composition. The Strzelecki Desert dunes (Della, Bosca and Teilta) are less well organized (more junctions and terminations, wavy crests), smaller (8-10 m) and more closely spaced (≈300 m). The dune crests share many of the characteristics of the Simpson dunes, including the plant species, but the interdunes have a different character (more rounded) and vegetation (different shrub and tree species).

The field area is one of moderate to low wind energy (Kalma et al., 1988). Ashkenazy et al. (2012) derived DP over Australia from 6 hourly observational data (NCDC) according to the method of Fryberger and Dean (1979). Although much of the Simpson and Strzelecki was an area of no data, areas to the southwest had DP values in excess of 250 vector units (intermediate energy environment of Fryberger and Dean) while areas to the northeast had DP less than 200 (low energy environment). The overall pattern is of declining sand transport potential towards the centre of the continent.

The Mayan and Della sites were chosen in 2002 to be 'representative' of their areas, in which dunes were largely vegetated and lacking mobile slip faces. However, there are bare areas of active sand movement, usually restricted in area and to the dune crests, throughout the dunefields including on dunes neighbouring Mayan and Della sites. In 2004 the Aztec (neighbouring Mayan) and Bosca (neighbouring Della) sites were selected to measure vegetation and sand dynamics on these bare areas as a comparison with the vegetated crest sites (Mayan and Della). At each site quadrats were established on the narrow crests and surveyed up to four times between 2002 and 2012 in winter or spring (Table 1). Quadrats were also measured on the flanks of Della and Mayan dunes in 2002 only (Table 1). In 2002 and 2004 total station surveys were made of each crest quadrat at 1 m intervals.

Figure 1

Weather observations from Bureau of Meteorology automatic weather stations (AWS) at Birdsville and Moomba were used to derive time series of several climatic variables. In addition, older observer-based stations nearby were used for long-term precipitation statistics only (Table 2). AWS records of 3-hourly wind speeds and directions, and daily maximum gust were utilised. The 3-hourly records of wind speed and direction were used to calculate the total sand drift potential (DP), resultant sand drift potential (RDP) and resultant drift directions (RDD) following a modification of the method of Fryberger and Dean (1979). With access to highly accurate metered observations it was decided not to bin observations into velocity or direction classes. The units are thus not comparable to previous studies which utilise binned data (e.g. Ashkenazy et al., 2012; Kalma et al., 1988).

Daily DP (DP_d) was calculated as the sum of the above-threshold wind measurements, converted to $m.s^{-1}$ (Bullard, 1997):

$$DP_d = \Sigma(V-V_t)V^2 a b^{-1} d^{-1} \quad (1)$$

Where V is the measured wind velocity at 10 m above ground height (converted to ms^{-1}), V_t is the threshold wind velocity, *a* is the number of above threshold wind observations each day, *b* is the number of wind observations that day, and *d* is the number of days per year. A threshold wind velocity of 22 kmh^{-1} (6.11 ms^{-1}) was adopted, being the metric equivalent of the threshold velocity of 11.6 knots adopted by Fryberger and Dean (1979) to describe the threshold velocity required to entrain a medium sand grain of 0.3 mm diameter. Monthly and annual DP values were calculated from the sum of the daily values. Monthly and annual RDP and RDD were calculated from the sum of DP_d vectors.

Table 1

Table 2

Measurement at each quadrat consisted of a combination of point and line intersection surveys (Hesse and Simpson, 2006). Presence or absence of ripples, loose sand, crust and vegetation was noted at each point on the 1 m grid (except where noted in Table 1) as well as the depth of loose sand above the crust, if present. The height, width and species (if determinable) of plants at each survey point and along each survey line were also recorded. Coverage was calculated as the percentage of points where vegetation, crust or ripples were recorded. Frontal area index (FAI) was calculated as the ratio of the sum of the silhouette areas (height x width) of each plant to the quadrat area. Although the survey method accounted for larger plants and clumps of plants, isolated small plants which did not overlie a grid point were not recorded resulting in an underestimation of cover by the line intercept method and, most likely, FAI. The identification of plants was particularly difficult in 2002 when most forbs were dead, in which case they were only recorded to structural group level (i.e. forbs, grass etc.). Crust was determined by physical resistance and the cohesion of sand grains into aggregates. In some cases the crust was clearly cyanobacterial, with visible filaments, but in other cases it was not and may have been physical, rather than biotic (Hesse and Simpson, 2006). Cyanobacterial crust was also found in interdunes of the eastern Simpson Desert by Strong et al. (2010). Mosses and lichens were not observed.

At each point vegetation was recorded as present if it was within the 'canopy' of the plant. This therefore includes ground, basal and foliar cover and was adopted because of the highly variable degree of porosity (in aerodynamic terms) of the dune vegetation.

Many small forbs occur as clumps or areas with overlapping or closely spaced canopies and the effect is of a continuous mat creating skimming air flow.

3 Results

3.1 Climate Variability

Analysis of daily meteorological observations at Birdsville Airport (since 2000) and Moomba Airport (since 1995) reveals very similar climatic characteristics (Figs 2, 3). Rainfall at these sites is highly variable at intra-annual and inter-annual timescales (van Etten, 2009) and there is no rainfall seasonality (Figs 2a and 3a): high rainfall or zero rainfall months have occurred at all times of year. There is a weak influence of El Niño Southern Oscillation (ENSO) in this area (Freeman et al., 2011). Major wet periods in the Simpson and Strzelecki rainfall record correlate with positive Southern Oscillation Index (SOI) (Wolter and Timlin, 2011) and two prominent wet periods associated with La Niña events are evident in the records in 1998-2001 and 2010-2012 (Figs 2d, 3d). The Millennium Drought (from around 2001 to 2009 in this area) was most severe in eastern and southern Australia (Timbal and Fawcett, 2013) and this is reflected in the diminished magnitude and duration of rainfall deficits in Birdsville compared with Moomba (Figs. 2d and 3d).

In contrast to precipitation, there is a strong and clear seasonal pattern to the wind climate, particularly at Birdsville (Figs 2b, 3b). Strong sand-transporting winds are experienced in spring and summer (August to March) although there is still pronounced inter-annual variability in summer maxima (Figs 2c, 3c). There is a seasonal shift from SE winds in summer to SW in winter (Fig. 12) consistent with the seasonal shift of the subtropical high pressure belt. Overall, the wind directionality is low (low RDP/DP;

Table 2) in the range associated with longitudinal dunes (Fryberger and Dean, 1979; Wasson and Hyde, 1983). Although there is a crude relationship between Interdecadal Pacific Oscillation (IPO) and variations of DP and RDD after 1960 (Hesse, 2010) there is no relationship between DP and precipitation on either seasonal or inter-annual time-scales.

Field observations were conducted between July 2002 and September 2012 (Table 1; Figs 2 and 3). The first two (Simpson) or three (Strzelecki) field seasons occurred within the worsening (Strzelecki) and continuing (Simpson) drought that began in 2001. The last field season in 2012 followed the 2010-2012 La Niña event in which higher than average rainfall was experienced at both sites. The observations, therefore, capture a full decadal drought cycle. Both sites recorded higher DP at the time of survey in 2002, declining a little in 2004 and 2005 and lowest in 2012 (Figs 2c, 3c).

Figure 2

Figure 3

3.2 Vegetation Species and Functional Groups

Although 26 species of plants were identified on the dune crest plots (Supplementary Table 1) there were, in addition, many unidentifiable plants, mostly dead, at most sites. Only a small number of species are common across the sites: principally *Zygochloa paradoxa*, an arenophilic hummock grass found on dune crests across the region. The well-known 'spinifex', *Triodia basedowii*, is more common on the lower flanks and interdunes and mostly occurred outside the surveyed quadrats.

For the purposes of this study it is appropriate to categorise the different species according to their aerodynamic properties (form) and persistence (Table 3). These are similar to previously identified plant functional types (PFT) in the Simpson Desert (Nano and Pavey, 2013) but explicitly recognize the aerodynamic properties and surface sheltering effects.

Table 3

Crust was observed at all sites. Evidence from shallow pits shows that cyanobacterial crust (identifiable by small filaments) can colonise, bind and stabilize sand to form laminated deposits. Forbs, together with smaller numbers of sub-shrubs and tussock grasses, form perhaps the most extensive but also most variable category of plants on the dunes. Generally less than 50 cm in height, and ephemeral (short-lived < 1yr), they often formed 'carpets' of living or dead plants. They were observed to provide effective cover such that although they colonized rippled dune surfaces they did not allow sand transport within the covered area (usually larger than 0.5 m diameter). This category, as has been noted previously (Crocker, 1946; Madigan, 1946), flourishes for short periods following rain and then dies within several months.

The hummock grass *Zygochloa paradoxa* is the most abundant persistent species observed on the dune crests. It was persistent (> 3 years) on all the dune crests throughout the drought cycle (Supp. Table 1), except for Teilta which is outside its range. This plant has multiple stems, with few leaves, emerging from the ground and is effective at trapping sand. Larger clumps may grow to become small nebkha with solid cores and develop scour around their upwind sides, but this effect is less common than in the less porous *Triodia basedowii*.

A smaller group of longer-lived (1-3 years) shrubs and sub-shrubs, of which the most common was *Crotalaria eremaea,* was found in variable abundance at most sites. While growing to over 2 m in height, this group usually has a very small basal area resulting in very little surface cover and appears to be either neutral in terms of sand accumulation or promotes scour. Dead *Crotalaria* persist for some time, with branchlets curled up and towards the trunk (reducing drag and basal area) before toppling to form more effective cover lying on the dune surface.

Woody shrubs and trees persist for 10 years or longer usually and have distinct trunks with very small basal area. The aerodynamic effects are variable: the crowns are mostly dense (low porosity), increasing drag, but the lack of foliage near the ground results in a very small basal area which decreases surface protection and can promote scour. Likewise, the ecological effects are complex. In the shaded area beneath the canopy of umbrella mulga (*Acacia brachystachya*) sub-shrubs (such as Chenopodiaceae) flourish (Fig. 4c, d) and can trap sand. However, beyond the canopy cover is lower, presumably because of root competition for water, and scour was commonly observed (Fig. 4c). Fallen branches were found to provide much better surface cover than living trees, mostly following death of the entire plant. Most quadrats avoided trees because their low number but comparatively large size would both dominate quadrats and be atypical of the greater length of most dune crests. Whitewood (*Atalaya hemiglauca)* on the margin of the Bosca North quadrat were rooted in the flank but were being covered by sand from the eastward advancing slip face.

Figure 4

3.3 Temporal Variation of Vegetation Cover

Three sites, Mayan Crest in the Simpson Desert and Della Crest and Bosca North in the Strzelecki Desert, were re-surveyed over ten years (Fig. 5). Mayan Crest, a vegetated dune with no slip faces, retained its vegetation cover over the ten years of survey however the composition and cover changed dramatically throughout this period. In 2002, crust cover was relatively low (53%) and hummock grasses (*Zygochloa paradoxa*) dominated the vegetation. In the 2004 survey, hummock grasses were still present (largely the same clumps) but the cover of forbs had increased dramatically and crust was present over 97% of the quadrat. The 2012 survey again found hummock grasses but they were much larger following the 2010 to 2012 La Niña event and a dramatic expansion of shrubs such as *Crotalaria* was evident. Only in 2012 was leaf litter present on the quadrat, often formed by or trapped by sub-shrubs and shrubs (e.g. Chenopodiaceae, *Crotalaria*). Crust was recorded covering 91% of the quadrat in 2012.

Della Crest shows many of the same trends as Mayan Crest: following the initial survey in 2002 there was an expansion of crust in later surveys and extensive cover of forbs in 2004 and 2005 as hummock grass clumps (*Zygochloa paradoxa*) simultaneously decreased in size during the prolonged drought. In 2012 recovery of the hummock grass and a dramatic expansion of the shrubs, particularly *Crotalaria* was evident. However, like Mayan Crest, forbs were scarce and litter was present for the first time.

The pattern at Bosca North, a bare area with slipface on the neighbouring dune to Della, was quite different. First surveyed in 2004, there was a moderate scatter of forbs on the left side of the quadrat, a largely bare crest with eastward facing slipface descending to a line of whitewood (*Atalaya hemiglauca)*. In 2005 there was an expansion of crust, a less prominent, symmetrical crest line, and reduced cover of forbs. In 2012 the slip face had re-established, at an oblique orientation, and was free of crust but forbs were absent from the quadrat (Fig. 5).

Figure 5

Vegetation height distributions (Fig. 6) reflect these changes of species composition and cover. At Mayan Crest, Della Crest and Bosca North the abundance of tall plants increased in 2012 while the abundance of small plants decreased. The total plant cover at Mayan Crest and Della Crest in 2012 was similar to 2002 but with quite different physical structure. However the greatest cover was found in 2004 and 2005, although the total silhouette area was lower than in 2012.

The trees and hummock grasses overwhelmingly survived the long drought, even though leaf area, silhouette area and height were reduced in most cases. Individual longer-lived shrubs and sub-shrubs, on the other hand, died and their numbers reduced during the drought but colonised crests to become a significant component of the plant cover following the 2010 to 2012 La Niña event. Conversely, forbs (largely Asteraceae) were most abundant in 2004 and 2005 during the drought and much less abundant in 2012. Crust was widespread during all surveys but least abundant in 2002.

Neither the vegetated Mayan Crest (Fig. 4a, b) or Della Crest (Fig. 4g, h) sites, or their broader areas, changed status during the drought to active dunes with slipfaces. Likewise, the bare Bosca dune quadrats (Fig. 4 I, j) did not change status to become vegetated in the 2010 to 2012 La Niña event. However the Aztec North quadrat was visited, but not surveyed, in 2012 and was well vegetated, effectively indistinguishable from Mayan Crest, and its slipface had disappeared (Fig. 4e, f).

Figure 6

Figure 7

3.4 Relationship Between Vegetation Cover and Sand Transport

Two proxy measures of sand movement were made: the coverage of ripples (by point count) and the coverage of loose sand measured as the percentage coverage (by point count) of loose sand deeper than 10 mm. Loose sand occurs above buried crust at many points allowing the measurement of loose sand depth and also leading to many points recording both ripples and (buried) crust. The depth of loose sand >10 mm was used in preference to the higher value >100 mm (Hesse and Simpson, 2006) because not all sites had sand deeper than 100 mm and a good relationship was found (Supplementary Figure 4) between the two measures.

The results for all sites show that crust cover has a strong relationship with the cover of loose sand > 10 mm depth (Fig. 7) but no clear relationships with either combined plant and crust cover or plant cover or FAI (Fig. 7). Ripple coverage, on the other hand, was strongly related to plant cover, rather than crust cover, combined plant and crust cover, or FAI (Fig. 7). A simple linear regression model (r^2 = 0.77, p <0.0001) was fitted to describe the relationship between ripple cover and plant cover. An alternative model, with a step change at around 50% plant cover is also conceivable.

3.5 Relationship Between Vegetation Cover and Antecedent Rainfall

The relationship between vegetation cover and antecedent rainfall was examined by considering both total plant cover, living plant cover and dead plant cover (Supplementary Figure 1) and the cover of different PFTs against varying lengths of antecedent rainfall (Supplementary Figs 2, 3). The earlier observations (section 3.3) that different vegetation types appeared to have increased or decreased independently of each other over the survey period suggested different responses to the amount of antecedent rainfall or the duration of their response. To examine this idea, the cover (% area based on point counting) of the different cover types (i.e. crust, forbs, shrubs, hummock grass and trees) were assessed against antecedent rainfall measured over the same month (30 days), 3 months (90 days), 12 months, 3 years and the previous summer (DJF) (Supplementary Figs 2 and 3). The analysis was also completed using the FAI of each component as the vegetation measure (not shown).

The only cover functional group that shows a somewhat clear response to antecedent rainfall is crust (Fig. 8; Supplementary Figs 2 and 3), which shows a relationship to rainfall over the previous 90 days. The relationship is weakened because of the poor distribution of rainfall values. For bare dune crests the crust cover appears to increase rapidly from 10 to 20 mm of rain in the previous 3 months, from 48% to 80% cover but only one site (Bosca North 2012) was surveyed at higher values and suggests a less dramatic response to further increases in rainfall. The same pattern appears to hold for the vegetated dune crests but the plots fall into two groups: much lower crust cover in 2002 (40-55%) and very high cover >90%. These results suggest that a crust may form over the dune surface within this 90 day period, or possibly shorter, in response to a quite small rainfall amount. A threshold, rather than continuous, response is tentatively suggested for both vegetated and bare crests with a rapid expansion of crust cover when rainfall in the previous 3 months exceeds 10 mm (or, conversely, degradation of crust when rainfall falls below 10 mm in the previous 3 months).

Figure 8.

Even this low level of association between cover and antecedent rainfall was not evident for other PFTs on either bare or vegetated dune crests (Supplementary Figs 2 and 3). Instead, a grouping of plants according to height (<50 cm and >50 cm) was investigated (Fig. 8). In no case is the relationship strong or are there enough observations to test for statistical significance. Partly this is, again, because most surveys (except 2012) had quite similar antecedent rainfall, especially over longer periods. In both vegetated and bare crests cases there is a possible threshold response in the coverage of tall plants (>50 cm) in response to rainfall over the previous three years > 400 mm (Fig. 8), even though the cover levels are much higher for the vegetated dune crests. This division of plants into height classes may capture both the recruitment of fast-growing shorter and longer-lived sub-shrubs and shrubs (such as *Crotalaria, Acacia murraya* and chenopods) as well as the recovery and growth of persistent species such as *Zygochloa paradoxa.* On vegetated crests there is a possible, but less clear, response of short plants (<50 cm) to rainfall over the previous 3 months but there is no such relationship on bare dune crests (Fig. 8).

4. Discussion

4.1 Sand transport response to vegetation cover

This extended data set, including observations from the drought period in 2005 and 2012, after the La Niña event, strengthens the conclusion (Fig. 7) that crust has a strong influence on the availability of loose sand on the dune crest. However, vascular plant cover is observed to exert the strongest influence on sand transport, as measured by the presence of ripples (Fig. 7). Both results (loose sand depth and ripple cover) show that some sand movement occurs at very high levels (80%) of plant cover and that loose sand cover decreases with increasing crust cover to around full (100%) cover. Hesse and Simpson (2006), using only 2002 and 2004 data, found that deep (>100 mm) loose sand coverage had a strong relationship with combined plant plus crust cover but the expanded data set here, although confirming the importance of crust, did not find any relationship between loose sand depth and either vegetation plus crust or vegetation alone (Fig. 7).

The relationship between vegetation cover and ripple coverage (recently mobilized sand) found here (Fig. 7) can be modeled by a simple linear regression (r^2 = 0.77). However, the distribution of residuals is not uniform and another model may be more suitable. Visually, it is possible to infer a break or change in the relationship at around 50% vegetation cover. Consequently, the data above and below 50% vegetation cover were split and linear regressions were fitted to each set of data (Fig. 7). The correlation coefficients (r^2) are 0.6 for quadrats with high cover but only 0.19 below 50% cover. An alternative non-linear model is suggested by the higher Spearman ρ = -0.90. A cubic regression model has the highest r^2 = 0.86 (compared with linear or quadratic), is significant, but has unusually high residuals and predicts a physically unrealistic reversal of ripple cover at low vegetation cover levels, a product of the small number of measurements. A further alternative is a simple clustering of points above and below 50% cover. We retain the linear model as having high explanatory power but acknowledge that alternative models are possible. The evidence here for a threshold response of sand movement (ripple cover) to vegetation cover, as has previously been proposed (e.g. 40% - Ash and Wasson, 1983; 16% - Lancaster and Baas, 1998; 14% - Wiggs et al., 1995; 16% - 40% Wolfe and Nickling, 1993), is therefore ambiguous and requires further data to be adequately tested.

The silhouette area (FAI) is not a good predictor of sand mobility (Fig. 7). The most likely reason for this finding relates to the complexity of plant growth forms on these dunes. A mixture of taller hummock grasses, shrubs and trees, with large frontal area but low areal cover, is mixed with shorter forbs and sub-shrubs with smaller frontal area but much larger areal coverage (Fig. 4). In 2012 the contribution of the taller plants was greater than previous surveys, following the wet La Niña of 2010-2012, but total surface cover due to plants was lowest because of the relative scarcity of forbs. This conclusion is different to some previous studies (e.g. Lancaster and Baas, 1998; Wolfe and Nickling, 1996) which have investigated, or simulated, much more uniform vegetation in which frontal area and areal coverage are more simply related.

The role of vegetation in contemporary Australian dune mobility and Quaternary dune evolution has been investigated since the 1980s (Ash and Wasson, 1983; Buckley, 1987; Wasson and Nanninga, 1986). Vegetation cover assessed from aerial photographs was determined to be lower than the level necessary to suppress wind transport (Ash and Wasson, 1983) leading to the conclusion that low wind energy (sand drift potential) was responsible for the very low levels of activity seen in Australian desert dunes. Hesse and Simpson (2006) found that biological crust and small forbs, not visible in aerial photography, is a major constituent of the surface vegetation cover on dune crests. They also concluded that numerous modern examples of active dunes in areas of vegetation disturbance illustrated the effectiveness of modern winds when vegetation was removed. The data presented here (Figure 7) strengthen the finding (Hesse and Simpson, 2006) that some sand movement does occur on these dunes even at relatively high cover levels (>40%) but all surveyed sites with active slip faces had less than 50% vegetation cover. Although there is an important morphodynamic distinction between dunes with 'active' crests (slip faces) and those without, some 'stable' crests also have less than 50% vegetation cover (Fig. 7). Such bi-stable states have been observed elsewhere and modeled as a hysteretic response to either the growth or destruction of vegetation (Bel and Ashkenazy, 2014; Yizhaq et al., 2007) or crust (Kinast et al., 2013).

4.2 Variability of vegetation cover in response to rainfall

These observations point to some of the complexity of response of this complex vegetation: short-lived forbs appear to behave quite independently of the longer-lived shrubs and persistent trees and hummock grasses. The unexpected finding of this study is that, despite large variations in the abundance of different plant functional groups on the dune crests, there was no clear relationship between cover and antecedent rainfall (Fig. 8; Supp. Figs. 1 and 2). There is the suggestion that thresholds of antecedent rainfall may account for dramatic changes in the cover of crust, small plants and tall plants (Fig. 8).

Possible reasons for the weak or non-existent relationships between areal cover (or FAI, not shown) of plant groups and antecedent rainfall include the persistence of dead vegetation, which has an important aerodynamic effect but imposes a lag on possible responsiveness of measures of vegetation growth (cover) to environmental drivers. A similar explanation was proposed by Lancaster and Helm (2000) for an observed lag between sand transport and the climatic index M in southwest USA. It is also possible that the concentration of our observations in the cooler months (June, July and September) has biased the observations, however winters are relatively warm and still capable of allowing recruitment and growth of plants, as observed at many sites. It is also possible that other characteristics of precipitation, such as storm magnitude and intervals between storms, and the timing of surveys following critical storms may have influenced plant cover levels but have not been detected by the analysis.

The severe drought from 2000 - 2009 caused a reduction in net primary productivity (NPP), at the biome scale, across all climatic zones from the most arid to the most humid in both Australia and the USA (Ponce Campos et al., 2013). Conversely, the 2010 – 2011 La Niña event caused a large increase in plant growth across Australia, including the Simpson and Strzelecki Deserts (Wardle et al., 2013). Monitoring vegetation on sand dunes in the NW Simpson Desert at the end of the Millennium Drought and into the following La Niña wet period, Nano and Pavey (2013) found different responses in different PFTs. With some subtleties, their findings supported the pulse-reserve model (PRM) that vegetation productivity responds to pulses of precipitation in arid environments. Generally, wetter years saw more vegetation on 50 m x 50 m plots on sand dunes compared with 'normal' (dry) years (Nano and Pavey (2013). However, the relationship they derived is not linear and the grouping of pulses of precipitation, as well as their seasonality, was shown to have an effect. They found that short-lived grasses respond to summer rains (even small events), dominant in gibber (desert pavement) non-dune sites, while shrubs (dominant on dunes) respond to winter rain storms, even while summer rainfall is dominant. Closely spaced storms in 2010 saw a bigger response than isolated but larger summer storms in 2011. They concluded that this is most likely because of higher and more persistent soil moisture. Importantly, the threshold for response in some ephemeral shallow-rooted species was found to be as low as 5 mm of rainfall. This result may offer an explanation for the observation (Fernandez, 2007) that not all rainfall results in net primary productivity and, that in some cases, this is because moisture is not limiting, while in others it may be that the amount of rainfall is insufficient to allow a response (i.e. be effectively utilised). In summary, the timing of sequential events may be as important or more important than amount.

Analysis of the Moomba meteorological records supports the difference in the distribution of storm magnitudes in dry and wet years (Fig. 9). Dry years have a similar frequency of small storms (~<15 mm) to wet years, or average years, but large storms (>15 mm) are only experienced (although still infrequently) in wetter than average years. This is in agreement with previous studies from other areas (Nano and Pavey, 2013; Schwinning and Sala, 2004) which concluded that dry years have many small events while wet years have more, larger events. Rainfall variability in western and southern Africa and northern Australia (tropical latitudes) is highest for MAP around 400-500 mm (D'Odorico et al., 2013). Hyper-arid areas (e.g. Sahara, northern Atacama, Taklamakan) have very low precipitation variability while neighbouring, less arid, areas have highest variability.

Figure 9

Reynolds et al. (2004) modeled plant response to pulsed rainfall for a variety of PFTs, all with modeled rooting depth to 60-80 cm. They used a threshold of 10 mm of rain for biologically meaningful pulses. Very complex responses in biomass production for different storm sizes and antecedent soil moistures were found. In the Negev Desert drought was found to impact on shrubs but not on biocrust, thus limiting the effect of drought on dune activity (Siegal et al., 2013). However, Kidron et al. (2017) observed the breakdown of crust and subsequent erosion by wind under drought conditions in the Negev Desert, which they attributed to degradation of the crust beneath patches of mobile sand. Measurements along a rainfall gradient (geographic) found some weak positive trends between precipitation (average P) and shrub cover but high scatter between sites weakened the long-term relationship (Siegal et la., 2013). Dune crests showed contrary behaviour to flanks and interdunes. In later drought years the average wettest sites had declining live vegetation and increasing dead vegetation. They found a correspondence between shrub cover and 9-year moving average of rainfall, suggesting a long lag before a response was seen in collapsing shrub cover (and a lag in recovery as well). Our analysis (Fig. 8), while somewhat different, also supports a lag, or buffer, between declining rainfall, up to three years, and the collapse of persistent plant cover.

Overall, then, the results of this study complement a range of other studies that have found weak, complex and lagged responses of desert vegetation and crust to antecedent rainfall. This finding strongly suggests that models, conceptual or quantified, of dune response to rainfall (e.g. Ashkenazy et al., 2012; Knight et al., 2004; Thomas et al., 2005) must recognize this complexity and be mindful that vegetation, and therefore sand transport, responses to climate variability will be complex.

4.3 Model for prediction of susceptibility to sand transport

Threshold antecedent rainfall response has been tentatively proposed (Fig. 8) to explain the vegetation cover on these Simpson and Strzelecki dune crests. Two thresholds are tentatively identified: for crust and small plants (mostly forbs) > 10 mm of rain over the previous three months seems to be sufficient to promote high cover levels. For taller plants a threshold of > 400 mm over the previous three years appears to be important. Taking these as a basis for estimating times of low cover, days were identified which satisfied both criteria of less than 10 mm of rainfall in the previous 90 days and less than 400 mm of rainfall in the previous three years (Fig. 10).

Figure 10

Figure 11

Figure 11 shows the annual and seasonal distribution of days of predicted bare dune crests at Birdsville. Predicted bare-crest days are strongly clustered in consecutive years separated by long intervals without any predicted bare-crest days. This clustering is largely determined by the 3-year antecedent rainfall totals (Fig. 10) that are influenced by longer-term climate variability modes. However, the Inter-decadal Pacific Oscillation (IPO) or related indices only appear to offer an explanation for some of these clusters. Notably, they do not explain the extended drought period from the early 1920s to the mid 1940s. An analysis of regime shifts (non-stationarity) in Australian precipitation records also found that IPO was important but not solely responsible for the observed changes (Verdon-Kidd and Kiem, 2015). The Millennium Drought of the 2000s emerges as having been as severe as any of the 20^{th} century dry periods, in terms of predicted bare-crest days, but of shorter duration than the 1920s-1940s drought (Fig. 11).

Predicted bare-crest days are strongly concentrated in the winter and spring months from May to November at Birdsville (Fig. 12). Potential sand drift (DP) (Fig. 12) is lowest in winter months, increasing from August through to November, and then declining through summer and autumn. Therefore, actual sand drift is likely to be greatest mostly in Spring (ASON) in drought years when winds are typically changing from SW to SE. If the dry period persists from winter through spring then the impact on vegetation may be stronger when the winds strengthen in spring.

The discrepancy between the calculated annual RDD (Table 2) and observed short and long-term sand drift direction (from dune morphology) may be explained by the seasonality of predicted bare-crest days in dry years (Fig. 12). The greatest susceptibility of the surface to sand transport in spring, when vegetation cover is low and DP is high, will favour transport by the dominant SW quarter winds of that season. It is likely that in many well-vegetated dunefields seasonal variations in cover may also introduce a discrepancy between observed drift direction and calculated potential drift directions.

Figure 12

The common perception is that in both the Simpson and Strzelecki deserts dunes are steeper to the right (when viewed looking down-dune (Hesse and Simpson, 2006)) (e.g. Rubin, 1990; Wopfner and Twidale, 1967), although Madigan (1946) noted differences across the Simpson Desert in 1939 with steeper faces to the left on the eastern side of the desert. However, the average annual RDD derived from meteorological observations at both Moomba and Birdsville is only slightly oblique to the local dune orientations (Table 2), to the right at Birdsville but to the left at Moomba. Aztec and Mayan dunes in the Simpson Desert are asymmetrical and steeper on the right flank, with small slipfaces on Aztec dune facing obliquely to the right of the crest line, consistent with the mean

RDD but particularly with spring (and winter) RDD at Birdsville (Fig. 12). Della and Bosca dunes in the Strzelecki Desert are also somewhat steeper on the right flank, although dune asymmetry is less marked (Hesse and Simpson, 2006), while the slip face at Bosca North faces to the right. However, while average annual RDD at Moomba is to the left of the dune orientation (Table 2), spring (and winter) RDD is also to the right (from the SW).

4.4 Stability of Dunes and Role of Vegetation and Climate Variability

In general, the dunes monitored in this study were very stable throughout the intense, decade-long Millennium Drought. The proportion of the vegetated dune crest surfaces experiencing sand transport (ripple cover) varied in inverse proportion to the vegetation cover (Fig. 7) but the vegetated dune crests did not develop mobile sand areas with slip faces. A short (50 cm) stake placed on the crest of Mayan Dune in 2002 was found lying on the surface in 2012, indicating some degree of scour (also observed on the upper flanks through exposed roots) but this was part of a patchy pattern of scour and deposition. This finding was also made by Craddock et al. (2015), who surveyed a dune in the central Simpson Desert from 2006 to 2014 and found up to a metre of deposition in places but a net dune crest accretion of only several centimetres and no change in dune morphodynamic status despite large variations in plant cover.

Likewise, of the bare dune crests surveyed in this study (Aztec and Bosca), Google Earth imagery showed a persistent active slip face at Bosca North (1/12/2010) during the 2010 - 2012 La Niña event. The slip face was oriented obliquely to the right of the crest line in 2004 and 2012 but had been blown back to a more symmetrical orientation in 2005 and was facing to the left in 2010 (Google Earth). Two other bare areas (in 2004 and 2005) on Bosca dune were bare in December 2010 (Google Earth) and remained bare in 2012 (personal observation). However Aztec North, in the Simpson Desert, was observed to have stabilized in 2012 following its survey in 2004. These observations of surficial reworking are consistent with observations in the Kalahari dunefield (Telfer, 2011) and modeling (Telfer et al., 2010) and may be the typical mode of activity within similar subtropical, vegetated dunefields.

Collectively these observations suggest that the threshold for changing morphodynamic state from 'stable' to 'active', or *vice versa*, is high but also somewhat stochastic. They support the model of bi-stable behavior (Bel and Ashkenazy, 2014; Yizhaq et al., 2007) where hysteresis imposed by the lag required to either grow or remove plants results in two stable states (active and stable) in an intermediate range of environmental forcing. However, the climatic data presented here suggest that variation in precipitation is the driving factor affecting vegetation response, rather than wind strength. Our data (Fig. 8) suggest that there may be an inherent threshold in the response of vegetation cover to antecedent rainfall which is likely to accentuate the 'flipping' from one state to the other, contributing to a patchy mosaic of active dune crest areas between vegetated segments.

Underlying this general resistance to change, or resilience, is the complexity of the vegetation community on dune crests in central Australia and the highly variable rainfall. Decadal-scale variability in precipitation, of uncertain origin, drives dry periods with high numbers of predicted bare-crest days where vegetation cover is reduced to the point that it offers lower resistance to sand transport. Nevertheless, the resistance to change from vegetated dunes to active crests with mobile sand areas and slip faces is created by the complexity of the vegetation cover. This is found in the high number of species surveyed on the crests which display a range of growth patterns and life-cycle lengths each with different responses to rainfall events and to drought periods. A less complex vegetation cover of, say, a single species would have a simpler climatic response. However, the combination of short-lived smaller species, capable of covering the dunes after only small storms, and persistent species capable of resisting drought for several years, confers meta-stability on the vegetation cover as a whole and on dune activity levels. This does not mean that there is no sand movement (Craddock et al., 2015; Hesse and Simpson, 2006) but simply that the magnitude and frequency of sand movement is restricted and cannot form self-reinforcing mobile crests without stochastic removal of persistent plants and suppression of short-lived plants and crust. Although we have investigated the role of drought in determining vegetation cover, other mechanisms which may also contribute to the observed vegetation cover, and susceptibility to wind erosion are grazing and fire.

The complex, and still poorly-defined, relationship between antecedent rainfall and plant cover on the dune crests may partly be the result of the presence of several functional plant types with different growth responses, resistance to dry spells, and persistence of plants offering aerodynamic protection of the surface after death. The threshold relationships between cover and antecedent rainfall tentatively identified here do offer a model of sand availability and transport which is consistent with field observations but which also requires further investigation. In particular, more observations (with replicates) over a wider range of antecedent rainfall conditions are required, preferably at a broader scale. Remote sensing techniques are likely to be highly suitable but care must be taken to adequately include small plants and crust contributing to surface protection.

5. Conclusions

The repeat surveys (in 2002, 2004, 2005 and 2012) of vegetation cover and mobile sand on dune crests in the Strzelecki and Simpson Deserts during the Millennium Drought

(2001 – 2009) and following the subsequent La Niña event (2010 – 2011) confirm and extend the earlier finding (Hesse and Simpson, 2006) of a relationship between vegetation cover and sand transport, even at very high cover levels. In addition, it is now possible to identify that crust (including cyanobacterial and physical crust) is largely responsible for limiting sand availability (depth of loose sand) on the crests while vascular plant cover (excluding crust) determines the degree of sand transport (surface covered by ripples) on both vegetated and 'bare' dune crests.

The vegetation covering the dune crests is complex, with 26 identified plant species falling into four classes of functional plant types (short-lived forbs, longer-lived sub-shrubs and shrubs, persistent hummock grasses, and persistent shrubs and trees) in addition to crust. Collectively this complex community shows only a weak response to antecedent precipitation. A threshold of 10 mm of rain over the previous 3 months was tentatively identified below which cover levels of crust and small plants (<50 cm) fell to low levels and above which they were very high (approaching total cover for crust). Tall plants (>50 cm) appeared to respond to a threshold of 400 mm of rain over the previous 3 years, above which cover levels were high. These proposed thresholds, amounting to below average rainfall for 3 years and for the preceding 3 months, suggest the complex conditions which must be met to reduce cover to a level where appreciable sand transport is possible.

The seasonality of days with predicted low vegetation cover levels on dune crests (defined by antecedent rainfall) combined with the seasonality of sand drift potential suggest a spring (ASON) maximum of sand movement in dry years. The predicted sand drift direction during this season (from the SW quarter) is consistent with observations of asymmetrical dunes and crests with steeper NE faces and resolves a mismatch between RDD calculated form meteorological data and the field observations of dominant drift direction.

The complexity of the vegetation cover, high response thresholds and variability of precipitation combine to make the dunes meta-stable and resistant to change of status from ‘stable’ vegetated to ‘active’ bare crests, even during the intense Millennium Drought. The observed patchiness of dune crest activity in these deserts is achieved through stochastic responses mediated by the threshold relationships of plant cover to precipitation. The findings of this study may be applicable to other dunefields where largely vegetated longitudinal dunes are found.

Acknowledgements

We would like to thank Levi Roberts, Lindsay Killin, Richard Roberts and Sam Marx for their hard work and cheerful company in the field. Santos gave assistance and access to sites in the Strzelecki Desert and Don Rowlands of the Queensland National Parks and Wildlife Service for permission to undertake fieldwork in Simpson Desert National Park. Plymouth University is thanked for funding MT under the International Research Network and Collaboration Scheme. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors. The constructive suggestions of two anonymous reviewers and the editor helped improve the paper greatly.

References

Ash, J.E., Wasson, R.J., 1983. Vegetation and sand mobility in the Australian dunefield. Z. Geomorph. N.F. Suppl. Bd. 45, 7-25.

Ashkenazy, Y., Yizhaq, H., Tsoar, H., 2012. Sand dune mobility under climate change in the Kalahari and Australian deserts. Climatic Change 112, 901-923.

Bagnold, R.A., 1941. The Physics of Blown Sand and Desert Dunes. Methuen, London.

Barchyn, T.E., Hugenholtz, C.H., 2013. Reactivation of supply-limited dune fields from blowouts: A conceptual framework for state characterization. Geomorphology 201, 172-182.

Bel, G., Ashkenazy, Y., 2014. The effects of psammophilous plants on sand dune dynamics. Journal of Geophysical Research: Earth Surface 119, 1636-1650.

Buckley, R., 1987. The effect of sparse vegetation on the transport of dune sand by wind. Nature 325, 426-428.

Bullard, J., 1997. A note on the use of the 'Fryberger Method' for evaluating potential sand transport by wind. J. Sed. Res. 67, 499-501.

Bullard, J.E., Thomas, D.S.G., Livingstone, I., Wiggs, G.F.S., 1997. Dunefield activity and interactions with climatic variability in the southwest Kalahari desert. Earth Surf. Proc. Landforms 22, 165-174.

Clarke, P.J., Latz, P.K., Albrecht, D.E., 2005. Long-term changes in semi-arid vegetation: Invasion of an exotic perennial grass has larger effects than rainfall variability. Journal of Vegetation Science 16, 237-248.

Craddock, R.A., Tooth, S., Zimbelman, J.R., Wilson, S.A., Maxwell, T.A., Kling, C., 2015. Temporal observations of a linear sand dune in the Simpson Desert, central Australia: Testing models for dune formation on planetary surfaces. Journal of Geophysical Research: Planets 120. DOI 10.1002/2015JE004892

Crocker, R.L., 1946. The Simpson Desert Expedition, 1939 Scientific Reports: No. 8 - The soils and vegetation of the Simpson Desert and its borders. Trans. Roy. Soc. S. Aust. 70, 234-258.

D'Odorico, P., Bhattachan, A., Davis, K.F., Ravi, S., Runyan, C.W., 2013. Global desertification: Drivers and feedbacks. Advances in Water Resources 51, 326-344.

Duran, O., Herrmann, H.J., 2006. Vegetation against dune mobility. Physical Review Letters 97, 0031-9007/0006/0097(0018)188001(188004).

Fernandez, R.J., 2007. On the frequent lack of response of plants to rainfall events in arid areas. Journal of Arid Environments 68, 688-691.

Forman, S.L., Spaeth, M., Marin, L., Pierson, J., Gomez, J., Bunch, F., Valdez, A., 2006. Episodic Late Holocene dune movements on the sand-sheet area, Great Sand Dunes National Park and Preserve, San Luis Valley, Colorado, USA. Quat. Res. 66, 97-108.

Freeman, R., Goodwin, I., Donovan, T.-M., 2011. The MQ-DECCW-NSW palaeoclimate database and its application to reconstructing past climate modes and variability in south-eastern Australia, Climate Futures Technical Report, Macquarie University, p. 82.

Fryberger, S.G., Dean, G., 1979. Dune forms and wind regime, in: McKee, E.D. (Ed.), A Study of Global Sand Seas. USGS, Washington.

Greenville, A.C., Dickman, C.R., Wardle, G.M., Letnic, M., 2009. The fire history of an arid grassland: the influence of antecedent rainfall and ENSO. International Journal of Wildland Fire 18, 631-639.

Gergis, J., Gallant, A.J.E., Braganza, K., Karoly, D.J., Allen, K., Cullen, L., D'Arrigo, R., Goodwin, I., Grierson, P., McGregor, S., 2012. On the long-term context of the 1997-2009 'Big Dry' in South-Eastern Australia: insights from a 206-year multi-proxy rainfall reconstruction. Climatic Change 111, 923-944.

Hesse, P.P., 2010. The Australian desert dunefields: formation and evolution in an old, flat, dry continent, in: Bishop, P., Pillans, B. (Eds.), Australian Landscapes. Geological Society, London, London, pp. 141-163.

Hesse, P.P., Simpson, R.L., 2006. Variable vegetation cover and episodic sand movement on longitudinal desert sand dunes. Geomorphology 81, 276-291.

Kalma, J.D., Speight, J.G., Wasson, R.J., 1988. Potential wind erosion in Australia: A continental perspective. Journal of Climatology 8, 411-428.

Kidron, G.J., Wang, Y., Starinsky, A., Herzberg, M., 2017. Drought effect on biocrust resilience: High-speed winds result in crust burial and crust rupture and flaking. Science of The Total Environment 579, 848-859.

Kinast, S., Meron, E., Yizhaq, H., Ashkenazy, Y., 2013. Biogenic crust dynamics on sand dunes. Physical Review E 87, 020701 (R).

Knight, M., Thomas, D.S.G., Wiggs, G.F.S., 2004. Challenges of calculating dunefield mobility over the 21st century. Geomorphology 59, 197-213.

Kuriyama, Y., Mochizuki, N., Nakashima, T., 2005. Influence of vegetation on aeolian sand transport rate from a backshore to a foredune at Hasaki, Japan. Sedimentology 52, 1123-1132.

Lancaster, N., 1988. Development of linear dunes in the southwestern Kalahari, Southern Africa. Journal of Arid Environments 14, 233-244.

Lancaster, N., Baas, A., 1998. Influence of vegetation cover on sand transport by wind: field studies at Owens Lake, California. Earth Surf. Proc. Landforms 23, 68-92.

Lancaster, N., Helm, P., 2000. A test of a climatic index of dune mobility using measurements from the southwestern United States. Earth Surface Processes and

Landforms 25, 197-2000.

Levin, N., Levental, S., Morag, H., 2012. The effect of wildfires on vegetation cover and dune activity in Australia's desert dunes: a multisensor analysis. International Journal of Wildland Fire 21, 459-475.

Madigan, C.T., 1946. The Simpson Desert Expedition: 1939 Scientific Reports, No. 6. : Geology. The Sand Formations. Trans. Roy. Soc. S. Aust. 70, 45-63.

Mangan, J.M., Overpeck, J.T., Webb, R.S., Wessman, C., Goetz, A.F.H., 2004. Response of Nebraska Sand Hills natural vegetation to drought, fire, grazing, and plant functional type shifts as simulated by the CENTURY model. Climatic Change 63, 49-90.

Nano, C.E.M., Pavey, C.R., 2013. Refining the 'pulse-reserve' model for arid central Australia: Seasonal rainfall, soil moisture and plant productivity in sand ridge and stony plain habitats of the Simpson Desert. Austral Ecology 38, 741-753.

Nield, J.M., Baas, A.C.W., 2008. The influence of different environmental and climatic conditions on vegetated aeolian dune landscape development and response. Glob. Planet. Change 64, 76-92.

Ponce Campos, G.E., Moran, M.S., Huete, A., Zhang, Y., Bresloff, C., Huxman, T.E., Eamus, D., Bosch, D.D., Buda, A.R., Gunter, S.A., Heartsill Scalley, T., Kitchen, S.G., McClaran, M.P., McNab, W.H., Montoya, D.S., Morgan, J.A., Peters, D.P.C., Sadler, E.J., Seyfried, M.S., Starks, P.J., 2013. Ecosystem resilience despite large-scale altered hydroclimatic conditions. Nature 494, 349-352.

Reynolds, J.F., Kemp, P.R., Ogle, K., Fernandez, R.J., 2004. Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. Oecologia 141, 194-210.

Rubin, D.M., 1990. Lateral migration of linear dunes in the Strzelecki desert, Australia.

Earth Surf. Proc. Landforms 15, 1-14.

Schwinning, S., Sala, O.E., 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141, 211-220.

Siegal, Z., Tsoar, H., Karnieli, A., 2013. Effects of prolonged drought on the vegetation cover of sand dunes in the NW Negev Desert: Field survey, remote sensing and conceptual modeling. Aeolian Research 9, 161-173.

Strong, C.L., Bullard, J.E., Dubois, C., McTainsh, G.H., Baddock, M.C., 2010. Impact of wildfire on interdune ecology and sediments: An example from the Simpson Desert, Australia. J. Arid Envir. 74, 1577-1581.

Telfer, M.W., 2011. Growth by extension, and reworking, of a south-western Kalahari linear dune. Earth Surf. Proc. Landforms 36, 1125-1135.

Telfer, M.W., Bailey, R.M., Burrough, S.L., Stone, A.E.S., Thomas, D.S.G., Wiggs, G.S.F., 2010. Understanding linear dune chronologies: Insights from a simple accumulation model. Geomorphology 120, 196-208.

Thomas, D.S.G., Burrough, S.L., 2012. Interpreting geoproxies of late Quaternary climate change in African drylands: Implications for understanding environmental change and early human behaviour. Quaternary International 253, 5-17.

Thomas, D.S.G., Knight, M., Wiggs, G.F.S., 2005. Remobilisation of southern African desert dune systems by twenty-first century global warming. Nature 435, 1218-1221.

Thomas, D.S.G., Tsoar, H., 1990. The geomorphological role of vegetation in desert dune systems, in: Thornes, J.B. (Ed.), Vegetation and Erosion. John Wiley and Sons Ltd, pp. 471-489.

Timbal, B., Fawcett, R., 2013. A historical perspective on Southeastern Australian rainfall since 1865 using the instrumental record. J. Clim. 26, 1112-1129.

Tsoar, H., Møller, J.T., 1986. The role of vegetation in the formation of linear sand dunes, in: Nickling, W.G. (Ed.), Aeolian Geomorphology. Allen and Unwin, Boston, pp. 75-95.

van Etten, E.J.B., 2009. Inter-annual rainfall variability of arid Australia: greater than elsewhere? Aust. Geog. 40, 109-120.

Verdon-Kidd, D.C., Kiem, A.S., 2015. Regime shifts in annual maximum rainfall across Australia - implications for intensity-frequency-duration (IFD) relationships. Hydrology and Earth System Sciences 19, 4735-4746.

Wardle, G.M., Pavey, C.R., Dickman, C.R., 2013. Greening of arid Australia: New insights from extreme years. Austral Ecology 38, 731-740.

Wasson, R.J., 1983. The Cainozoic history of the Strzelecki and Simpson dunefields (Australia), and the origin of the desert dunes. Zeitschrift fur Geomorphologie N.F. Suppl. Bd. 45, 85-115.

Wasson, R.J., Hyde, R., 1983. Factors determining desert dune type. Nature 304, 337-339.

Wasson, R.J., Nanninga, P.M., 1986. Estimating wind transport of sand on vegetated surfaces. Earth Surf. Proc. Landforms 11, 505-514.

Wiggs, G.F.S., Livingstone, I., Thomas, D.S.G., Bullard, J.E., 1996. Airflow and roughness characteristics over partially vegetated linear dunes in the southwest Kalahari Desert. Earth Surf. Proc. Landforms 21, 19-34.

Wiggs, G.F.S., Thomas, D.S.G., Bullard, J.E., Livingstone, I., 1995. Dune mobility and vegetation cover in the southwest Kalahari Desert. Earth Surf. Proc. Landforms 20, 515-529.

Wolfe, S.A., Nickling, W.G., 1993. The protective role of sparse vegetation in wind erosion. Progress in Physical Geography 17, 50-68.

Wolfe, S.A., Nickling, W.G., 1996. Shear stress partitioning in sparsely vegetated desert canopies. Earth Surf. Proc. Landforms 21, 607-619.

Wolter, K., Timlin, M.S., 2011. El Nino/Southern Oscillation behaviour since 1871 as diagnosed in an extended multivariate ENSO index (MEI.ext). Int. J. Climatol. 31, 1074-1087.

Wopfner, H., Twidale, C.R., 1967. Geomorphological history of the Lake Eyre Basin, in: Jennings, J.N., Mabbutt, J.A. (Eds.), Landform studies from Australian and New Guinea. Australian National University Press, Canberra, pp. 119-143.

Yizhaq, H., Ashkenazy, Y., Tsoar, H., 2007. Why do active and stabilised dunes coexist under the same climatic conditions? Physical Review Letters 98, 0031-9007/0007/0098(0018)/188001 (188004).

Yizhaq, H., Ashkenazy, Y., Tsoar, H., 2009. Sand dune dynamics and climate change: A modeling approach. J. Geophys. Res. 114, F01023.

Yizhaq, H., Ashkenazy, Y., Levin, N., Tsoar, H., 2013. Spatiotemporal model for the progression of transgressive dunes. Physica A: Statistical Mechanics and its Applications 392, 4502-4515.

Figure Captions

Figure 1. Location of field sites in the Simpson and Strzelecki Deserts of central eastern Australia. Dunefield boundaries interpreted from ESRI satellite imagery, dune crests modified from data from Geoscience Australia.

Figure 2. Precipitation and sand-transporting winds at Moomba Airport Automatic Weather Station (7/95 – 1/14 (precipitation), 12/14 (wind)). (a) Seasonal distribution of monthly precipitation and (b) sand drift potential observations between 1995 and 2014. (c) Time series of monthly (black line) and annual (July to June) sand drift potential (light grey) and annual (J-J) resultant drift potential (dark grey). (d) Time series of monthly and annual (J-J) precipitation. Horizontal line represents the median annual (J-J) precipitation for the period shown. Inverted triangles represent the timing of field observations.

Figure 3. Precipitation and sand-transporting winds at Birdsville Airport Automatic Weather Station (7/00 – 1/14 (precipitation) and 12/14 (wind)). (a) Seasonal distribution of monthly precipitation and (b) drift potential observation between 1995 and 2014. (c) Time series of monthly (black line) and annual (July to June) sand drift potential (light grey) and annual (J-J) resultant drift potential (dark grey). (d) Time series of monthly and annual (J-J) precipitation. Horizontal line represents the median annual (J-J) precipitation for the period shown. Inverted triangles represent the timing of field observations.

Figure 4. Photographs of the study sites during the drought (2002-2005, left hand side) and after the La Niña wet period in 2012 (right hand side). (a) Mayan Crest, 2004, (b) Mayan Crest, 2012, (c) Mayan Right Flank, 2002, (d) Mayan Right Flank, 2012, (e) Aztec North, 2004, (f) Aztec North, 2012, (g) Della Crest, 2005, (h) Della Crest, 2012, (i) Bosca North, 2004, (j) Bosca North, 2012.

Figure 5. Distribution of vegetation in each of the functional groups on Mayan, Della and Bosca North dune crest quadrats. Crust is shown as present (grey squares) or absent (white) but other categories are shown as circles scaled to the height of the plant. All quadrats are shown oriented with the downwind direction (roughly north) to the top, and at the same scale. Solid black lines and dashed line on Bosca North plot indicate the slipface crest and rounded, symmetrical crest respectively.

Figure 6. Vegetation height distributions for Mayan Crest, Della Crest and Bosca North quadrats. The x-axis is the percentage of the quadrat (as points) with plants taller than a given height (H) on the y-axis. Apparent differences in the tree heights at Bosca North are partly due to minor differences in the location of the quadrat boundary and partly due to progressive burial by the advancing slip face.

Figure 7. Vegetation cover indices versus loose sand and ripple cover on all quadrats and all surveys. Triangles are bare dune crest plots (Aztec and Bosca), filled circles are vegetated dune crest plots (Mayan and Della) and empty circles are vegetated dune flanks (Mayan and Della). One outlier (Mayan Crest 2004) was excluded from the regression of ripple cover against plant cover, where forbs and crust had colonised

ripples rendering them immobile. Two additional regressions (dashed lines) for points >50% cover (r^2 = 0.68) and <50% cover (r^2 = 0.19) are also shown.

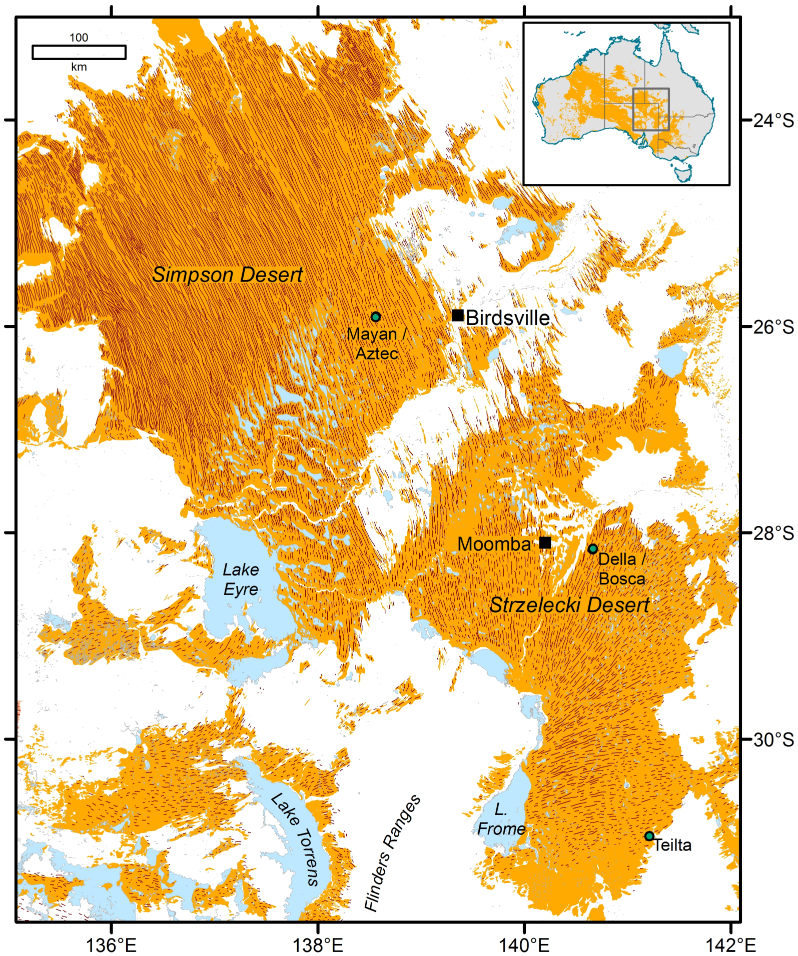
Figure 8. Response of vegetation and crust to antecedent rainfall on vegetated crests and bare crests. Dashed vertical lines indicate the proposed threshold antecedent rainfall values.

Figure 9. Frequency of storms of different magnitude (in 5 mm increments) at Moomba for average (1995/6 to 2000/1), drier than average (2001/2 to 2009/10) and wetter than average (2009/10 to 2011/12) years. Storms are defined as consecutive days of rainfall.

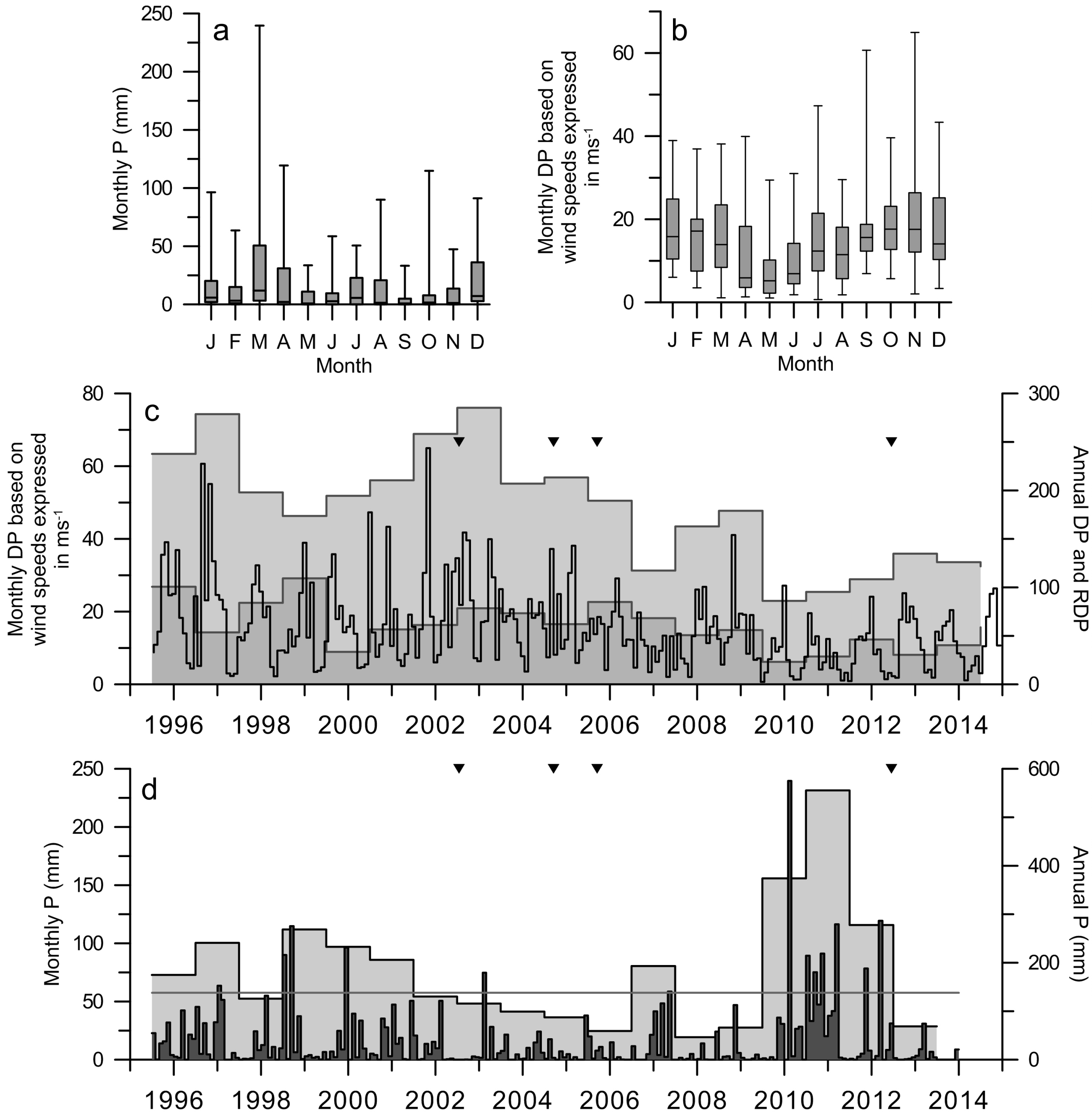
Figure 10. Prediction for days when dune crests are bare (points), and susceptible to high rates of sand transport, with both 90 day antecedent rainfall < 10 mm and three year antecedent rainfall < 400 mm. Several gaps in the daily rainfall record are evident but all occur during relatively wet periods and are unlikely to affect the prediction of bare-crest days.

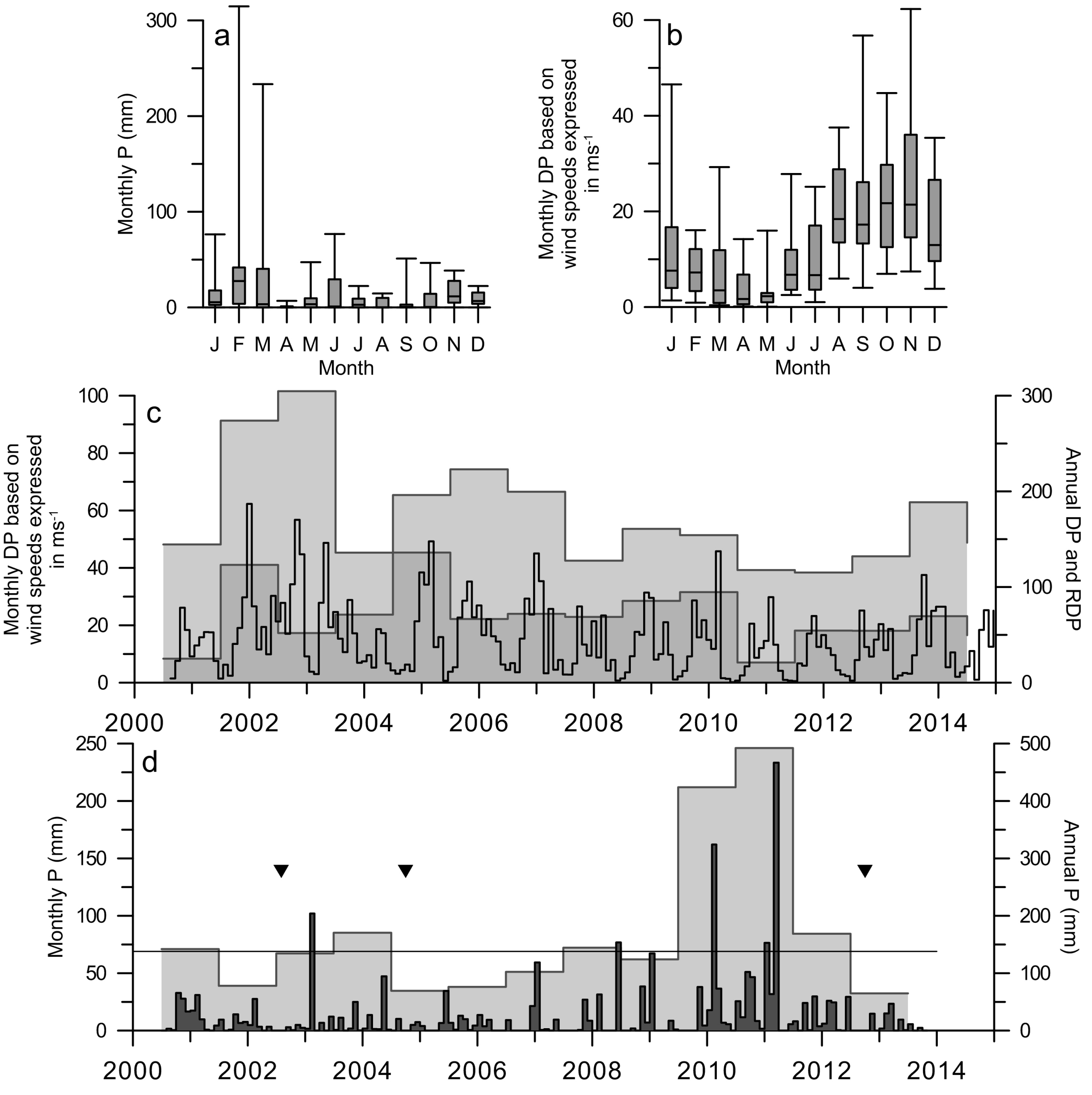
Figure 11. Annual and seasonal distribution of predicted bare-crest days at Birdsville. Predicted bare-crest days are defined as days where the preceding 90 days' precipitation is < 10 mm and the preceding three years' precipitation is < 400 mm. Note the gap in data between 1918 and 1923, and around 1950 (see Fig. 10). The lower panel shows the monthly SOI record (Wolter and Timlin, 2011) and the 11 –year filtered IPO index (A Colman, UK Met Office).

Figure 12. Seasonal distribution of predicted bare-crest days, monthly sand drift potential and monthly resultant drift direction (RDD) at Birdsville. RDD is the direction from which potential sand-moving winds blow.

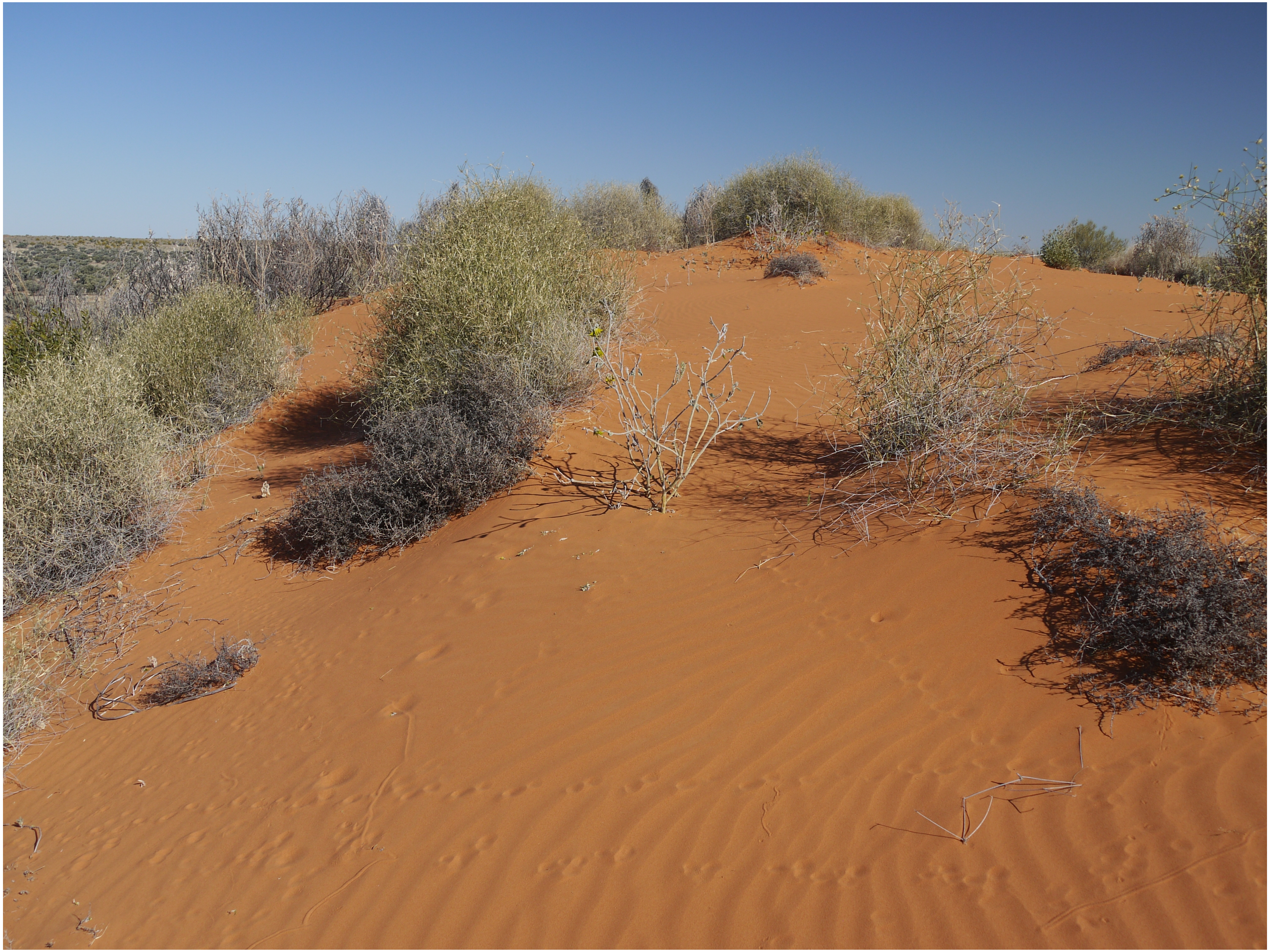


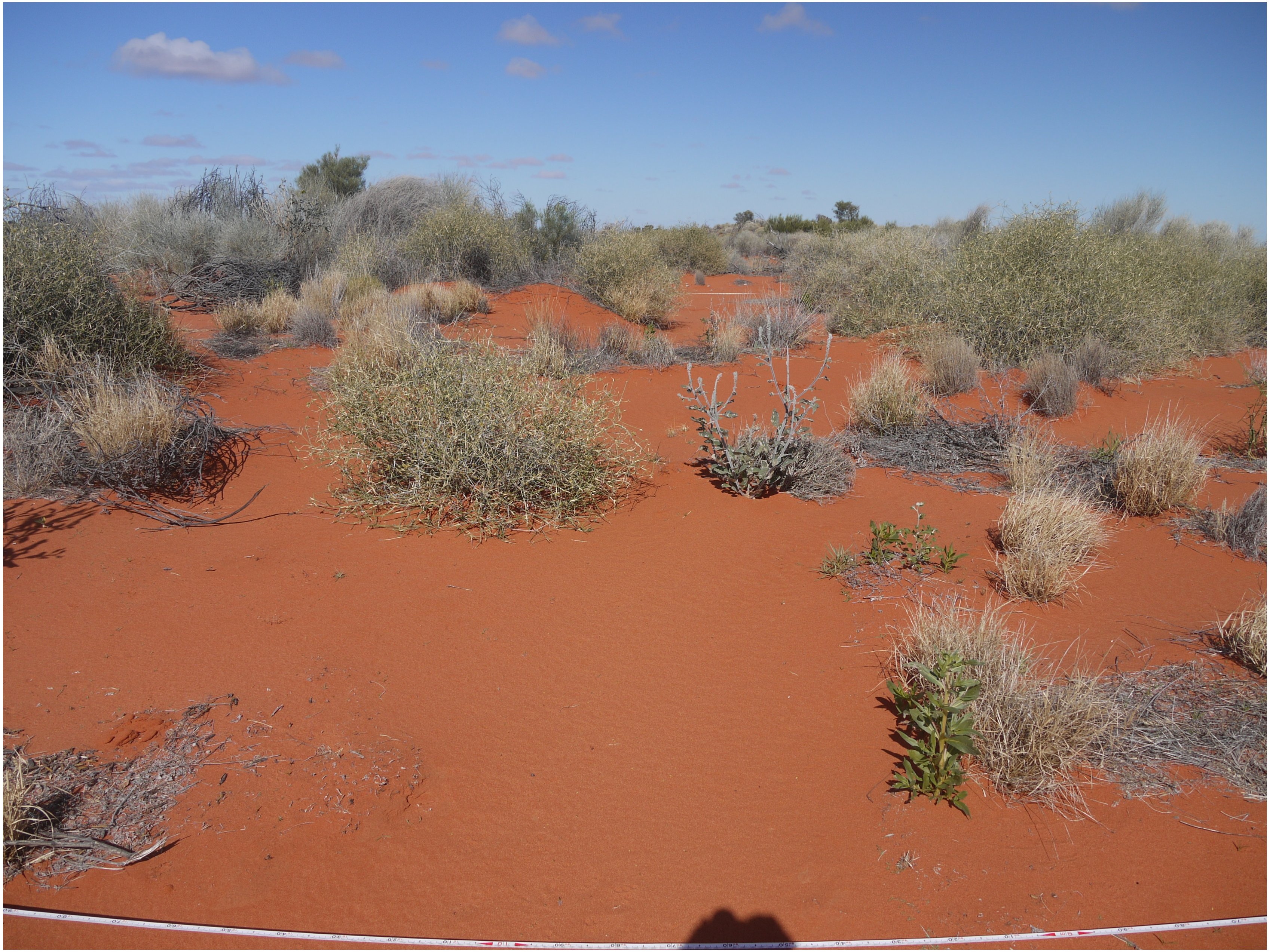
100
km
24°S
26°S
28°S
30°S
136°E
138°E
140°E
142°E
Simpson Desert
Mayan /
Aztec
Birdsville
Moomba
Della /
Bosca
Strzelecki Desert
Lake
Eyre
Lake Torrens
Flinders Ranges
L.
Frome
Teilta

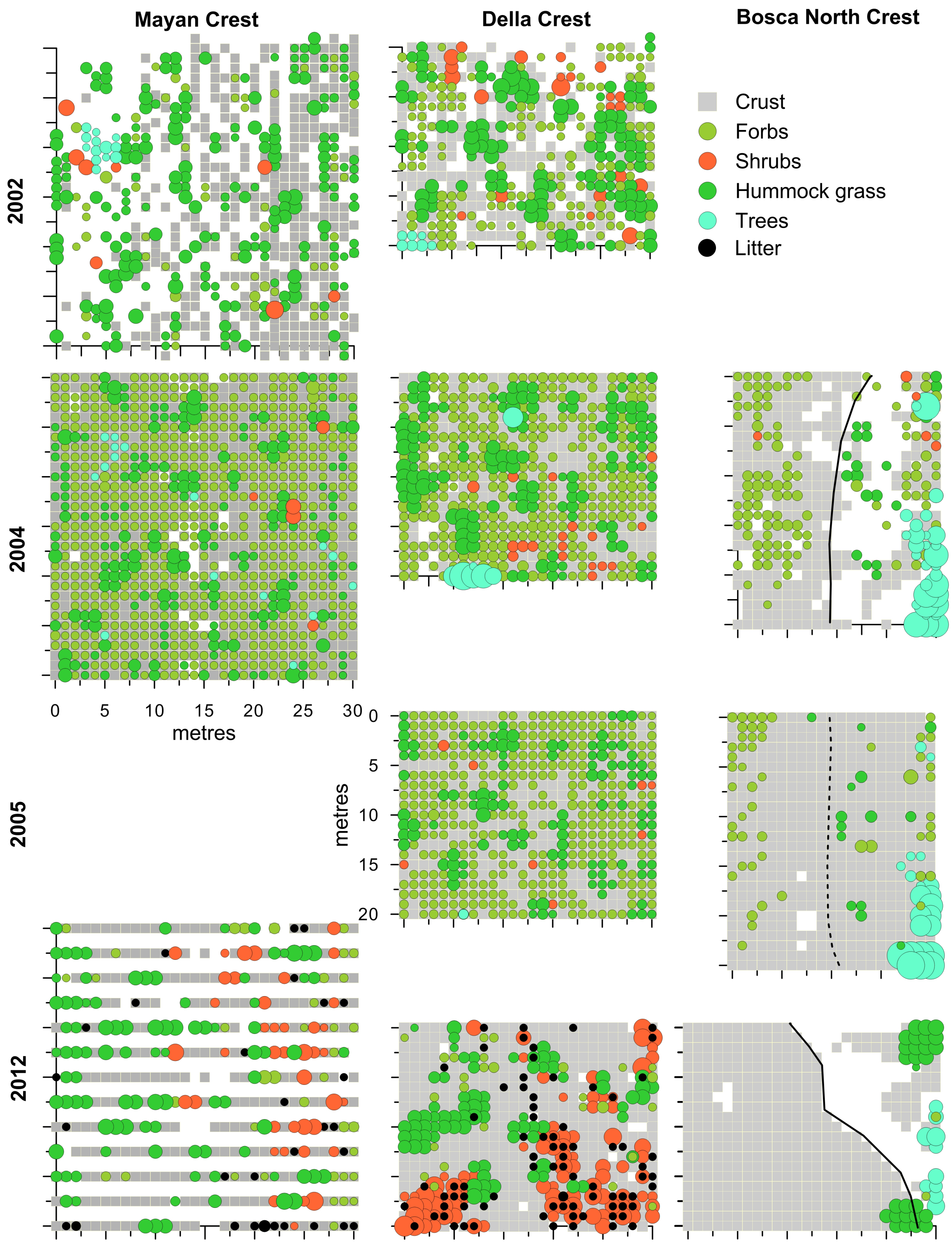

a
Monthly P (mm)
250
200
150
100
50
0
J F M A M J J A S O N D
Month
b
Monthly DP based on wind speeds expressed in ms-1
60
40
20
0
J F M A M J J A S O N D
Month
c
Monthly DP based on wind speeds expressed in ms-1
Annual DP and RDP
80
60
40
20
0
300
200
100
0
1996 1998 2000 2002 2004 2006 2008 2010 2012 2014
d
Monthly P (mm)
Annual P (mm)
250
200
150
100
50
0
600
400
200
0
1996 1998 2000 2002 2004 2006 2008 2010 2012 2014



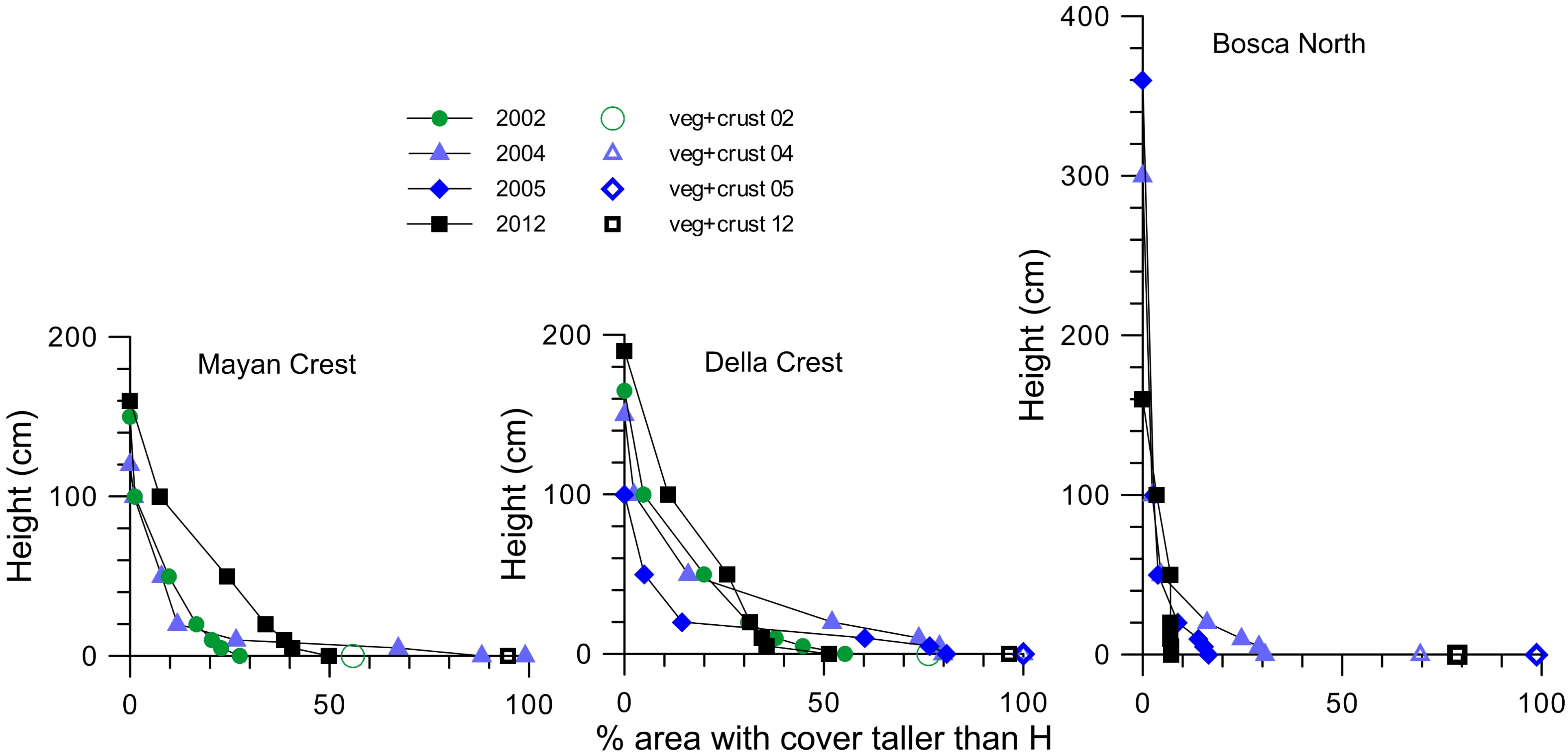
a
Monthly P (mm)
Month
J F M A M J J A S O N D
b
Monthly DP based on wind speeds expressed in ms^{-1}
Month
J F M A M J J A S O N D
c
Monthly DP based on wind speeds expressed in ms^{-1}
Annual DP and RDP
d
Monthly P (mm)
Annual P (mm)
2000 2002 2004 2006 2008 2010 2012 2014



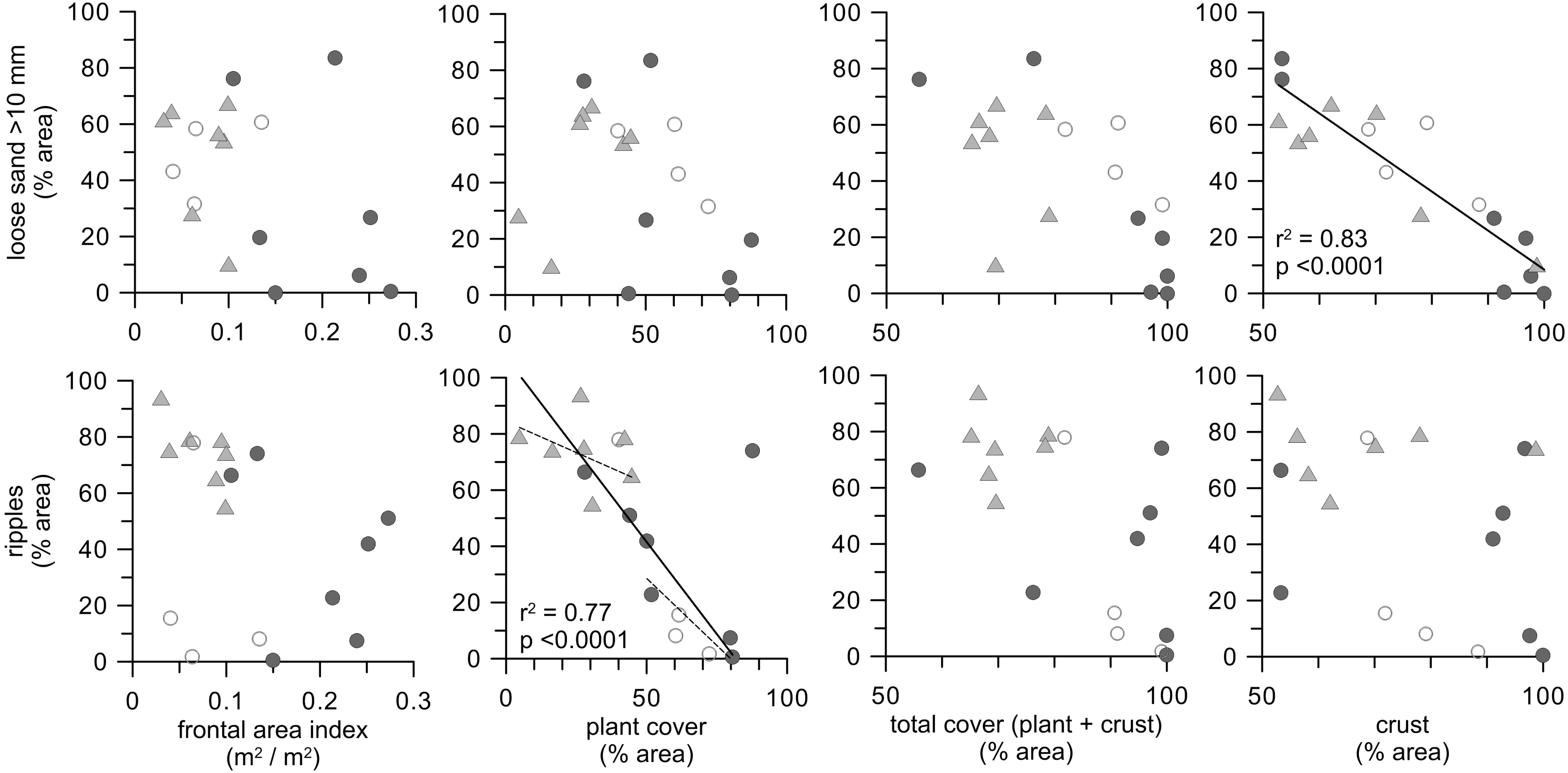




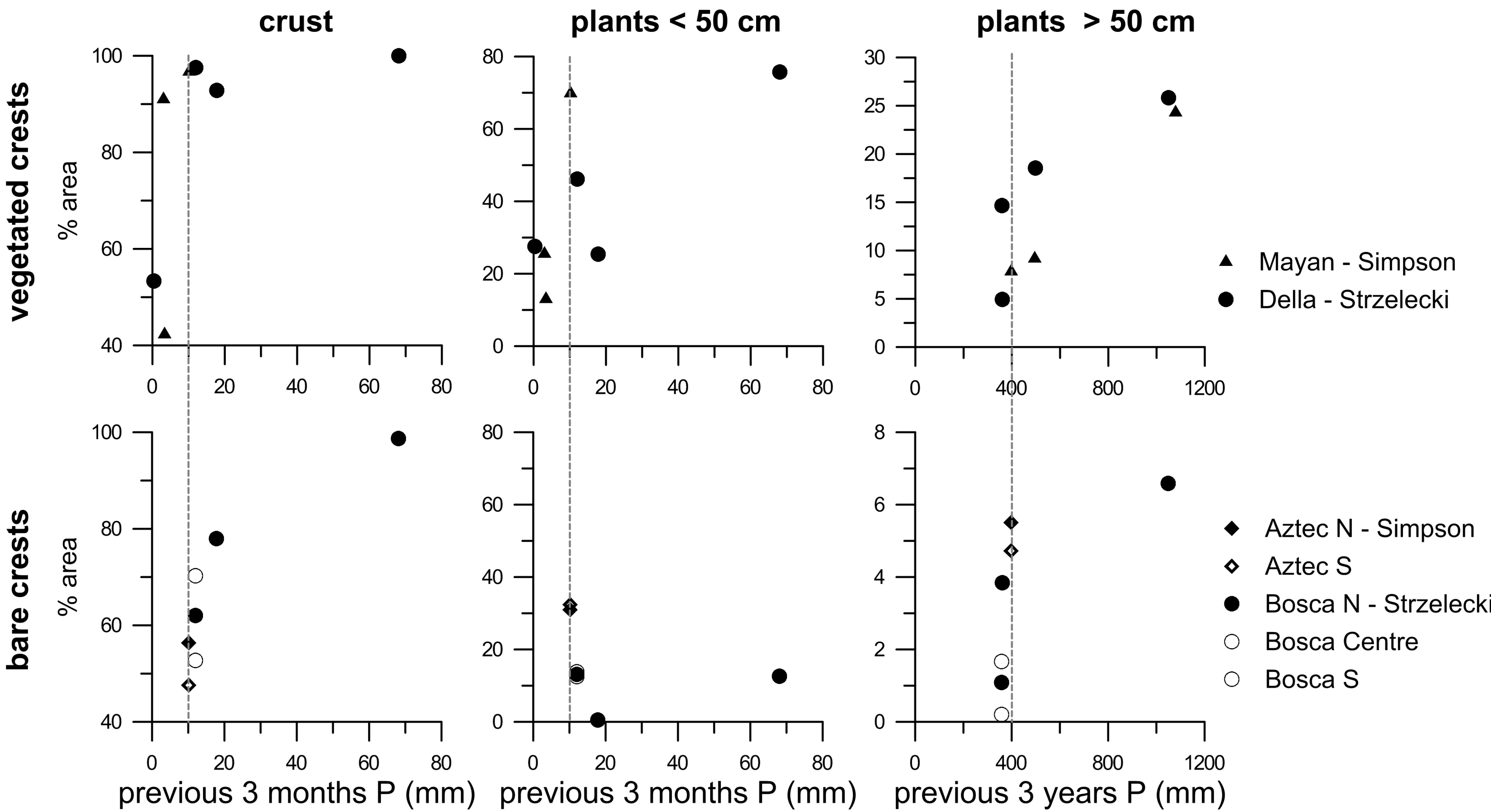
Mayan Crest
Della Crest
Bosca North Crest
Crust
Forbs
Shrubs
Hummock grass
Trees
Litter
2002
2004
2005
2012
0 5 10 15 20 25 30
metres
0 5 10 15 20
metres



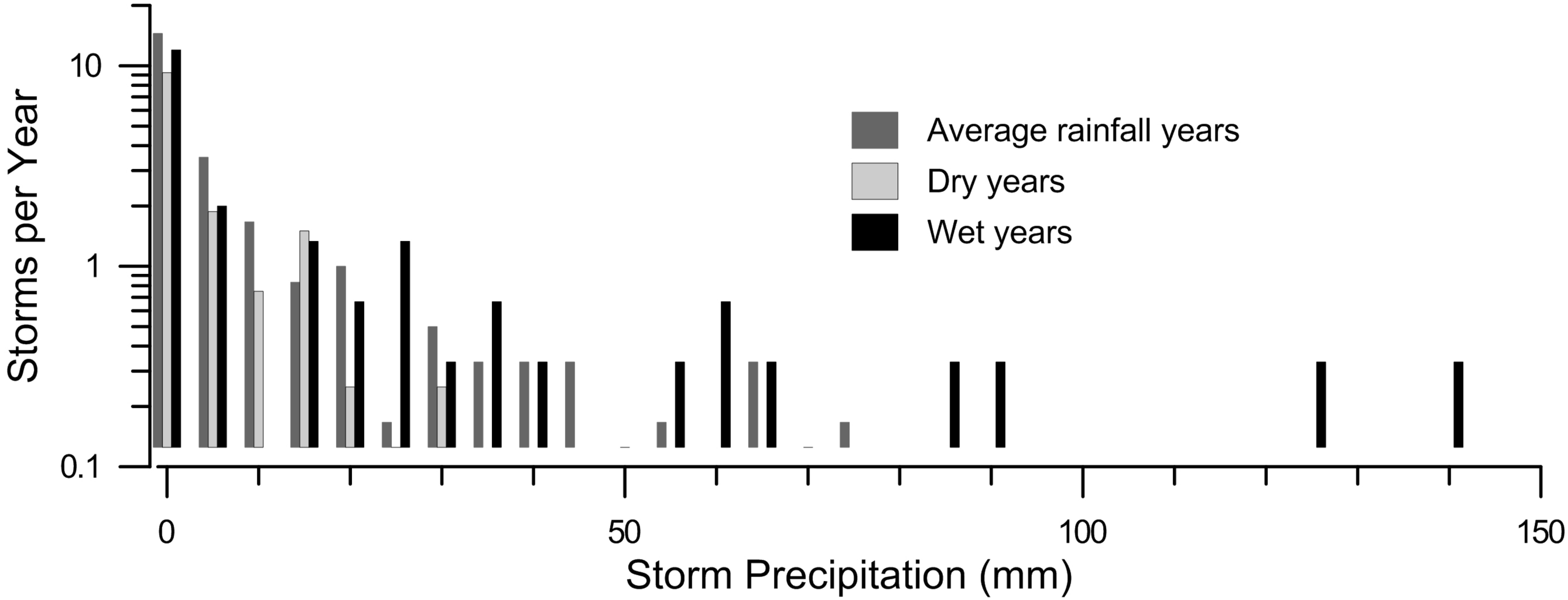
2002
2004
2005
2012
veg+crust 02
veg+crust 04
veg+crust 05
veg+crust 12
Mayan Crest
Della Crest
Bosca North
Height (cm)
Height (cm)
Height (cm)
% area with cover taller than H
0
50
100
200
300
400



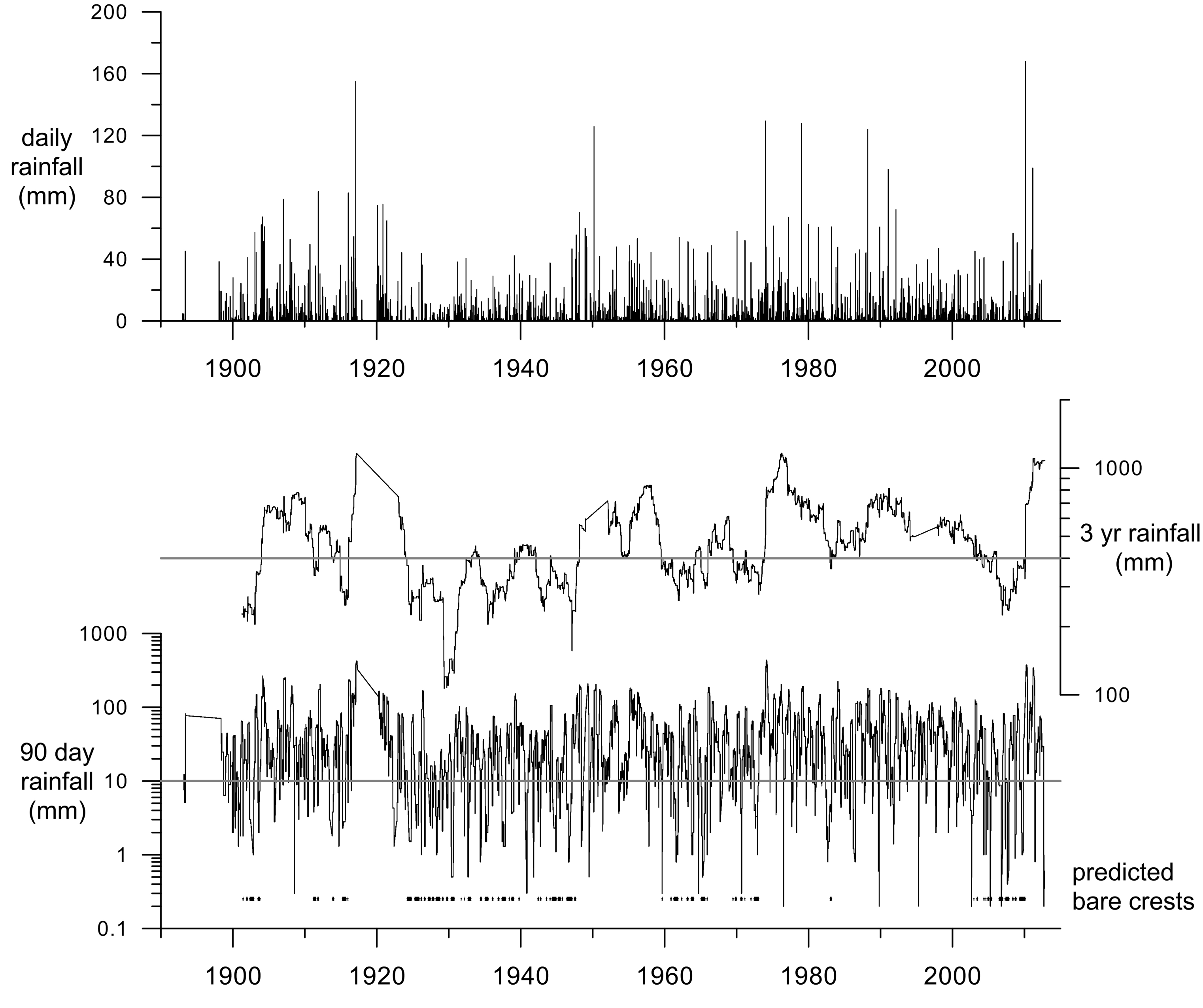
loose sand >10 mm (% area)
ripples (% area)
r² = 0.83
p <0.0001
r² = 0.77
p <0.0001
frontal area index (m² / m²)
plant cover (% area)
total cover (plant + crust) (% area)
crust (% area)



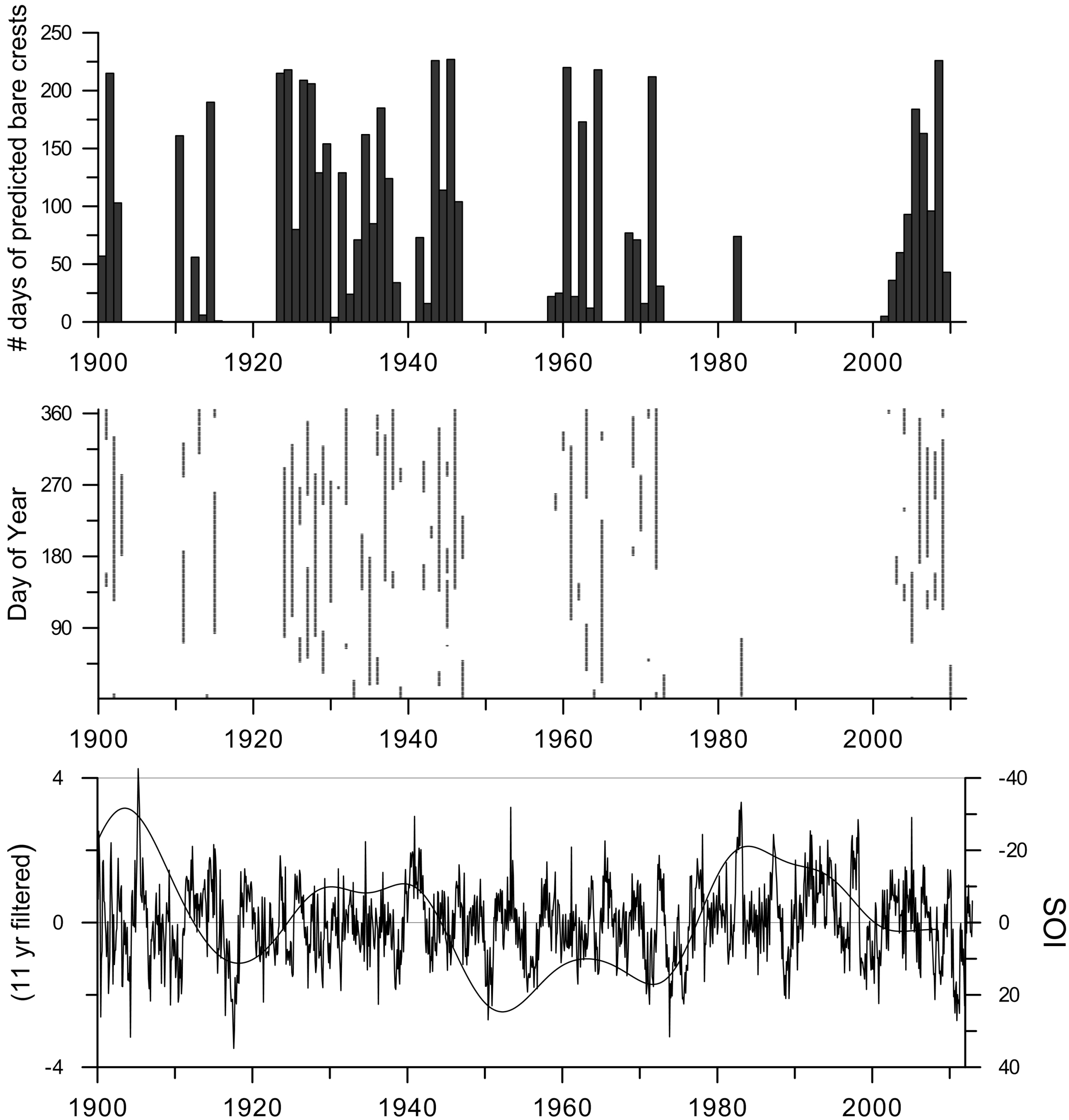
crust
plants < 50 cm
plants > 50 cm
vegetated crests
bare crests
% area
previous 3 months P (mm)
previous 3 months P (mm)
previous 3 years P (mm)
Mayan - Simpson
Della - Strzelecki
Aztec N - Simpson
Aztec S
Bosca N - Strzelecki
Bosca Centre
Bosca S



Storms per Year
10
1
0.1
Average rainfall years
Dry years
Wet years
0
50
100
150
Storm Precipitation (mm)



daily rainfall (mm)
200
160
120
80
40
0
1900
1920
1940
1960
1980
2000
1000
100
3 yr rainfall (mm)
1000
100
10
1
0.1
90 day rainfall (mm)
predicted bare crests
1900
1920
1940
1960
1980
2000



days of predicted bare crests
250
200
150
100
50
0
1900
1920
1940
1960
1980
2000
Day of Year
360
270
180
90
1900
1920
1940
1960
1980
2000
IPO index
(11 yr filtered)
4
0
-4
-40
-20
0
20
40
SOI
1900
1920
1940
1960
1980
2000

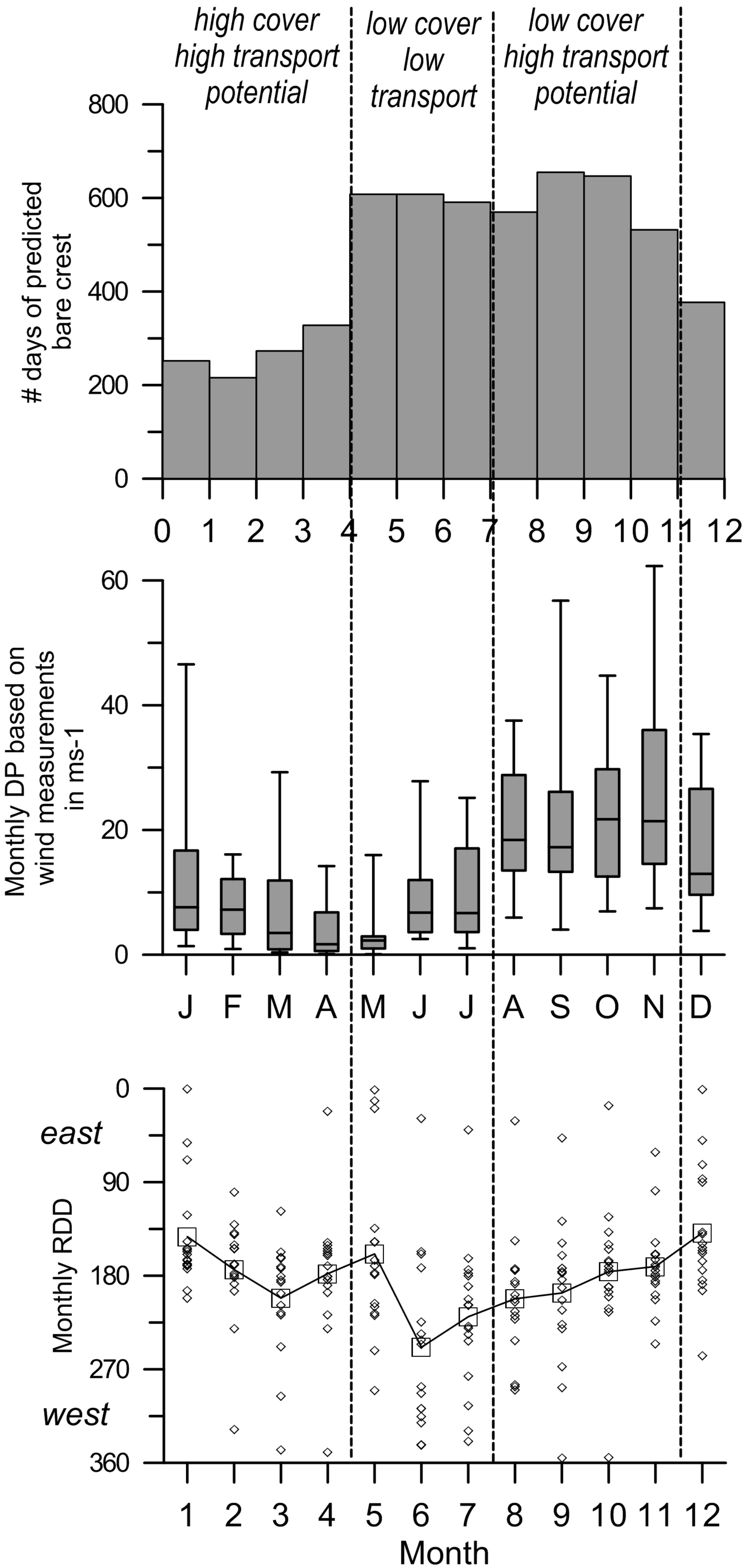

high cover
high transport
potential
low cover
low
transport
low cover
high transport
potential
days of predicted
bare crest
800
600
400
200
0
0 1 2 3 4 5 6 7 8 9 10 11 12
Monthly DP based on
wind measurements
in ms-1
60
40
20
0
J F M A M J J A S O N D
Monthly RDD
0
east
90
180
270
west
360
1 2 3 4 5 6 7 8 9 10 11 12
Month

Table 1 Site Location and sampling details

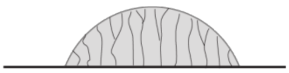
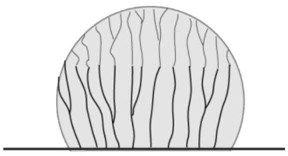
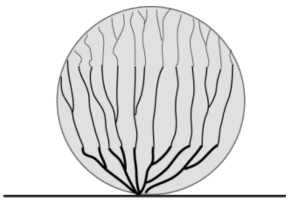
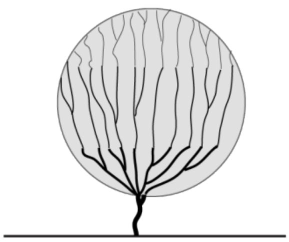
Name	Type	Latitude (WGS84)	Longitude (WGS84)	2002	2004	2005	2012
Simpson Desert							
Mayan Crest	1 m grid 30x30	S25.90639	E138.56199	13-Jul	10-Sep		13-Sep (1x2.5 m grid)
Mayan Left flank	1 m grid 20x20			15-Jul			
Mayan Right flank	1 m grid 20x20			14-Jul			
Aztec North	1 m grid 25x20	S25.90864	E138.55549		12-Sep		
Aztec South	1 m grid 25x20	S25.91377	E138.55774		13-Sep		
Strzelecki Desert							
Della Crest	1 m grid 25x20	S28.16128	E140.65839	19-Jul	17-Sep	4-Sep	23-Jun
Della Left Flank	1 m grid 20x20			19-Jul			
Della Right Flank	1 m grid 20x20			20-Jul			
Bosca Centre	1 m grid 25x20	S28.16171	E140.66148		18-Sep		
Bosca North	1 m grid 25x20	S28.15757	E140.66228		19-Sep	5-Sep	23-Jun
Bosca South	1 m grid 25x20	S28.16414	E140.66106		17-Sep		
Teilta	5 m grid 75 x 130	S30.939822	E141.208794	23-Jul			

Table 2 Birdsville and Moomba Average Climate Data

Location	Birdsville		Moomba	
BoM station	AP (AWS) 38026	PS 38002	AP (AWS) 17123	17096
Annual (J-J) Precipitation (mm)	2002/03 – 2011-/12	1960/61 – 2012/13	2002/03 – 2011/12	1973/74 – 2012/13
Range	69 – 492	31 – 592	46 – 555	46 – 871
Mean	191	182	187	188
Median	140	156	108	147
SD	146	110	168	124
SE	46	15	53	20
AWS Wind Data	07/2002 – 07/2012		07/2002 – 07/2012	
Mean wind speed (all obs) (km/h)	16.7		17.3	
Mean midday wind speed (km/h)	20.2		20.1	
% All wind observations >Vt[1]	25.3		26.8	
% Midday wind observations >Vt	40.7		41.6	
Mean max daily wind gust km/h	41.25		40.5	
% Daily max wind gust >Vt	98.4		98.2	
Mean ± SD J-J DP	174 ± 59		164 ± 63	
Mean ± SD J-J RDP	72 ± 30		57 ± 20	
Mean ± SD J-J RDP/DP	0.44 ± 0.18		0.36 ± 0.10	
Mean J-J ± SD RDD (bearing)	172 ± 17		171 ± 19	
Mean dune direction ± SD (bearing)	159 ± 4		182 ± 6	
Divergence (dune – RDD) (degrees)	-13		11	

1 - Vt = 22 km/h; 6.11 m/s

Table 3 Categorisation of vegetation functional types and effects on sand movement

Vegetation form		Longevity[1]	Effect on sand surface	Examples
	Cyanobacterial crust	Persistent (as population)	Binding; low drag; high cover	Not identified to taxa
	Forbs, sub-shrubs & tussock grass	Short-lived (<1yr) to longer-lived (1 – 3 yrs)	Low drag; shelter; high cover (as patch)	*Aristida* (Poac.), Aster., Brassic.; Chenopod., Portulac., Zygophyll.
	Hummock grass	Persistent (>3 yrs)	High drag; sheltering; high contact cover; scour at margins	*Zygochloa*, *Triodia* (Poac.)
	Sub-shrubs & shrubs	Longer-lived (1 – 3 yrs) to Persistent	High drag; low contact cover; scour beneath	*Crotalaria*, *Swainsona* (Fab.), *Acacia* (Mimos.)
	Trees & tall shrubs	Persistent (>3 yrs)	High drag; low contact cover; scour; shading (beneath canopy); root competition (beyond canopy)	*Acacia* (Mimos.), *Grevillea* (Protea.), *Dodonaea*, *Atalaya* (Sapind.), *Eremophila* (Scrophularia.)

1 – after Nano and Pavey (2013) and Clarke et al. (2005).

Supplementary Material

Table S1 Summary of Vegetation and Surface Data from All Sites

Location	Bare (%)	Vegetation Cover (%)	Crust Cover		Veg Height					FAI	Veg <50 cm (%)	Veg >50 cm (%)	Max veg height (cm)	Living veg cover (%)	Dead veg cover (%)
			No crust (%)	**Crust (%)**	**0-5 cm (%)**	**6-20 cm (%)**	**21-50 cm (%)**	**51-100 cm (%)**	**>100 cm (%)**						
Simpson Desert															
Mayan Crest 2002	70.2	28.0	47.2	52.8	2.5	5.1	5.5	7.9	1.3	0.11	13.1	9.2	150	9.0	13.3
Mayan Crest 2004	11.9	87.6	3.2	96.7	17.1	50.2	2.7	6.9	1.0	0.13	69.9	7.9	120	15.2	60.2
Mayan Crest 2012	49.6	50.1	8.9	90.8	9.2	6.7	9.7	16.9	7.4	0.25	25.6	24.3	160	25.3	34.5
Mayan Right 2002	38.5	61.5	28.1	71.9	32.3	6.3	2.5	2.2	0.0	0.04	41.1	2.2	100	2.0	42.0
Mayan Left 2002	59.9	40.1	31.3	68.7	11.4	3.2	4.7	4.1	1.0	0.06	19.3	5.1	140	4.8	34.9
Aztec North 2004	58.1	42.1	43.6	56.4	5.8	18.2	7.1	4.8	0.8	0.10	31.0	5.5	120	16.9	19.7
Aztec South 2004	54.9	44.7	42.3	57.7	7.8	19.0	5.7	4.3	0.4	0.09	32.5	4.7	110	20.0	17.2
Northern Strzelecki Desert															
Della Crest 2002	46.1	51.8	45.0	55.1	7.8	11.6	8.2	13.5	5.1	0.23	27.6	18.6	165	20.2	26.0
Della Crest 2004	19.6	79.9	0.7	99.3	0.3	19.2	26.8	12.1	2.6	0.26	46.2	14.7	150	15.6	45.3
Della Crest 2005	18.9	80.6	0.0	100.0	4.2	62.1	9.5	5.0	0.0	0.15	75.8	5.0	100	41.2	39.2
Della Crest 2012	66.9	44.0	7.1	92.9	15.6	4.2	5.7	14.8	11.0	0.27	25.5	25.8	180	21.8	28.2
Della Left 2002	27.7	72.3	11.6	88.4	39.7	19.2	2.9	1.1	0.2	0.06	61.8	1.3	110	39.5	36.1
Della Right 2002	39.7	60.3	20.9	79.1	31.4	6.8	5.3	5.9	2.3	0.14	43.5	8.2	200	14.5	46.3
Bosca North 2004	71.4	30.8	37.7	62.3	0.3	6.0	6.8	0.9	0.2	0.11	13.1	1.1	300	6.0	8.2
Bosca North 2005	86.3	16.5	1.1	99.0	1.1	6.6	5.0	1.1	2.8	0.10	12.7	3.9	360	12.1	7.0
Bosca North 2012	94.9	4.8	12.0	78.0	0.0	0.2	0.4	3.1	3.5	0.06	0.5	6.6	160	7.0	0.0
Bosca Central 2004	72.0	27.7	29.7	70.3	3.7	7.1	3.2	1.1	0.6	0.04	13.9	1.7	150	4.2	2.9
Bosca South 2004	73.3	26.6	47.3	52.7	1.1	5.4	6.1	0.2	0.0	0.03	12.5	0.2	60	4.5	5.9
Southern Strzelecki Desert															
Teilta contact	55.3	44.7	78.7	21.3	13.2	6.4	11.6	6.1	2.1	0.01	31.2	8.3	250	8.0	41.6
		canopy height classes			<50	50-100	101-200	201-300	>301						
Teilta canopy		23.2			1.4	5.9	8.8	6.2	3.5	0.07	1.4	24.4	500	18.4	4.7
Teilta total cover		67.9								0.09					

Table S2 Plant Species Identified at Each Site and in Each Survey

Form	Longevity[1]	Species	Mayan Crest			Mayan L flank	Mayan R flank	Aztec N	Aztec S	Della Crest				Della L Flank	Della R Flank	Bosca S	Bos
			2002	2004	2012	2002	2002	2004	2004	2002	2004	2005	2012	2002	2002	2004	20
Crust		unidentified cyanobacteria	y	y	y	y	y	y	y	y	y	y	y	y	y	y	y
Hummock grasses	persistent	*Zygochloa paradoxa*	y	y	y	y	y	y	y	y	y	y	y	y	y	y	y
Hummock grasses	persistent	*Triodia basedowii*												y	y		
Subshrubs	persistent	*Lechenaultia divaricata*			y												
Grasses	short-lived	*Aristida contorta*			y	y							y	y	y	y	y
Grasses	short-lived	unidentified tussock grass											y				
Forbs	short-lived	*Blennodia canescens*		y							y					y	y
Forbs	short-lived	*Calandrinia balonensis*									y						
Forbs	short-lived	*?Hibbertia sp*			y												
Forbs	short-lived	*Polycalymma stuartii*		y				y	y	dead	y			y	y	y	y
Forbs	short-lived	*?Senecio*		y													
Forbs	short-lived	*Tribulus terrestris*			y												
Forbs	short-lived	*Trichodesma zeylanicum*	y		y						y					y	
Forbs	short-lived	*Zygophyllum howittii*		y							y			y		y	y
Forbs	short-lived	unidentified (dead)	y	y	y	y	y	y	y	y	y	y	y	y	y		y
Subshrubs	longer-lived	*Enchylaena tomentosa*									y						
Subshrubs	longer-lived	*Maireana sp*									y	y				y	y
Subshrubs	longer-lived	*Rhagodia spinescens*		y													
Subshrubs	longer-lived	unidentified chenopod	y	y	y	y	y		y		y						
Subshrubs	longer-lived	*Crotalaria eremaea*	y	y	y	y			y	y	y	y	y	y	y	y	y
Subshrubs	longer-lived	*Crotalaria cunninghamii*	y					y		y			y				
Shrubs	longer-lived	*Swainsona laxa*			y												
Shrubs	persistent	*Acacia murrayana*	?dead	?dead	y	?dead		y	y			nearby					
Shrubs	persistent	*Dodonaea viscosa subsp. angusstissima*								dead	dead	dead				dead	dea
Shrubs	persistent	*Grevillea stenobotrya*															y
Trees	persistent	*Acacia brachystachya*	nearby	nearby	nearby	nearby											
Trees	persistent	*Acacia ligulata*								y							
Trees	persistent	*Atalaya hemiglauca*															
Trees	persistent	*Callitris glaucophylla*															
Trees	persistent	*Pittosporum angustifolium*															

1. short-lived – annual/ephemeral < 1 year; longer-lived – up to 3 years; persistent - > 3 years (after P Clarke, P Latz and D Albrecht, 2005. J Veg Sci. 16: 237-248)

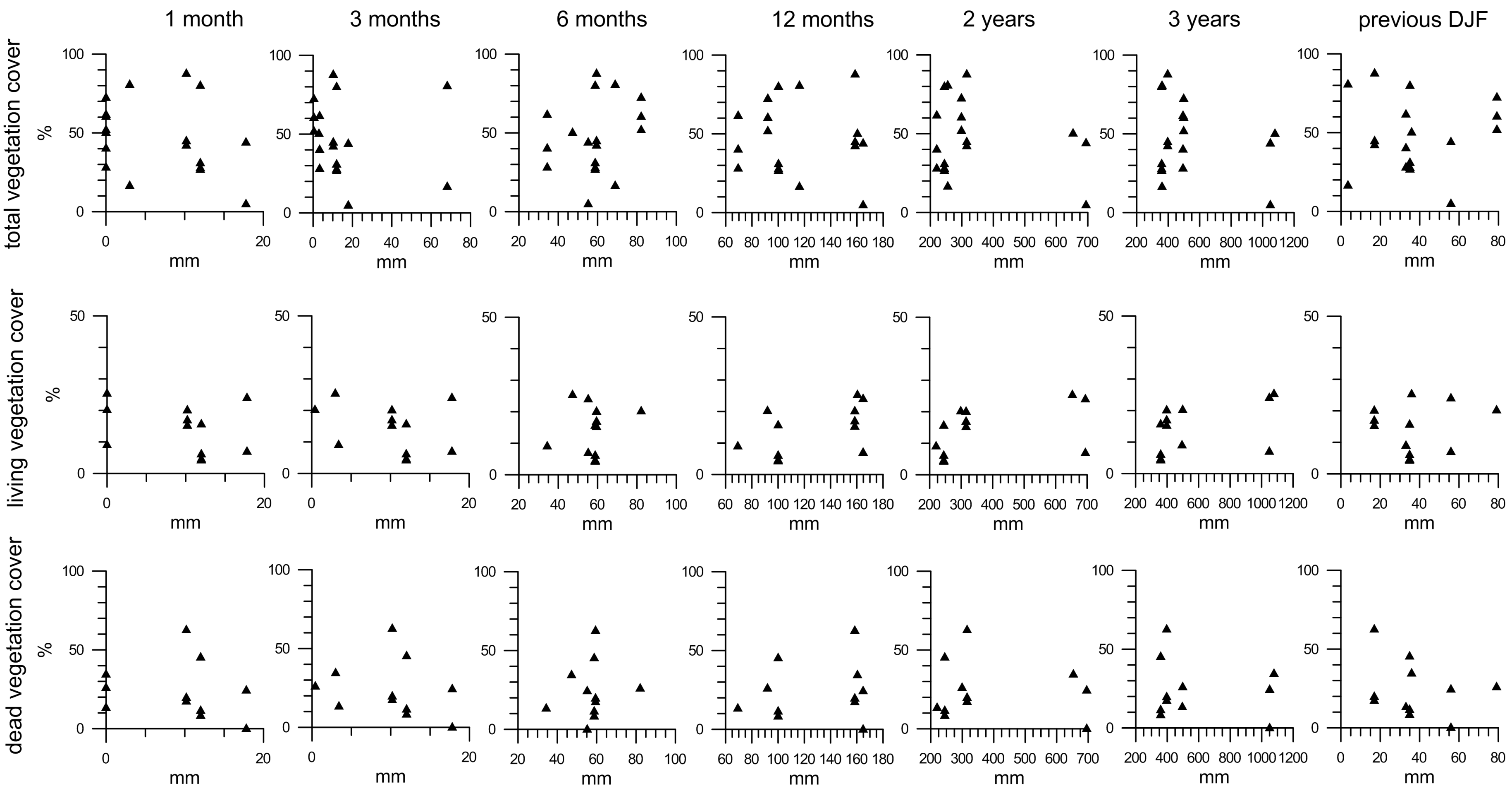


Figure S1 Graphs of Antecedent Rainfall and Total, Living and Dead Vegetation Cover for all Surveys

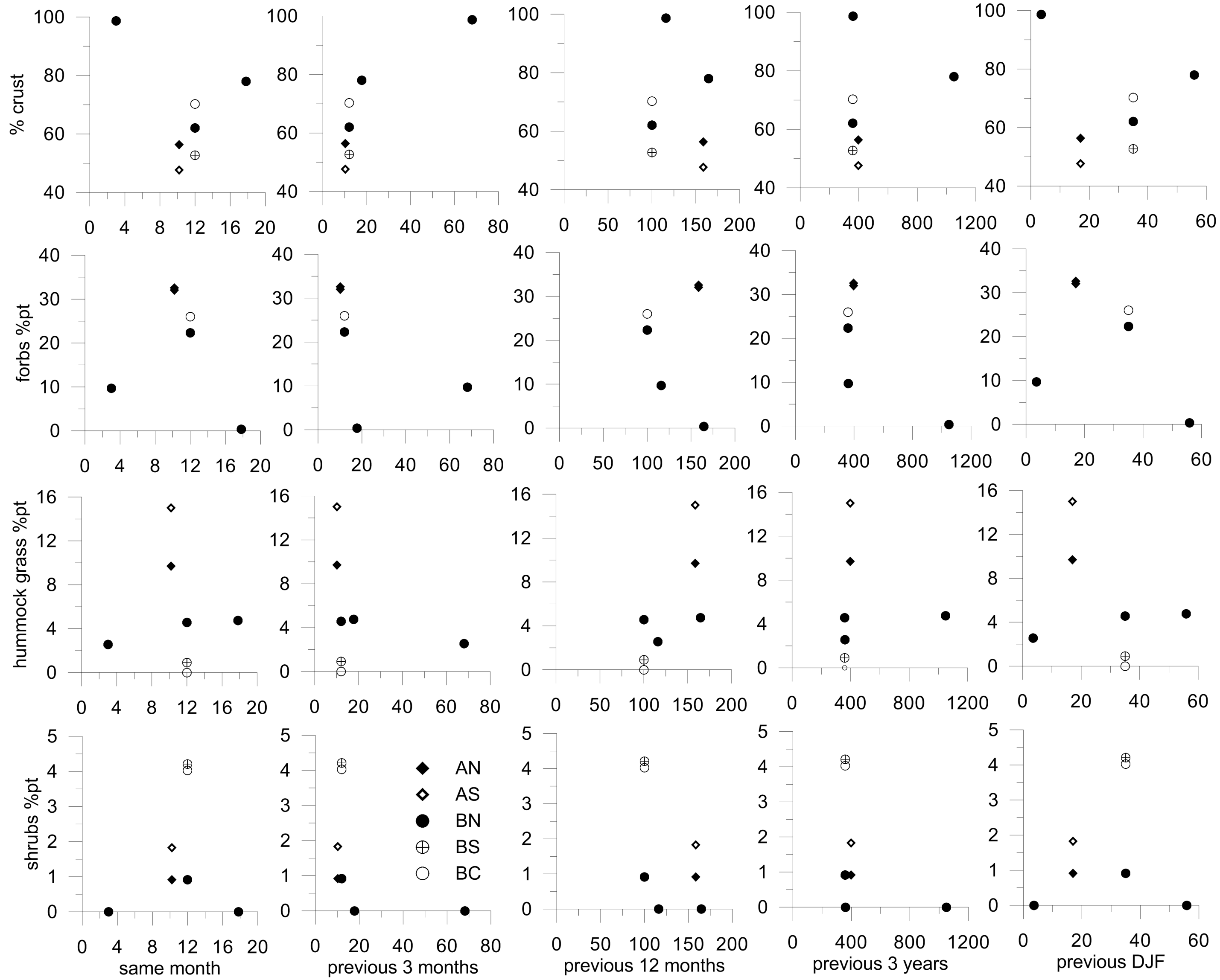


Figure S2. Coverage of different PFTs on bare crests for different periods of antecedent rainfall.

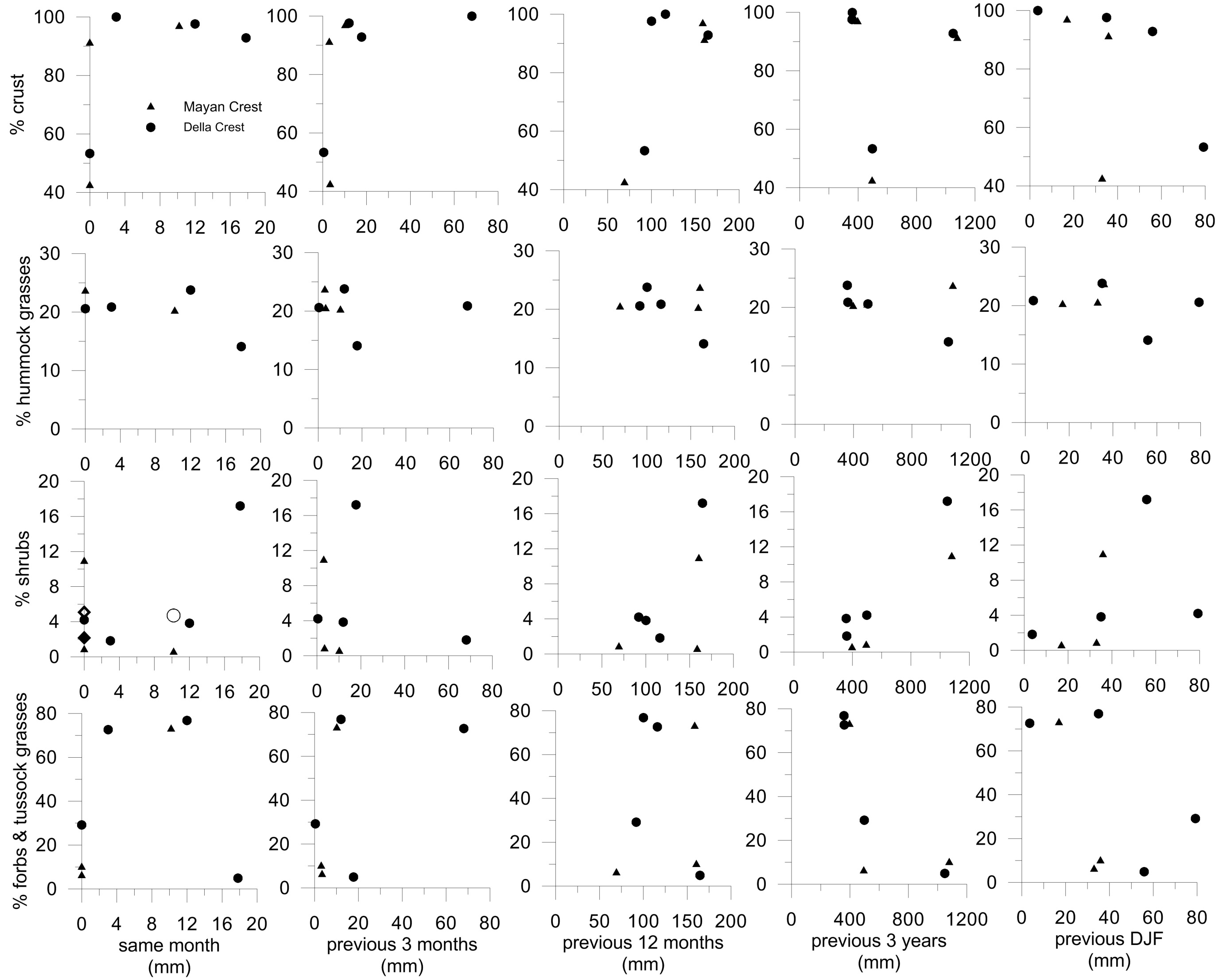
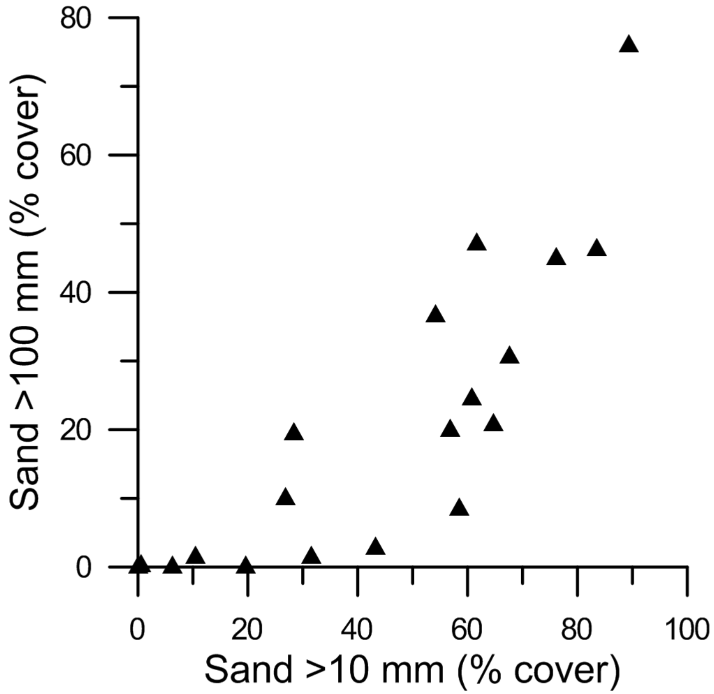


Figure S3. Coverage of different PFTs on vegetated crests for different periods of antecedent rainfall.



Supplementary Figure 4. Relationship between cover of loose sand deeper than 10 mm and cover of loose sand deeper than 100 mm for all sites.

- Sand movement on dune crests is limited by crust (biotic and/or physical) and plant cover
- Vegetation on desert dune crests over a drought cycle varied greatly between surveys
- Crust & small plants expand above a threshold of 10 mm rain in the preceding 90 days
- Tall plants (>50 cm) increase above >400 mm rain over preceding 3 years.
- Both thresholds restrict at-risk days to decadal droughts, leading to meta-stability

Complexity confers stability: Climate variability, vegetation response and sand transport on longitudinal sand dunes in Australia's deserts

Paul P **Hesse**[a], Matt W **Telfer**[b], Will **Farebrother**[a]

[a] Department of Environmental Sciences, Macquarie University, Sydney, NSW 2109, Australia

[b] School of Geography, Earth and Environmental Sciences, University of Plymouth, Drake Circus, Plymouth, Devon PL4 8AA, UK

* Corresponding author paul.hesse@mq.edu.au

matt.telfer@plymouth.ac.uk

willfarebro@gmail.com