

CHAPTER 2

The African Pollen Database (APD) and tracing environmental change: State of the Art

Anne-Marie Lézine

Laboratoire d'Océanographie et du Climat, Expérimentation et Approche numérique/IPSL, Sorbonne Université, CNRS-IRD-MNHN, Paris, France

Sarah J. Ivory

Department of Geosciences, Pennsylvania State University, University Park, USA

William D. Gosling

Institute for Biodiversity and Ecosystems Dynamics, University of Amsterdam, Amsterdam, The Netherlands

Louis Scott

Department of Plant Sciences, University of the Free State, Bloemfontein, South Africa

ABSTRACT: The African Pollen Database is a scientific network with the objective of providing the international scientific community with data and tools to develop palaeoenvironmental studies in sub-Saharan Africa and to provide the basis for understanding the vulnerability of ecosystems to climate change. This network was developed between 1996 and 2007. It promoted the collection, homogenization and validation of pollen data from modern (trap, soils, lake and river mud) and fossil materials (Quaternary sites) and developed a tool to determine pollen grains using digital photographs from international herbaria. Discontinued in 2007 due to a lack of funding, this network now resumes its activity in close collaboration with international databases: Neotoma, USA, Pangaea, DE, and the Institut Pierre Simon Laplace, FR.

2.1 INTRODUCTION

International cooperation in research and decision-making is critical for solving global environmental problems linked to climate and/or human impact on ecosystems, particularly at regional level. These environmental problems include forest degradation, accelerating loss of biodiversity and water resources, instability of transitional ecological domains, and change in coastal zones. Tropical ecosystems are especially at risk as future states are likely to be beyond the range of observations, yet their preservation is of crucial importance for the maintenance of the Earth's biosphere and climate. For example, the role of the equatorial and tropical forests

in global exchanges, such as the global carbon cycle, is widely recognised (Detwiler and Hall 1988). Research developed within the general framework of international scientific programmes (e.g., the International Geosphere Biosphere Programme, IGBP – <http://www.igbp.net/>) have long highlighted the need to provide quantitative understanding of the Earth's past environment in order to define the envelope of natural environmental variability within which we can assess anthropogenic impact on the Earth's biosphere, geosphere and atmosphere. Following these recommendations, the scientific community has developed a set of analytical techniques to recover high-resolution environmental and ecological records from different natural archives such as tree-rings, and lake and ocean sediments, thus providing accurate scientific information for the development of predictive models of regional and global change. The use of these data to test Earth system model simulations requires the collection, assemblation, standardization and subsequently the access to the wider scientific and modelling community in the form of specific regional databases.

2.2 MAIN ACHIEVEMENTS

The African Pollen Database (APD) was first developed in 1996 in close cooperation with its European counterpart (EPD) (European Pollen Database; <http://www.europeanpollendatabase.net>) and the Global Pollen Database hosted at the National Oceanic and Atmospheric Administration (NOAA) Paleoclimatology Database (USA) (<https://www.ncdc.noaa.gov/data-access/paleoclimatology-data>). The initial workshop and subsequent work, funded by the French National Centre for Scientific Research (CNRS), the European Union (International Cooperation for development (INCO-DEV) and European network of research and innovation centres (ENRICH) programmes and the UNESCO International Geoscience Programme (PICG), established methods of collating pollen data, developed a standardized pollen nomenclature (Vincens *et al.* 2007), generated updated age models, composed images of pollen grains from internationally recognized herbaria, and created a searchable web interface. In the first stage of its development, the APD contained 288 fossil sites and 1985 modern samples (Figure 1). Among the numerous achievements of the APD one can highlight the following topics.

2.2.1 Pollen based biome reconstructions

Jolly *et al.* (1998) first demonstrated that the 'biomization' method for assigning pollen taxa to plant functional types and biomes was able to predict the potential natural vegetation of tropical Africa, despite uncertainty and variability of pollen production and dissemination (Ritchie 1995) of an extremely biodiverse flora (26,000 plant species; Lebrun and Stork 1991–1997). This allowed palaeoecologists working in Africa to participate in the 'BIOME 6000' project sponsored by IGBP (Prentice and Webb 1998). This project aimed to use palaeoecological data from the mid-Holocene as a benchmark to evaluate simulations with coupled climate-biosphere models and thus to assess the extent of biogeophysical (vegetation-atmosphere) feedbacks in the global climate system (Prentice *et al.* 2000). After the validation of the modern pollen dataset (Gajewski *et al.* 2002; Jolly *et al.* 1998), the biomization method was successfully applied to reconstruct modern (Lézine *et al.* 2009; Vincens *et al.* 2006) and past biomes for selected time periods, typically the Last Glacial Maximum (LGM) and the Holocene (Jolly *et al.* 1998; Elenga *et al.* 2000). Past biome reconstructions have also been performed for the Plio-Pleistocene (Bonnefille *et al.* 2004; Novello *et al.* 2015) and more recent time periods such as the last glacial-interglacial cycle and the Holocene (Amaral *et al.* 2013; Izumi and Lézine 2016; Lebamba *et al.* 2012; Lézine *et al.* 2019).

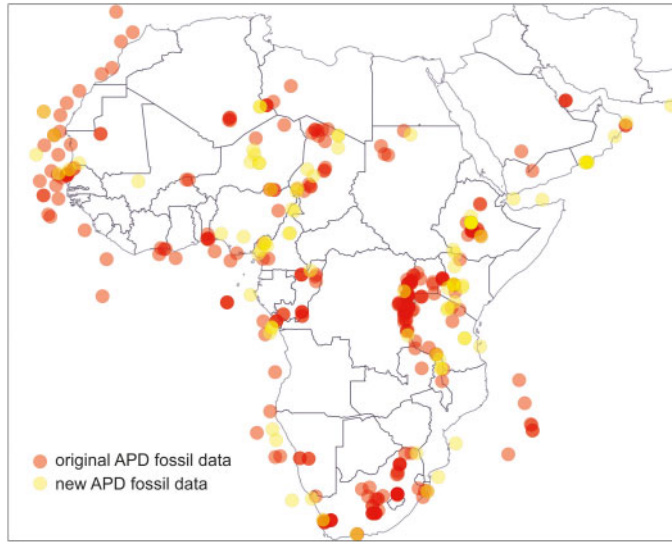


Figure 1. Late Quaternary African Pollen Database (APD) sites. In red: pollen data gathered during the first phase of the APD (1994–2007). In yellow: new pollen sites to be entered into the new version of APD, in construction).

2.2.2 Quantitative reconstructions of climate variables from pollen data

Modern-analogue, regression, and model-inversion techniques have been developed to reconstruct past climates from pollen assemblages or pollen-based reconstructed biomes worldwide. Using the APD modern pollen dataset, Peyron *et al.* (2007) provided the first quantitative pollen-based reconstruction of precipitation for all of Africa at 6000 yr BP based on the Modern Analogues Technique (MAT) and the Plant-Functional Types (PFT) climate relationships. Results were then compared with atmospheric general circulation model output and coupled ocean atmosphere-vegetation models developed in the frame of the Paleoclimate Model Inter-comparison Project (PMIP) international project (Joussaume and Taylor 1995). More recently, Wu *et al.* (2007) then Izumi and Lézine (2016) developed an inverse modelling approach based on the BIOME model to quantitatively reconstruct past climates based on pollen biome scores. The advantage of this method was to provide quantitative climate reconstructions for periods when CO₂ concentrations were different from today. While reconstruction attempts of climate by means of pollen data in South Africa, were mostly qualitative (Scott *et al.* 2012), Chevalier and Chase (2015) applied a method that related the pollen to plant distribution data to obtain quantitative estimates.

2.2.3 Vegetation reconstructions from pollen data

Palaeoecological data from the APD led to a series of reconstructions of vegetation at a continental scale. Site-based global biome maps for Africa for the mid-Holocene and LGM were first completed within the framework of the ‘BIOME 6000’ project (Prentice *et al.* 2000). More recently, APD palaeoecological data was included in a global synthesis of changes in composition and structure of past vegetation since the LGM performed by Nolan *et al.* (2018). This study provided a baseline for evaluation of the magnitudes of ecosystem transformations under future emission scenarios.

At a regional scale, APD data were used to reconstruct the Green Sahara and evaluate plant migration rates during the African Humid Period (Hély *et al.* 2014; Watrin *et al.* 2009). In

East Africa, compilation of pollen and archaeological data was used to discuss the cumulative effects of climate and land-use on the environment (Marchant *et al.* 2018). Furthermore, with the increasing recognition that fossil data can improve information about fundamental climatic tolerances, modern and palaeoecological data from the APD have been included in estimates of climatic niches of at-risk plant taxa (Ivory *et al.* 2016). This information was then used to provide forecasts of future impacts to ranges under climate and land-use trajectories for the end of the 21st century (Ivory *et al.* 2019).

2.3 CHALLENGES AND FUTURE DEVELOPMENTS

All these realizations suffer from (1) an highly uneven geographic distribution of data. Pollen data are relatively abundant in Eastern and Southern Africa where palynological research has been ongoing since the early 1950s (Hedberg 1954; van Zinderen Bakker and Coetzee 1952). In the former region, the abundance of lakes and swamps also provides favourable conditions for pollen preservation and long-time series. In North and Central Africa, on the other hand, data are less numerous and often discontinuous in time. The drying out of Holocene lakes in the Sahara, the difficulties of access to the sites, and their rarity are all limitations to regional geographical reconstructions; (2) the scarcity of long time series beyond the LGM (Ivory *et al.* 2017; Lézine *et al.* 2019; Miller and Gosling 2014; Scott 2016), and therefore long-term vegetation changes are mostly derived from marine cores (e.g., Dupont and Kuhlmann 2017; Hessler *et al.* 2010).

Thanks to a recent funding from the Belmont Forum for Science-driven e-infrastructure innovation for the project ‘Abrupt Change in Climate and Ecosystems: Where are the Tipping points?’, the APD is now being relaunched and developing further collaborations with international databases (‘NEOTOMA’, ‘PANGAEA’) and the French Institute Pierre Simon Laplace (IPSL). One of the priorities is to gather and validate data published since 2007, the date of the closure of the French data centre Medias-France where APD was stored. Today, 67 new late Quaternary, 17 Plio-Pleistocene and 20 marine new pollen series have been collated. Strong links are being developed with NEOTOMA (<https://www.neotomadb.org/>) and PANGAEA (<https://pangaea.de/>) databases.

These new datasets benefit from improved dating techniques and age modelling methods. The result of which is that newly acquired pollen series have reduced temporal uncertainty and improved resolution, allowing to more precision in interpretation of local and regional ecosystem dynamics and climate-vegetation interactions. All this allows to envisage new scientific developments of which one can cite three examples here:

2.3.1 Better understanding of ecosystem-human interactions

The identification and quantification of human-induced alterations to the Earth’s surface are critical to understand the role of land-use change on ecosystems and climate. The Land Cover 6k (6000 yrs BP) project of IGBP PAGES (<http://www.pastglobalchanges.org/science/wg/landcover6k>) described in Gaillard *et al.* (2018) is a unique opportunity to develop a methodological approach to carefully reconstruct land cover change from pollen data and evaluate anthropogenic land-cover change scenarios for palaeoclimate modelling. The major limitation of such a quantification in tropical Africa is that ‘with very few exceptions, tropical trees have zoophilous pollinating systems and relatively low pollen productivity’ (Ritchie 1995; p. 487). The relationship between pollen percentages in diagrams and actual vegetation cover is thus extremely difficult to assess. Within the equatorial forest for instance, many tree taxa are under-represented or even absent from the pollen assemblages.

The reliability of any landscape reconstruction requires the spatial scale represented by the pollen assemblage to be carefully taken into account. This requires the most accurate possible

evaluation of pollen productivity of species and pollen-rain settling time. Following the work of Duffin and Bunting (2008) in South Africa, Gaillard and colleagues are currently applying the LOVE (Local Vegetation Estimates) and REVEALS (Regional Estimates of Vegetation Abundance from Large Sites) models developed by Sugita (2007a,b) in Central Africa. The development of such an approach as well as the compilation of pollen and archaeological data (Marchant *et al.* 2018) can greatly improve the involvement of the palynological community in the study of land-use as a climate forcing.

2.3.2 Improved constraint of climate variability over the last millennia

The recent publication of Nash *et al.* (2016) within the framework of the PAGES 2ka working group (<http://www.pastglobalchanges.org/science/wg/2k-network>) showed that Africa is one of the world's most poorly documented regions in terms of climate reconstructions over the last millennia. Historical archives are very rare, as are natural archives with adequate temporal resolution and age control. Time frames where historical records overlap the prehistorical data are important to obtain seamless reconstructions and validate reconstructions. Improving the spatial coverage and resolution of palaeoecological records is crucial for studying natural decadal (or multi-decadal) climate variability and associated mechanisms. It is also essential to analyze the complexity of spatial hydroclimate patterns, such as that suggested for the Little Ice Age (1250–1750 CE) in Africa, for which wet or dry regions have been identified.

2.3.3 Understanding vegetation responses to abrupt climate change

The evolution of northern Africa from a 'Green Sahara' state to one of the most arid deserts today (Kröpelin *et al.* 2008) or the collapse of the equatorial forests (e.g., Lézine *et al.* 2013) occurred at the end of the African Humid Period. These are among the most emblematic examples of the extreme changes that can affect the global environment with dramatic consequences for human populations. The tipping points and climatic drivers between extreme states remain to be studied, as do the early warning signals of these environmental crises, which may date back several millennia, and still need to be identified. Long-term, high-resolution and evenly distributed pollen records are critical to address these questions.

2.4 CONCLUSION

The African Pollen Database aims at providing the scientific community, students and teachers with scientific and educational tools (pollen grain determination tools, modern and fossil data duly validated and dated, publications) to address key issues for understanding the vulnerability of ecosystems facing climate change. It ensures interoperability with international databases for multi-proxy reconstructions of the past environment. Beyond these activities, the African Pollen Database is a scientific network to develop the sharing of data and knowledge between researchers in different countries.

REFERENCES

- Amaral, P.G.C., Vincens, A., Guiot, J., Buchet, G., Deschamps, P., Doumnang, J.C. and Sylvestre, F., 2013, Palynological evidence for gradual vegetation and climate changes during the African Humid Period termination at 13° N from a Mega-Lake Chad sedimentary sequence. *Climate of the Past*, **9**(1), pp. 223–241, 10.5194/cp-9-223-2013.

- Bonnefille, R., Potts, R., Chalié, F., Jolly, D. and Peyron, O., 2004, High-resolution vegetation and climate change associated with Pliocene *Australopithecus afarensis*. *Proceedings of the National Academy of Sciences*, **101**(33), pp. 12125–12129, 10.1073/pnas.0401709101.
- Chevalier, M. and Chase, B.M., 2015, Southeast African records reveal a coherent shift from high- to low-latitude forcing mechanisms along the east African margin across last glacial-interglacial transition. *Quaternary Science Reviews*, **125**, pp. 117–130, 10.1016/j.quascirev.2015.07.009.
- Detwiler, R.P. and Hall, C.A., 1988, Tropical forests and the global carbon cycle. *Science*, **239**(4835), pp. 42–47, 10.1126/science.239.4835.42.
- Duffin, K.I. and Bunting, M.J., 2008, Relative pollen productivity and fall speed estimates for southern African savanna taxa. *Vegetation History and Archaeobotany*, **17**(5), pp. 507–525, 10.1007/s00334-007-0101-2.
- Dupont, L.M. and Kuhlmann, H., 2017, Glacial-interglacial vegetation change in the Zambezi catchment. *Quaternary Science Reviews*, **155**, pp. 127–135, 10.1016/j.quascirev.2016.11.019.
- Elenga, H., Peyron, O., Bonnefille, R., Jolly, D., Cheddadi, R., Guiot, J., Andrieu, V., Bottema, S., Buchet, G., De Beaulieu, J.L., Maley, J., Marchant, R., Perezbiol, R., Reille, M., Riollet, Scott, L., Strake, H., Taylor, D., Van Campo, E., Vincens, A., Laarif, F., Jonson, H. and Hamilton, A.C., 2000, Pollen-based biome reconstruction for southern Europe and Africa 18,000 yr BP. *Journal of Biogeography*, **27**(3), pp. 621–634, 10.1046/j.1365-2699.2000.00430.x.
- Gaillard, M.-J., Morrison, K.D., Madella, M. and Whitehouse, N., 2018, Past land-use and land-cover change: the challenge of quantification at subcontinental to global scale. *PAGES Magazine*, **26** (1), p. 3, 10.22498/pages.26.1.3.
- Gajewski, K., Lézine, A.-M., Vincens, A., Delestan, A. and Sawada, M., 2002, Modern climate–vegetation–pollen relations in Africa and adjacent areas. *Quaternary Science Reviews*, **21** (14–15), pp. 1611–1631, 10.1016/S0277-3791(01)00152-4.
- Hedberg, O., 1952, A pollen-analytical reconnaissance in tropical East Africa. *Oikos* **5**(2), pp. 137–166, 10.2307/3565157.
- Hély, C., Lézine, A.-M. and APD contributors, 2014, Holocene changes in African vegetation: tradeoff between climate and water availability. *Climate of the Past* **10**, pp. 681–686, 10.5194/cp-10-681-2014.
- Hessler, I., Dupont, L., Bonnefille, R., Behling, H., González, C., Helmens, C.F., Hooghiemstra, H., Lebamba, J., Ledru, M.-P., Lézine, A.-M., Maley, J., Marret, F. and Vincens, A., 2010, Millennial-scale changes in vegetation records from tropical Africa and South America during the last glacial. *Quaternary Science Reviews*, **29** (21–22), pp. 2882–2899, 10.1016/j.quascirev.2009.11.029.
- Ivory, S. J., Early, R., Sax, D. F., and Russell, J., 2016, Niche expansion and temperature sensitivity of tropical African montane forests. *Global Ecology and Biogeography*, **25**(6), pp. 693–703, 10.1111/geb.12446.
- Ivory, S. J., Russell, J., Early, R. and Sax, D. F., 2019, Broader niches revealed by fossil data do not reduce estimates of range loss and fragmentation of African montane trees. *Global Ecology and Biogeography*, **28**(7), pp. 992–1003, 10.1111/geb.12909.
- Ivory, S.J., McGlue, M.M., Ellis, G.S., Boehlke, A., Lézine, A.-M., Vincens, A. and Cohen, A.S., 2017, East African weathering dynamics controlled by vegetation-climate feedbacks. *Geology*, **45**(9), pp. 823–826, 10.1130/G38938.1.
- Izumi, K. and Lézine, A.-M., 2016, Pollen-based biome reconstructions over the past 18,000 years and atmospheric CO₂ impacts on vegetation in equatorial mountains of Africa. *Quaternary Science Reviews*, **152**, pp. 93–103, 10.1016/j.quascirev.2016.09.023.
- Jolly, D., Prentice, C., Bonnefille, R., Ballouche, A., Bengo, M., Brenac, P., Buchet, G., Burney, D., Cazet, J.-P., Cheddadi, R., Ederh, T., Elenga, H., Elmoutaki, S., Guiot, J., Laarif, F., Lamb, H., Lézine, A.-M., Maley, J., Mbenza, M., Peyron, O., Reille, M., Reynaud-Farrera, I., Riollet, G., Ritchie, J.C., Roche, E., Scott, L., Ssemmanda, I., Straka, H., Umer, M.,

- Van Campo, E., Vilimumbalo, S., Vincens, A. and Waller, M., 1998, Biome reconstruction from pollen and plant macrofossil data for Africa and the Arabian Peninsula at 0 and 6000 years. *Journal of Biogeography*, **25**, pp. 1007–1027, 10.1046/j.1365-2699.1998.00238.x.
- Joussaume, S. and Taylor, K.E., 1995, *Status of the Paleoclimate Modeling Intercomparison Project (PMIP)*, WCRP-92, WMO/TD 732, (Geneva: World Climate Research Programme), pp. 425–430.
- Kröpelin, S., Verschuren, D., Lézine, A.-M., Eggermont, H., Cocquyt, C., Francus, P., Cazet, J.P., Fagot, M., Rumes, B., Russell, J.M. and Darius, F., 2008, Climate-driven ecosystem succession in the Sahara: the past 6000 years. *Science*, **320**(5877), pp. 765–768, 10.1126/science.1154913.
- Lebamba, J., Vincens, A. and Maley, J., 2012, Pollen, vegetation change and climate at Lake Barombi Mbo (Cameroon) during the last ca. 33,000 cal yr BP: a numerical approach. *Climate of the Past*, **8**(1), pp. 59–78, 10.5194/cp-8-59-2012.
- Lebrun, J.-P. and Stork, A.L., 1991-1997. *Énumération des plantes à fleurs d'Afrique tropicale*. Vol. 1–4, (Geneva : Conservatoire et Jardin botaniques de la Ville de Genève).
- Lézine, A.-M., Izumi, K., Kageyama, M. and Achoundong, G., 2019, 90,000-year record of Afromontane forest responses to climate change. *Science*, **363**, pp. 177–181, 10.1126/science.aav6821.
- Lézine, A.-M., Watrin, J., Vincens, A., Hély, C. and APD contributors, 2009, Are modern pollen data representative of west African vegetation? *Review of Palaeobotany and Palynology*, **156**(3–4), pp. 265–276, 10.1016/j.revpalbo.2009.02.001.
- Marchant, R., Richer, S., Boles, O., Capitani, C., Courtney-Mustaphi, C.J., Lane, P., Prendergast, M.E., Stump, D., De Cort, G., Kaplan, J.O. and Phelps, L., 2018, Drivers and trajectories of land cover change in East Africa: Human and environmental interactions from 6000 years ago to present. *Earth-Science Reviews*, **178**, pp. 322–378, 10.1016/j.earscirev.2017.12.010.
- Miller, C.S. and Gosling, W.D., 2014, Quaternary forest associations in lowland tropical West Africa. *Quaternary Science Reviews*, **84**, pp. 7–25, 10.1016/j.quascirev.2013.10.027.
- Nash, D.J., De Cort, G., Chase, B.M., Verschuren, D., Nicholson, S.E., Shanahan, T.M., Asrat, A., Lézine, A.M. and Grab, S.W., 2016, African hydroclimatic variability during the last 2000 years. *Quaternary Science Reviews*, **154**, pp. 1–22, 10.1016/j.quascirev.2016.10.012.
- Nolan, C., Overpeck, J.T., Allen, J.R., Anderson, P.M., Betancourt, J.L., Binney, H.A., Brewer, S., Bush, M.B., Chase, B.M., Cheddadi, R., Djamali, M., Dodson, J.E., Edwards, M.E., Gosling, W.D., Haberle, S., Hotchkiss, S.C., Huntley, B., Ivory, S.J., Kershaw, A.P., Soo-Hyun, K., Latorre, C., Leydet, M., Lézine, A.-M., Liu, K.-B., Liu, Y., Lozhkin, A.V., McGlone, M.S., Marchant, R., Momohara, A., Moreno, P., Müller, S., Otto-Bliesner, B., Shen, C., Stevenson, J., Takahara, H., Tarasov, P., Tipton, J., Vincens, A., Weng, C. Xu, Q., Zheng, Z. and Jackson, S.T., 2018, Past and future global transformation of terrestrial ecosystems under climate change. *Science*, **361**(6405), pp. 920–923, 10.1126/science.aan5360.
- Novello, A., Lebatard, A.E., Moussa, A., Barboni, D., Sylvestre, F., Bourlès, D.L., Paillès, C., Buchet, G., Decarreau, A., Düringer, P. and Ghienne, J.F., 2015, Diatom, phytolith, and pollen records from a 10Be/9Be dated lacustrine succession in the Chad basin: Insight on the Miocene–Pliocene paleoenvironmental changes in Central Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **430**, pp. 85–103, 10.1016/j.palaeo.2015.04.013.
- Peyron, O., Jolly, D., Braconnot, P., Bonnefille, R., Guiot, J., Wirmann, D. and Chalié, F., 2006, Quantitative reconstructions of annual rainfall in Africa 6000 years ago: Model-data comparison. *Journal of Geophysical Research: Atmospheres*, **111**, 10.1029/2006JD007396, article: D24110.
- Prentice, I. C., D. Jolly and BIOME 6000 Participants, 2000, Mid-Holocene and glacial-maximum vegetation geography of the northern continents and Africa. *Journal of Biogeography*, **27**, pp. 507–519, 10.1046/j.1365-2699.2000.00425.x.

- Prentice, I.C and Webb T., III, 1998, BIOME 6000: reconstructing global mid-Holocene vegetation patterns from palaeoecological records. *Journal of Biogeography*, **25**(6), pp. 997–1005, 10.1046/j.1365-2699.1998.00235.x.
- Ritchie, J.C., 1995, Current trends in studies of long-term plant community dynamics. *New Phytologist*, **130**(4), pp. 469–494, 10.1111/j.1469-8137.1995.tb04325.x.
- Scott, L., 2016, Fluctuations of vegetation and climate over the last 75,000 years in the Savanna Biome, South Africa: Tswaing Crater and Wonderkrater pollen sequences reviewed. *Quaternary Science Reviews*, **145**, pp. 117–133, 10.1016/j.quascirev.2016.05.035.
- Scott, L., Neumann, F.H., Brook, G.A., Bousman, C.B., Norström, E. and Metwally, A.A., 2012, Terrestrial fossil pollen evidence of climate change during the last 26 thousand years in southern Africa. *Quaternary Science Reviews*, **32**, pp. 100–118, 10.1016/j.quascirev.2011.11.010.
- Sugita, S., 2007a, Theory of quantitative reconstruction of vegetation I: Pollen from large sites REVEALS regional vegetation composition. *The Holocene*, **17**(2), pp. 229–241, 10.1177/0959683607075837.
- Sugita, S., 2007b, Theory of quantitative reconstruction of vegetation II: All you need is LOVE. *The Holocene*, **17**(2), pp. 243–257, 10.1177/0959683607075838.
- van Zinderen Bakker. E.M. and Coetzee, J.A., 1952, Pollen spectrum of the southern middleveld of the Orange Free State. *South African Journal of Science*, **48**, pp. 275–281.
- Vincens, A., Bremond, L., Brewer, S., Buchet, G. and Dussouillez, P., 2006, Modern pollen-based biome reconstructions in East Africa expanded to southern Tanzania. *Review of Palaeobotany and Palynology*, **140**(3-4), pp. 187–212, 10.1016/j.revpalbo.2006.04.003.
- Vincens, A., Lézine, A.-M., Buchet, G., Lewden, D. and Le Thomas, A., 2007, African pollen database inventory of tree and shrub pollen types. *Review of Palaeobotany and Palynology*, **145**(1-2), pp. 135–141, 10.1016/j.revpalbo.2006.09.004.
- Watrin, J., Lézine, A.-M. and Hély, C., 2009, Plant migration and plant communities at the time of the ‘green Sahara’. *Comptes Rendus Geoscience*, **341**(8–9), pp.656–670, 10.1016/j.crte.2009.06.007.
- Wu, H., Guiot, J., Brewer, S., Guo, Z., Peng, C., 2007, Dominant factors controlling glacial and interglacial variations in the treeline elevation in tropical Africa. *Proceedings of the National Academy of Sciences*, **104**(23), pp. 9720–9724, 10.1073/pnas.0610109104.