The demise of the largest and oldest African baobabs

Adrian Patrut[®]^{1*}, Stephan Woodborne[®]², Roxana T. Patrut³, Laszlo Rakosy³, Daniel A. Lowy⁴, Grant Hall⁵ and Karl F. von Reden[®]⁶

The African baobab is the biggest and longest-living angiosperm tree. By using radiocarbon dating we identified the stable architectures that enable baobabs to reach large sizes and great ages. We report that 9 of the 13 oldest and 5 of the 6 largest individuals have died, or at least their oldest parts/ stems have collapsed and died, over the past 12 years; the cause of the mortalities is still unclear.

The African baobab (*Adansonia digitata* L.) has a natural distribution in the savannah regions of Africa between the latitudes 16° N and 26° S. It is also found outside Africa in tropical areas, where it has been introduced¹⁻³. The biggest and oldest specimens may have wood volumes of $300-500 \text{ m}^3$ and reach ages close to 2,000 years; by these values the African baobab is the largest and longest living angiosperm tree^{4,5}.

In 2005 we started an in-depth research programme to elucidate several controversial or poorly understood aspects of the architecture, growth and age of the African baobab. The research is based on our new approach, which is not limited to fallen specimens, but allows live specimens to be investigated and dated. The approach consists of accelerator mass spectrometry (AMS) radiocarbon dating of small wood samples collected from inner cavities and/or from different areas of their trunk/stems⁴.

This research has revealed that big African baobabs are always multistemmed. The majority of baobabs start growing as singlestemmed trees. Over time, single-stemmed individuals become multistemmed, owing to the baobabs' ability to periodically produce new stems, in much the same way other tree species produce branches. With this special ability, baobabs develop architectures of increasing complexity over time. Therefore, we focused on the investigation of superlative individuals: very large and potentially old baobabs. One should emphasize that neither the identification of such very complex architectures nor the accurate age determination of old baobabs is possible via traditional dendrochronological methods based on tree ring investigation. The radiocarbon investigation of large African baobabs has revealed that their architecture is much more complex and idiosyncratic than previously believed^{6.7}.

Our research has identified a new type of architecture that enables African baobabs to reach great ages and large sizes. In this architecture, the multiple stems define a circle or an ellipse at ground level, with an empty space between them; we named it the ring-shaped structure (RSS). There are two subtypes of RSSs. The only one obvious to visual observation is the open RSS in which the stems are fused or knitted at the base, are pointed sideways, have quasi-cylindrical shapes and quasi-circular transversal sections^{5,7}. The most frequent is, however, the closed RSS in which the stems are pointed upwards and are fused almost perfectly. The fused stems are disposed in a ring with an empty space inside. We called this natural empty space between the fused stems the false cavity^{6,7}.

According to dating results, open and closed RSSs have formed progressively and closed over time as they usually consist of three to eight stems belonging to several generations. Certain individuals have additional stems outside the ring(s).

Many old baobabs have large hollow parts, mainly in the central area of their trunk/stems. Large normal cavities are formed by wood loss (because of fungi decay, fire, elephant damage) and the pith/centre is located inside the cavity. The ages of samples collected from normal cavities decrease continuously from the cavity walls towards the outer part of the trunk/stem⁷.

In most cases we found, however, that the age sequence shows a continuous increase from the cavity walls up to a certain distance into the wood, after which it decreases towards the outer part. The only reasonable explanation is that such cavities are in fact false cavities: natural empty spaces between fused stems disposed in a closed RSS. The thickness of the fused stems that define the false cavity is only 1-2 m. The oldest part of the fused stems is located between the false cavity walls and the outer part/exterior of each stem, always closer to the cavity, in an area that would be accessible to the increment borer and allows very old samples to be collected^{6,7} (Supplementary Fig. 1a–d).

The first noticeable difference between false and normal cavities is the presence or absence of bark inside the cavity. Normal cavities become larger over time because of continuous decay, but false cavities become smaller because of stem growth. Similarly to the closed RSSs, the false cavities close progressively. Several false cavities have closed completely over time, retaining only one or several small openings. The closed RSSs with their false cavities represent the most enigmatic architecture of the African baobab. We found that this structure is a characteristic exclusive to baobabs: trees that belong to the *Adansonia* genus^{6–8}.

In the period 2005–2017, we investigated and dated practically all known very large and potentially old African baobab specimens (over 60 trees) from northern and southern continental Africa, the African islands and outside Africa^{4–8}. The main data and dating results of the oldest 13 specimens (numbered 1–13) and of the largest 6 specimens, in terms of wood volume (marked 21–26), are shown in Table 1 (see also Supplementary Tables 1 and 2).

The most unexpected and intriguing fact is that since 2005, 8 of the 13 oldest African baobab specimens and 5 of the 6 largest

The Nature trademark is a registered trademark of Springer Nature Limited.

¹Faculty of Chemistry and Chemical Engineering, Babes-Bolyai University, Cluj-Napoca, Romania. ²iThemba LABS, Johannesburg, South Africa. ³Faculty of Biology and Geology, Babes-Bolyai University, Cluj-Napoca, Romania. ⁴Department of Science and Engineering, Nova University, Alexandria, VA, USA. ⁵Mammal Research Institute, University of Pretoria, Pretoria, South Africa. ⁶NOSAMS Facility, Department of Geology & Geophysics, Woods Hole Oceanographic Institution, Woods Hole, MA, USA. ^{*}e-mail: apatrut@gmail.com

BRIEF COMMUNICATION

NATURE PLANTS

No.	Tree (location)	Girthª (m)	Height (m)	Volume (m ³)	Radiocarbon age ^ь (¹⁴ C yr BP)	Sample age⁵ (cal yr)	Calculated age of tree/stem (cal yr)	Status
1/24	Panke (Mbuma, Zimbabwe)	25.50	15.5	(400)	2,429 [±14]	2,450 [+ 45, -40] (in 2011)	+2,500	All stems toppled and died in 2010-2011
2	Dorslandboom (Khaudum Park, Namibia)	(+30) ^c	14.3	(200)	1,956 [±21]	1,915 [+25] (in 2006)	2,100	The oldest two stems toppled and died in 2006
3/23	Glencoe tree (Hoedspruit, South Africa)	(+30) ^c	16.0	(400)	1,931 [±14]	1,905 [±40] (in 2009)	+2,000	The main old part split and died in 2009
4/26	Holboom (Nyae Nyae Conservancy, Namibia)	35.10	30.2	(340)	1,760 [±18]	1,700 [±60] (in 2012)	1,800	Several stems and cavity walls broke off since 2012
5	Humani Bedford Old baobab (Savé Valley, Zimbabwe)	23.65	18.2	(240)	1,655 [±14]	1,585[+35, –25]	1,800	Alive
6	Makuri Leboom (Nyae Nyae Conservancy, Namibia)	34.23	14.5	(200)	1,602 [±17]	1,510 [+35, -40]	1,600	Several old stems toppled and/or broke off
7/25	Grootboom (Nyae Nyae Conservancy, Namibia)	30.60	32.0	(350)	1,575 [±14]	1,455 [±20] (in 2005)	1,500	All stems toppled and died in 2004-2005
8	Matendere Big baobab (Savé Valley, Zimbabwe)	26.30	22.5	(300)	1,529 [±14]	1,430 [±45]	1,500	Alive
9	Luna tree (Venetia Limpopo NR, South Africa)	20.02	17.2	(170)	1,507 [±22]	1,405 [±20]	1,500	Alive
10	Lebombo Eco trail baobab (Limpopo NP, Mozambique)	21.44	18.5	(220)	1,425 [<u>+</u> 24]	1,360 [±10]	1,400	Alive
11	Chapman baobab (Makgadikgadi Pans, Botswana)	25.90	22.6	(275)	1,381 [±22]	1,345 [+10,- 15] (in 2016)	1,400	All stems toppled and died in 2016
12	Makulu Makete Big baobab (Makulu Makete Reserve, South Africa)	22.25	23.0	(220)	1,277 [±21]	1,195 [+45] (in 2008)	1,250	All stems toppled and died in 2008
13	Lundu baobab (South Luangwa NP, Zambia)	26.01	24.6	(300)	1,221 [±26]	1,190 [+75, –55]	1,250	Several stems and cavity walls broke off since 2014
21	Platland tree/Sunland baobab (Modjadjiskloof, South Africa)	34.11	18.9	501	978 [±14]	930 [+50,– 70]	1,100	The largest unit toppled and died in 2016-2017
22	Sagole Big tree (Zwigodini/ Mutale, South Africa)	34.35	20.3	414	781 [±29]	740 [±15]	850	Alive

Table 1 | Main data, radiocarbon and calibrated ages of the oldest and largest African baobabs

Specimens that toppled completely or partially have a bold name and number; estimated values are in round brackets. ¹⁴C yr BP, radiocarbon years before present (before AD 1950); cal yr, clalibrated calendar years. ^aCircumference at 1.30 m. ^bOf the oldest dated sample/segment. ^cUnmeasurable because of collapsed stems.

individuals (marked in bold in Table 1) have died or at least their largest and/or oldest parts/stems have collapsed and died. All 15 superlative trees listed in Table 1 are or were located in southern Africa (5 in South Africa, 4 in Namibia, 3 in Zimbabwe and 1 each in Botswana, Mozambique and Zambia), which is the home of the oldest and largest African baobabs. Nine individuals exhibit or exhibited a closed RSS (Panke, Holboom, Humani Bedford, Matendere, Luna, Lebombo, Lundu, Platland, Sagole), and four individuals have or had an open RSS (Dorslandboom, Glencoe, Makuri Leboom, Chapman). Finally, one specimen had an incomplete RSS (Grootboom) and another a cluster structure (Makulu Makete).

All stems of four African baobabs have toppled and died (Panke in 2010–2011, Grootboom in 2004–2005, Chapman in 2016 and

Makulu Makete in 2008). The largest and oldest stems of the other six individuals have collapsed and died, but other smaller and younger stems survived, and are still alive (Dorslandboom in 2006, Glencoe in 2009, Makuri Leboom since 2005, Holboom since 2012, Lundu since 2014 and Platland in 2016–2017).

Here we present briefly three superlative trees, which were the oldest, the largest and the most famous African baobabs, that have collapsed and died recently.

Panke (no. 1 and 24 in Table 1 and Supplementary Fig. 2) was a sacred baobab located in a remote area of Matabeleland North, Zimbabwe^{9,10}. It had a closed RSS, with a ring defined by three fused stems around a false cavity with a low entrance; it also had three additional stems. In 2010, the remaining branches started to break

BRIEF COMMUNICATION

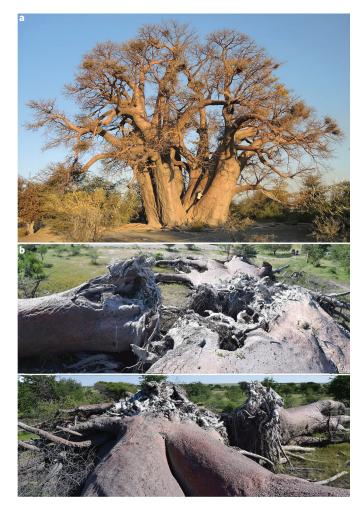


Fig. 1 | Life and death of the historic Chapman baobab. a, The Chapman baobab in June 2015, showing its open RSS, which consisted of six stems. **b,c**, Photographs showing the baobab just after its sudden collapse in January 2016. The tree lies on the ground almost intact, with unbroken stems and branches.

off and collapsed successively; next, the stems split and toppled one after another over a period of more than one year. We collected and dated several samples from its remains. The oldest sample had a radiocarbon age of $2,419 \pm 14$ BP, which corresponds to a calibrated calendar age of approximately 2,450 years. By this value, Panke becomes the oldest African baobab and angiosperm with accurate dating results.

The Platland tree, also known as Sunland baobab (no. 21; Supplementary Fig. 3), situated in Limpopo province, South Africa, was probably the most promoted and visited African baobab^{4,11}. Platland was the biggest known African baobab and angiosperm⁴, with a total wood volume of 501 m³. Its huge trunk has a double closed RSS and consists of two units, composed of two rings with two interconnected false cavities. The largest unit split four times in 2016 and 2017 and all its five stems toppled and died.

The most famous historic baobab, the Chapman baobab (no. 11; Fig. 1), was located close to the Makgadikgadi Pans of Central Botswana⁷. It was named after the South African hunter James Chapman, who visited the tree in 1852. The Chapman baobab had an open RSS, with six partially fused stems that belonged to three generations that were 1,400, 800–1,000 and 500–600 years old. On 7 January 2016, the six stems of Chapman toppled simultaneously and died.

The deaths of the majority of the oldest and largest African baobabs over the past 12 years is an event of an unprecedented magnitude. These deaths were not caused by an epidemic and there has also been a rapid increase in the apparently natural deaths of many other mature baobabs. We suspect that the demise of monumental baobabs may be associated at least in part with significant modifications of climate conditions that affect southern Africa in particular¹². However, further research is necessary to support or refute this supposition.

Methods

Metric measurements. The height of the investigated baobabs was measured when they still had standing stems using a Bosch Professional laser rangefinder and a Suunto clinometer. The circumference at breast height, at 1.30 m above ground level (cbh), was measured with graduated tapes. The overall wood volume was determined accurately for the two largest specimens (Platland, Sagole)⁴using Criterion survey lasers. For the other individuals, the overall volume was estimated from laser measurements of both the stems and large branches at different heights. For two specimens that toppled completely and died before our initial investigations (Panke, Grootboom), we adopted the dimensions measured previously by other researchers.

Sample collection. Several tiny wood samples were collected from the inner cavities and/or different areas of the outer part of stems at convenient heights between 1.00 m and 2.20 m, as well as from fallen/broken stems of live baobabs. Sampling was performed using Haglöf increment borers with lengths of 0.60–1.50 m (inner diameter 0.54–1.08 cm). In some cases, we also collected samples from the remains of dead specimens. Millimetre-length segments were extracted from determined positions of the original samples.

Radiocarbon measurements. After pretreatment, the sample segments were finally reduced to graphite^{7,8}. The AMS radiocarbon investigation of the graphite samples was performed at the NOSAMS Facility of the Woods Hole Oceanographic Institution, Woods Hole, MA, USA, using the Pelletron Tandem 500 kV AMS system. The obtained fraction modern values corrected for isotope fractionation were ultimately converted to radiocarbon ages. Radiocarbon ages of the oldest sample segments originating from each of the investigated baobabs are listed in Table 1 and Supplementary Table 2. Radiocarbon ages and errors were rounded to the nearest year.

Calibration. Radiocarbon ages were calibrated and converted into calendar ages with the OxCal v4.3 for Windows¹³, using the SHCal13 atmospheric dataset¹⁴ for the Southern Hemisphere.

Calibrated ages. The 1o probability distribution (68.2%) was typically selected to derive calibrated age ranges. For seven sample segments the 1σ distribution is consistent with one range of calendar years, and for other three segments the 1σ distribution corresponds to two ranges. For these three segments, the confidence interval of one range is considerably greater than that of the others; therefore, it was selected as the calibrated AD age (cal AD) range of the sample segment (marked in italics) for the purpose of this discussion. However, for five sample segments, there are several 1σ ranges with close confidence intervals. In these special cases (Glencoe, Holboom, Matendere, Lundu, Platland), we used the higher 2σ probability distribution (95.4%) for calibration, which corresponds to one or two ranges of calendar years for each date. We selected the range with the highest probability as the cal AD range of each sample segment (Supplementary Table 2; marked in italics) for the purpose of this discussion. The cal AD ranges for all 15 radiocarbon ages are displayed in Supplementary Table 2. For obtaining single age values, which each correspond to an assigned year, we derived a mean value for the 15 selected age ranges; this mean value divides the range graphically in two equal areas7. The assigned years for the 15 sample segments are presented in Supplementary Table 2.

Sample ages. Sample ages, expressed in calendar years, represent the difference between AD 2017 (or the year when the stem died) and the mean value of the selected range. Sample ages and errors were rounded to the nearest 5 years.

Tree/stem ages. The tree/stem ages were calculated by extrapolating the oldest sample ages to the calculated position of the stem's pith. Sample ages and tree/stem ages are shown in Table 1 and Supplementary Table 2.

Reporting Summary. Further information on experimental design is available in the Nature Research Reporting Summary linked to this article.

Data availability. The authors declare that all data supporting the findings of this study are available within the article. The NOSAMS Accession Numbers for the disclosed radiocarbon measurements are included in Supplementary Table 2.

NATURE PLANTS | VOL 4 | JULY 2018 | 423-426 | www.nature.com/natureplants

The Nature trademark is a registered trademark of Springer Nature Limited.

BRIEF COMMUNICATION

NATURE PLANTS

Received: 2 January 2018; Accepted: 4 May 2018; Published online: 11 June 2018

References

- 1. Wickens, G. E. & Lowe, P. *The Baobabs: Pachycauls of Africa, Madagascar and Australia* (Springer, Dordrecht, 2008).
- 2. Wickens, G. E. Kew Bull. 47, 173-209 (1983).
- 3. Baum, D. A. Ann. Mo. Bot. Gard. 82, 440-471 (1995).
- 4. Patrut, A. et al. Ann. For. Sci. 68, 993-1003 (2011).
- Patrut, A., von Reden, K. F., Mayne, D. H., Lowy, D. A. & Patrut, R. T. Nucl. Instrum. Methods Phys. Rev. B 294, 622–626 (2013).
- 6. Patrut, A. et al. *PLoS ONE* **10**, e0117193 (2015).
- 7. Patrut, A. et al. *Radiocarbon* **59**, 435–448 (2017).
- Patrut, A. et al. Tree Physiol. 27, 1569–1574 (2007).
 Alexander, J., McGregor, J. A. & Ranger, T. Violence & Memory, One Hundred
- Years in the 'Dark Forests' of Matabeleland (Currey, Oxford, 2000).
- 10. Mullin, L. J. Historic Trees of Zimbabwe (CBC, Bath, 2003).
- 11. Patrut, A. et al. *Radiocarbon* **52**, 717–726 (2010).
- 12. Engelbrecht, F. et al. Environ. Res. Lett. 10, 085004 (2015).
- 13. Bronk Ramsey, C. et al. *Radiocarbon* **51**, 337–360 (2009).
- 14. Hogg, A. G. et al. Radiocarbon 55, 1889-1903 (2013).

Acknowledgements

The investigation and collection of samples from the trees was approved and authorised by the South African National Parks, the Kruger National Park, the Mapungubwe National Park, the Ministry of Environment and Tourism of Namibia and the Department of Wildlife and National Parks of Botswana, the South Luangwa National Park. We thank H. and D. van Heerden, P. Philips and J. Chidgey, C. and Y. Liversage, L. Duplessis and R. and A. Whittall for granting permission for on-site investigation of baobabs located on their private lands. We also thank D.H. Mayne, M. Hofmeyr, S. Venter, A. Alberts, R. Wittmann, D. Dube and O. (Leon) Tsamkgao for helping to obtain permits and for participating at several field investigations. Special thanks go to J. Alexander for providing the photograph of Panke. This research was supported by the Romanian Ministry of National Education CNCS-UEFISCDI under grant PN-II-ID-PCE-2013-76 and by the Romanian Ministry of Research and Innovation CNCS-UEFISCDI under grant PN-III-P4-ID-PCE-2016-0776, no. 90/2017.

Author contributions

A.P. conceived the research. A.P., S.W., R.T.P., L.R. and G.H. performed field investigations and collected samples. K.F.v.R. performed AMS measurements. A.P., S.W., R.T.P. and D.A.L. interpreted results and wrote the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41477-018-0170-5.

Reprints and permissions information is available at www.nature.com/reprints.

Correspondence and requests for materials should be addressed to A.P.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

natureresearch

Corresponding author(s): Professor Adrian Patrut

Life Sciences Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form is intended for publication with all accepted life science papers and provides structure for consistency and transparency in reporting. Every life science submission will use this form; some list items might not apply to an individual manuscript, but all fields must be completed for clarity.

For further information on the points included in this form, see Reporting Life Sciences Research. For further information on Nature Research policies, including our data availability policy, see Authors & Referees and the Editorial Policy Checklist.

Please do not complete any field with "not applicable" or n/a. Refer to the help text for what text to use if an item is not relevant to your study. <u>For final submission</u>: please carefully check your responses for accuracy; you will not be able to make changes later.

Experimental design

.....

⊥.	Sample size					
	Describe how sample size was determined.	The typical sample size for AMS radiocarbon dating, which involves pretreatment, graphitisation and AMS masurement is between 0.002 - 0.005 g. This amount of wood is extracted from predetermined positions of larger samples. One should mention that each position of the sample has a distinct radiocarbon age, which changes continuously along the sample.				
2.	Data exclusions					
	Describe any data exclusions.	No data were excluded from the analysis.				
3.	Replication					
	Describe the measures taken to verify the reproducibility of the experimental findings.	The radiocarbon measurements reported by the world's leading laboratories are not questioned. The results are subject to internal verification before a final value with the corresponding error is reported. In certain cases, such as Dorslandboom, Glencoe tree, etc. listed in the tables, we successfully replicated the radiocarbon measurements.				
4.	Randomization					
	Describe how samples/organisms/participants were allocated into experimental groups.	The superlative African baobabs around the world, out of which we presented the 15 oldest and/or largest individuals, were investigated and sampled by our international research team. Currently, we are the only team which performs this type of research.				
5.	Blinding					
	Describe whether the investigators were blinded to group allocation during data collection and/or analysis.	Blinding is not relevant to our study, which refers to the oldest and/or largest African baobabs.				

Note: all in vivo studies must report how sample size was determined and whether blinding and randomization were used.

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a	Confirmed
\boxtimes	The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
	A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
\boxtimes	A statement indicating how many times each experiment was replicated
\boxtimes	The statistical test(s) used and whether they are one- or two-sided Only common tests should be described solely by name; describe more complex techniques in the Methods section.
\square	A description of any assumptions or corrections, such as an adjustment for multiple comparisons
\boxtimes	Test values indicating whether an effect is present Provide confidence intervals or give results of significance tests (e.g. P values) as exact values whenever appropriate and with effect sizes noted.
	A clear description of statistics including <u>central tendency</u> (e.g. median, mean) and <u>variation</u> (e.g. standard deviation, interquartile range)
\boxtimes	Clearly defined error bars in <u>all</u> relevant figure captions (with explicit mention of central tendency and variation)

See the web collection on statistics for biologists for further resources and guidance.

Software

Policy information about availability of computer code

7. Software

Describe the software used to analyze the data in this study.

Radiocarbon ages were calibrated and converted into calendar ages with the OxCal v4.3 for Windows, by using the SHCal13 atmospheric data set, as mentioned in the Methods section.

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). *Nature Methods* guidance for providing algorithms and software for publication provides further information on this topic.

Materials and reagents

Policy information about availability of materials

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a third party. The main finding of our research was that almost all oldest and/or largest African baobabs have died or at least their oldest parts/stems have collapsed and died over the past 12 years. Hence, these individuals are no longer extant. Under natural conditions, baobabs decay shortly after death, usually disappearing without a trace within several years. However, our research group is in possession wood samples collected from the investigated specimens, which are stored under dry conditions.

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

No antibodies were used.

10. Eukaryotic cell lines

- a. State the source of each eukaryotic cell line used.
- b. Describe the method of cell line authentication used.
- c. Report whether the cell lines were tested for mycoplasma contamination.
- d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by ICLAC, provide a scientific rationale for their use.

No eukar	votic	COLL	linde	MORD	LICOU.
NO Eukai	your	CEII	IIII C3	WEIE	useu.

No eukaryotic cell lines were used.

No eukaryotic cell lines were used.

No commonly misidentified cell lines were used.

Animals and human research participants

Policy information about studies involving animals; when reporting animal research, follow the ARRIVE guidelines

11. Description of research animals

Provide all relevant details on animals and/or animal-derived materials used in the study.

No animals were used.

Policy information about studies involving human research participants

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.

The study did not involve human research participants.

Nature Research, brought to you courtesy of Springer Nature Limited ("Nature Research")

Terms and Conditions

Nature Research supports a reasonable amount of sharing of content by authors, subscribers and authorised or authenticated users ("Users"), for small-scale personal, non-commercial use provided that you respect and maintain all copyright, trade and service marks and other proprietary notices. By accessing, viewing or using the nature content you agree to these terms of use ("Terms"). For these purposes, Nature Research considers academic use (by researchers and students) to be non-commercial.

These Terms are supplementary and will apply in addition to any applicable website terms and conditions, a relevant site licence or a personal subscription. These Terms will prevail over any conflict or ambiguity with regards to the terms, a site licence or a personal subscription (to the extent of the conflict or ambiguity only). By sharing, or receiving the content from a shared source, Users agree to be bound by these Terms.

We collect and use personal data to provide access to the nature content. ResearchGate may also use these personal data internally within ResearchGate and share it with Nature Research, in an anonymised way, for purposes of tracking, analysis and reporting. Nature Research will not otherwise disclose your personal data unless we have your permission as detailed in the Privacy Policy.

Users and the recipients of the nature content may not:

- 1. use the nature content for the purpose of providing other users with access to content on a regular or large scale basis or as a means to circumvent access control;
- 2. use the nature content where to do so would be considered a criminal or statutory offence in any jurisdiction, or gives rise to civil liability, or is otherwise unlawful;
- 3. falsely or misleadingly imply or suggest endorsement, approval, sponsorship, or association unless explicitly agreed to by either Nature Research or ResearchGate in writing;
- 4. use bots or other automated methods to access the nature content or redirect messages; or
- 5. override any security feature or exclusionary protocol.

These terms of use are reviewed regularly and may be amended at any time. We are not obligated to publish any information or content and may remove it or features or functionality at our sole discretion, at any time with or without notice. We may revoke this licence to you at any time and remove access to any copies of the shared content which have been saved.

Sharing of the nature content may not be done in order to create substitute for our own products or services or a systematic database of our content. Furthermore, we do not allow the creation of a product or service that creates revenue, royalties, rent or income from our content or its inclusion as part of a paid for service or for other commercial gain. Nature content cannot be used for inter-library loans and librarians may not upload nature content on a large scale into their, or any other, institutional repository.

To the fullest extent permitted by law Nature Research makes no warranties, representations or guarantees to Users, either express or implied with respect to the nature content and all parties disclaim and waive any implied warranties or warranties imposed by law, including merchantability or fitness for any particular purpose.

Please note that these rights do not automatically extend to content, data or other material published by Nature Research that we license from third parties.

If you intend to distribute our content to a wider audience on a regular basis or in any other manner not expressly permitted by these Terms please contact us at

onlineservice@springernature.com

The Nature trademark is a registered trademark of Springer Nature Limited.