A dendrochronological and radiocarbon analysis of two African *Acacia* species

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Abstract

Little research has been done on the dendrochronological potential of southern African trees, particularly the aging of wild-growing African *Acacia* species. Such data would provide ecologists and resource managers with valuable insight into the functioning of the savanna ecosystems where they occur. Sawn discs of wild-growing adult *Acacia nilotica* and *Acacia nigrescens* trees of unknown age from the Hluhluwe-Umfolozi Game Reserve were analysed using dendrochronological methods to determine age, growth rate, age: diameter relationship, and relationship with climate. Six sample rings from four discs of the two species were sent for radiocarbon dating in order to measure the accuracy of ring counts. Ring counts for *A. nilotica* ranged from 29 to 36 years and for *A. nigrescens* 46 to 83 years. Radiocarbon age showed moderate inaccuracy of ring counts for both species, although the faster-growing A. nigrescens about 90% accurate. Growth rates determined for both species were far lower than rates determined for the same two species in other studies in Africa, probably due to differences in environmental pressures encountered by wild-growing specimens. Relationships between age and diameter for individual species was not significantly correlated, but the combined regression was strongly correlated. A larger sample size may have provided better correlations for individual species, but it is likely that diameter is a suitable indicator of age only between species, and not within species. Positive correlations between determined age and climate were found for only one of the *A. nigrescens* samples and none of the *Acacia nilotica* samples. The difficulty of detecting and isolating annual growth structures in these species caused inaccuracy of dating which would account for the poor relationship with climate data. Alternatively inaccuracy could be explained by an underground water source that enables these trees to grow independently of rainfall. Radiocarbon dating results suggest that ring counts provide an improvement in accuracy over stem diameter measurement, but poor potential for dendroclimatology.

Introduction

Very little is known about the age attained by African *Acacia* species, and little research on this topic conducted in South Africa has been published. Despite the ecological and economic importance of these trees (Ross 1979, Gourlay 1995, Midgley & Bond 2001), only a handful of studies worldwide have attempted to age them.

Longevity is an important aspect of the demography and the ecology of such prominent trees (Midgley & Bond 2001), and therefore needs to be understood in order to conserve them effectively. Knowledge of their ecology is important not only for the conservation of the genus, but also of the systems of which they form such a conspicuous part. *Acacia karroo*, for example, is responsible for a great deal of habitat alteration in southern Africa through the process of bush encroachment, which has significant ecological as well as environmental consequences (Skowno *et al.* 1999, Moleele *et al.* 2002). In savannas they form an important part of the tree-grass co-existence that characterises these systems.

Part of the reason for the shortage of information on these species is that African *Acacia*, like the vast majority of tropical trees, present a host of obstacles to even the process of ring counting, the most basic step in dendrochronological analysis (Lilly 1977, Martin & Moss 1997). Ring counting is the most practical and widely used technique for aging trees. It is impeded because anatomical characters that clearly denote annual growth rings in temperate trees, such as ring-porous wood and pronounced cell wall thickness and dimensional changes, are uncommon in tropical species, including *Acacia* species (Gourlay 1995).

One feature of the genus *Acacia*, common to all South African hardwoods with any potential for dendrochronology (Lilly 1977) are thin rings of marginal, or boundary parenchyma, a form of axial parenchyma. These rings are laid down annually at either the beginning or the end of the dry season and are indicative of annual growth (Gourlay & Kanowski 1991). Marginal parenchyma rings are distinguishable from frequent intra-seasonal banded parenchyma by their comparative fineness. They are also more regularly spaced, and have a more even appearance than the irregular, wavy bands (Gourlay 1995). Marginal parenchyma also forms continuous rings around the disc whereas banded parenchyma is generally discontinuous. Marginal parenchyma contains calcium oxalate (CaC_2O_4) crystals, which enhances their visibility (Gourlay & Kanowski 1991). Several other forms of parenchyma exist in *Acacia* species. Besides marginal parenchyma, the two main forms are banded parenchyma: apotracheal bands that are independent of the wood vessels, and paratracheal bands that are associated with the vessels (Gourlay 1995). The prominence of banded parenchyma is perhaps the greatest hindrance to the detection of the finer marginal parenchyma.

Dendrochronological studies so far conducted on African *Acacia* have used known-age trees (Wyant & Reid 1992, Gourlay 1995, Gourlay *et al.* 1996, Martin & Moss 1997) where a significant degree of accuracy was attained. Most of these studies did not utilise wild-growing trees.

Another method for determining growth rate rather than absolute age of trees, involves the injuring of trees. When they are felled years later, the injury is detected on the sawn disc, and the ring count is compared to the number of years that have passed between injury and felling (Wyant & Reid 1992). A third method involves using radiocarbon analysis to cross-date isolated and extracted rings that have been counted. It is an independent proof of the annual nature of tree rings (Worbes & Junk 1989). Using an accelerator mass spectrometer to measure the $^{14}C_3$ content of the wood taken from a single annual ring, the age of the wood can be determined to within a year or two in the case of material that post-dates 1950. It is this method that was employed in this study.

Discs cut from wild-growing adult *Acacia nigrescens* and *Acacia nilotica* trees of unknown age were used in the study. As far as is known these trees established naturally, and grew in an environment where they were subject to herbivory, frequent fires, and other pressures encountered by wild-growing specimens. It was suspected that the environmental pressures encountered by these trees would result in their longevity and growth rate differing from cultivated, irrigated, or tended specimens.

It is important to note that the "age" discussed in this study is not total age, but the age from when the tree reached the height at which the disc was cut. Fire in particular may keep small trees low through continual damage for years before circumstances – for example a longer than usual rest between fires combined with high rainfall – allow them to grow tall enough to escape the so-called "fire trap" (Bond & van Wilgen 1996). Tribal elders in northern Kenya estimated *Acacia tortilis* escape age to be in the region of ten years (Martin & Moss 1997).

The main objective of this study was to establish the age obtained since time of release from the fire trap of *A. nilotica* and *A. nigrescens* by counting annual rings of marginal parenchyma and verifying the accuracy of these counts through radiocarbon dating. This verification would in turn serve as an indicator to determine the suitability of dendrochronology compared to stem diameter measurement as a tool for aging wild-growing African *Acacia* and to determine their growth rate relative to non-wild-growing specimens previously studied. Lastly the study aimed to determine whether ring counts of wild-growing specimens were accurate enough for dendroclimatological inferences to be made. Accuracy of the ring counts was measured against radiocarbon ages.

Study area

The study used discs sawn from trees from the Hluhluwe-Umfolozi Game Reserve (28°00'-28°26' S, 31°43'-32°09'E) in Zululand in northern Kwazulu-Natal, South Africa. This Reserve covers an area of about 900km^2, with a variation in altitude from 60m to 750m above sea level (Whately & Porter 1983). Most of Hluhluwe, the northern section, is at higher altitude than Umfolozi in the south. The area has a summer rainfall regime, with peaks between October and March. Rainfall increases with altitude, with an average of about 990mm per year on Hluhluwe, and on Umfolozi around 720mm per year (Whately & Porter 1983). Hluhluwe and Umfolozi are regarded as mesic and arid savanna respectively within the context of Zululand savanna. The vegetation on the Reserve is predominantly Lowveld, a sub-category of Bushveld, while most of the remainder is Zululand Thornveld (Acocks 1988).

Acacia species, distributed in a matrix of grass, visibly dominate much of the landscape. Some individual *Acacia* species form stands dominated by adults of fairly uniform size. Besides grass, the often-sparse understorey in these stands is generally composed of juvenile or resprouted *Acacia* of the same or different species to the adults composing the stand. Other resprouting trees such *as Dichrostachys cinerea* and *Euclea* species are also sometimes present. *A. nilotica* and *A. nigrescens* are two species that form stands on the Reserve. *A. nilotica* is found throughout the area but is more abundant on Hluhluwe, where stands of this species are also far more common. *A. nigrescens* is found only on the Umfolozi portion of the Reserve. All *A. nilotica* discs examined came from the same stand on Hluhluwe, while the *A. nigrescens* discs were collected from three different localities (Fig 1) on Umfolozi.

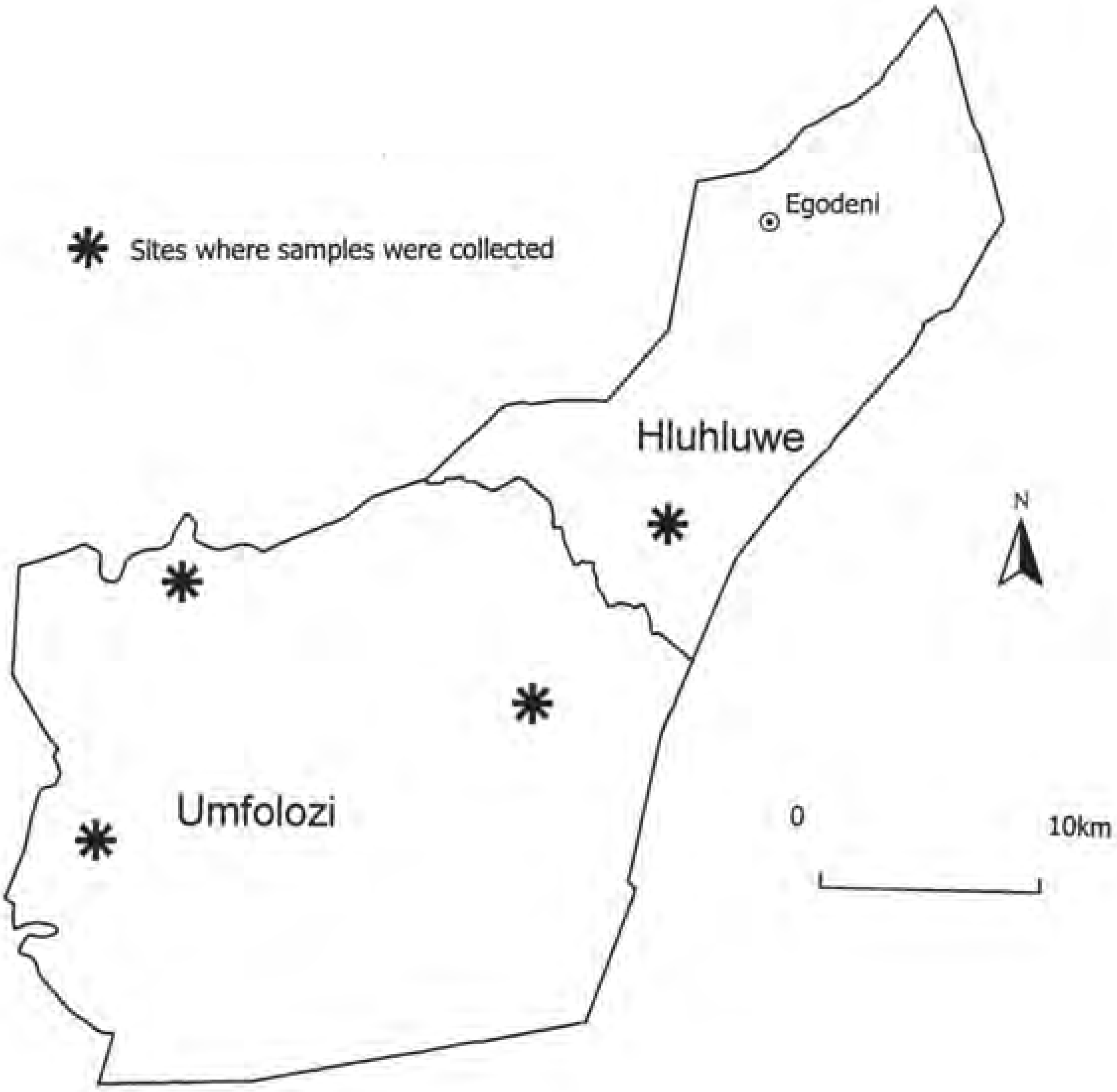

Fig 1 Map showing distribution of sample sites and location of rainfall station at Egodeni

Materials and methods

A chainsaw was used to cut discs from six living adult *A. nilotica* trees and six living adult *A. nigrescens* trees at a height of between 0.5m and 1.5m from their base. All of these trees had been pushed over by elephants. The fact that their branches had not been burned suggests they had been toppled since the last fire in their respective locations – generally no more than two years previously. The trees represented the average size (stem diameter and height) of adults of their species in stands, and on the Reserve as a whole. *A. nilotica* is the smaller of the two species, typically reaching a height of about 4 m and a stem diameter of between 10 and 20mm in the study area. Most adult *A. nigrescens* in the area are about 8m in height, with a stem diameter of usually between 20 and 30mm.

In the laboratory the discs were prepared by sanding with a belt sander using progressively finer paper, starting with 60-grit sandpaper and ending with 400 grit. Nine grades of paper were used. In some cases a palm sander with 400 grit sandpaper was also used for a final polish. Following preparation each disc was given a unique number. *A. nilotica* discs were labeled HAN (**H**luhluwe ***A**cacia* ***n**ilotica*) 01 to 06 and *A. nigrescens* were labeled UNG (**U**mfolozi ***A**cacia* ***n**igrescens*) 01 to 06.

Two or four radii were marked on the polished surfaces, roughly at right angles to each other, from the pith to the bark. Using a Leica MZ75 stereo microscope with magnification ranging from 6.3 to 50x, rings of marginal parenchyma were located and marked. After the rings were counted, ring widths were measured on a computer-linked Velmex stage. After manually matching the ring width variations among radii so as to identify the exact year in which each ring was formed (cross-dating), the computer programme COFECHA (Holmes 1983) was used to identify problems in measurement and to verify cross-dating. This programme allows for computer-assisted quality control of the dating and measurements of the original indices. The software develops a master dating series and then compares each individual tree ring measurement index to that series. This was done in order to compensate for the many factors such as competition and disease, which can influence tree growth other than climate (Gourlay 1995). This index data was used for chronologies comparing ring width with rainfall, while original measurements in millimeters were used when comparisons were made between ring width (and diameter) and ring count to determine suitability for age determination.

Tree age and ring count accuracy

All *A. nilotica* samples had some damage from woodborer beetle larvae, and two of the *A. nigrescens* had pith rot. The *A. nigrescens* discs with pith rot presented an obstacle to total age determination because of their missing centres, meaning that radial transects were incomplete. This was overcome by projecting the age determined for the rest of each of the incomplete transects of the respective discs, based on the proportions of the transects, constituted by these measurements in the other discs.

To verify ring counts, samples were sent off to the Quaternary Dating Unit (QUADRU) of the CSIR in Pretoria for radiocarbon dating. The two least damaged discs of each species were selected. A minimum of 20 grams is required from a single ring for radiocarbon dating, and despite the substantial density of the wood, in the case of the smaller *A. nilotica* discs only one ring per disc was thick and long enough to provide enough material. One ring from each of two *A. nilotica* samples was extracted, and two rings from each of two *A. nigrescens* samples. These rings were carefully chipped out using a chisel. Rings estimated to age less than about 50 years were used, partly because outer (more recent) rings are longer and therefore more likely to contain 20 grams of wood. Another reason for these more recent rings being selected was that the accuracy of radiocarbon dating for samples post-dating 1950 is far greater than for before that period. The reason for this is that the radiocarbon content of wood reflects the radiocarbon content of the atmosphere, which rose dramatically with nuclear weapons testing around 1950, and then dropped sharply with mitigation of this practice in about 1965 (Nydal & Lövseth 1983). By measuring the radiocarbon content of a wood sample and comparing the corresponding value from the so-called "bomb spike" graph of atmospheric radiocarbon content, a set of dates may be obtained (Nydal & Lövseth 1983, Hua *et al.* 2000, Worbes *et al.* 2003). It is the sharpness of the curve that accounts for the accuracy of dating of material from after 1950. Accuracy before that date is to only to within about 20 years (CSIR Pretoria). With a genus like *Acacia*, some species of which are believed to date only decades (Gourlay 1995), high-precision dating is essential.

Ring count: stem diameter relationships

Diameter of the discs was measured from the pith outwards, excluding the bark. Diameter was compared to ring count in order to establish whether a correlation existed between stem thickness and age. By then comparing stem diameter and ring count to radiocarbon ages, it was also determined which was a better indicator of actual tree age.

Growth rate

By comparing ring widths to the age of each tree as determined through ring counts and radiocarbon dating, annual increment was determined.

Ring width: rainfall relationships

The only rainfall data for the Reserve spanning most of the tree chronologies were from Egodeni on Hluhluwe (see Fig 1). These data spanned the period from 1934 to 2000. Average annual rainfall was used for comparison with the discs from the nearby *A. nilotica* site, as well as the various *A. nigrescens* sites. Despite the lower rainfall expected at the latter sites, and their distance from Egodeni (about 30km on average), no other data of comparable consistency or extent were available, and it was assumed that the rainfall at these sites was proportionately equivalent to the rainfall measured at Egodeni.

Rainfall data were compared to ring widths of corresponding years and to rainfall one year before, in order to determine whether any correlations existed between ring counts and rainfall.

Results

Tree age and ring count accuracy

Age determination through ring counts indicated a range of ages from 29 to 36 years for *A. nilotica* from the same stand, and a range of 46 to 83 years for *A. nigrescens* from three different localities. Ease of recognition of marginal parenchyma rings varied from sample to sample, but overall those in the *A. nilotica* discs were more readily detected and distinguished. As is often the case with annual ring structures in trees, it was at the pith and towards the bark that ring identification became most difficult (Gourlay 1995, Martin & Moss 1997). Other parenchyma bands often obscured the fine lines of marginal parenchyma, especially in the outermost rings of the *A. nilotica* samples. In the *A. nigrescens* samples this was less of an obstacle. *A. nigrescens* was, however, more problematic overall because of the difficulty involved in distinguishing between a double marginal parenchyma line representing one year (sometimes the result of occasional rainfall bimodality (Gourlay 1995)), and two closely-spaced lines from separate years. Such closely spaced lines could result from consecutive years of stressful conditions due to drought or herbivory (Zahner 1968, Gourlay 1995).

Radiocarbon results revealed that both *A. nilotica* samples sent for radiocarbon dating were older than ring counts suggested, while one *A. nigrescens* was older and the other slightly younger than predicted (Fig 2; see Appendix 1 for tabulated values).

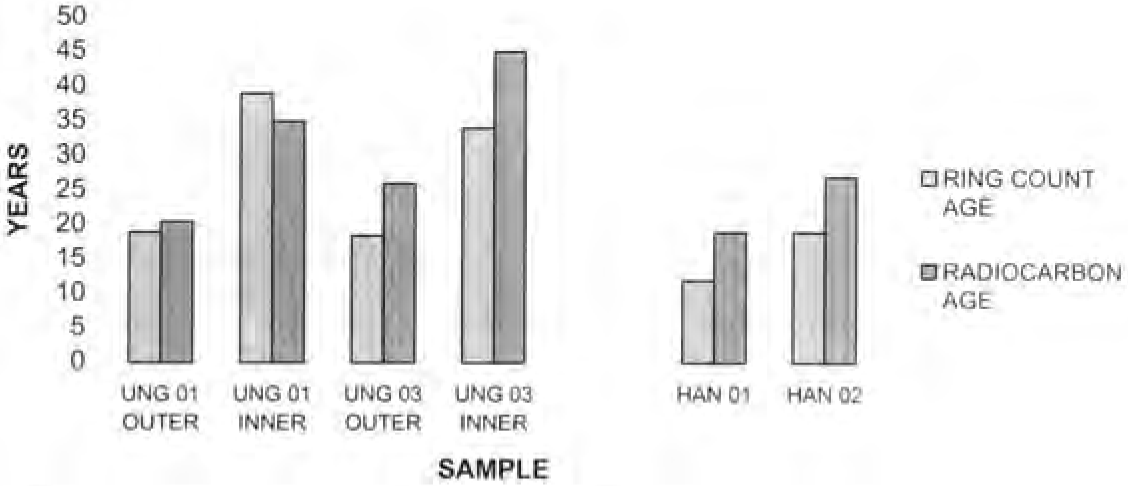

Fig 2 Ring counts and radiocarbon ages for sample rings of *A. nilotica* and *A. nigrescens*.

The ring count for the sample ring from sample HAN 01 estimated it to be 12 years old, while the radiocarbon age of the ring was 19 years. The ring count for the sample ring from sample HAN 02 was 19 years compared to the radiocarbon age of 27 years. Assuming radiocarbon ages to be completely accurate, ring count ages for these sample rings represent an accuracy of 63% and 70% for HAN 01 and HAN 02 respectively. For the outer ring of sample UNG 01 (called UNG 01 OUTER) 19 rings were counted, and an age of 20.5 years was determined by radiocarbon analysis. The ring count of the inner ring of this sample (UNG 01 INNER) was 39, while radiocarbon analysis determined it to be 35 years old. For these two rings from the same disc accuracy was 93% and 90% respectively. The ring count for the outer ring of sample UNG 03 (UNG 03 OUTER) was 18.5 years while the radiocarbon age 26 years, and the ring count age of the inner ring of this sample (UNG 03 INNER) was 34 years compared with the radiocarbon age of 45 years. The ring count accuracy for this sample was 71% and 76% for outer and inner rings respectively. Based on the accuracy obtained through ring counts, a total age was projected for each of the four discs. Figures 3 and 4 illustrate the relative values for *A. nilotica* and *A. nigrescens* respectively (see Appendix 1 for tabulated values), as well as the ring count ages of the other samples not sent for radiocarbon analysis.

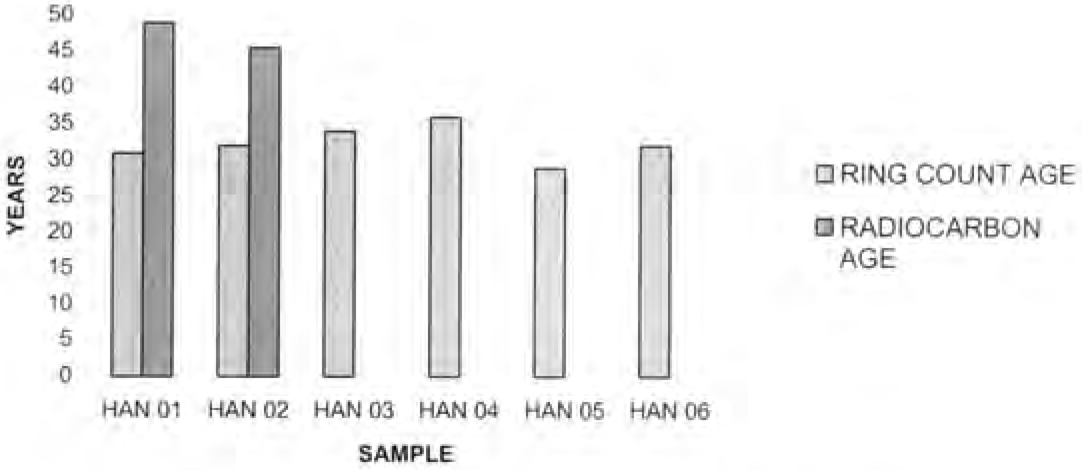

Fig 3 Ring counts and projected radiocarbon ages for *A. nilotica* samples that were radiocarbon dated.

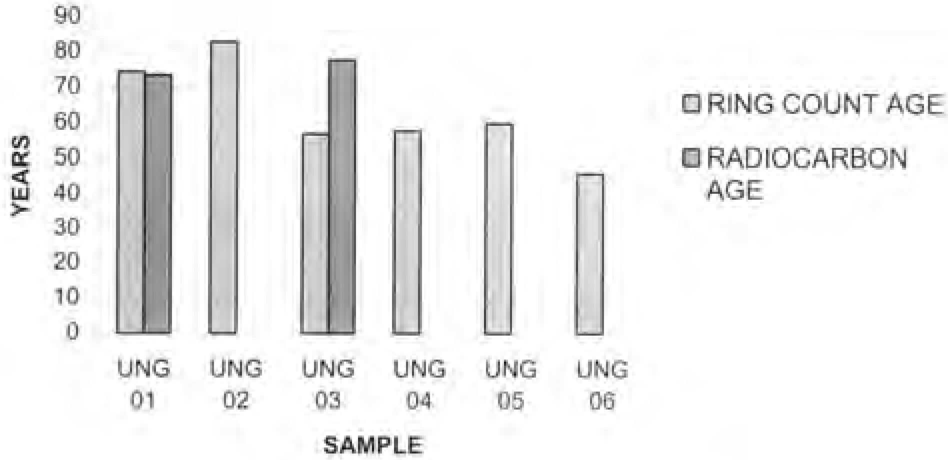

Fig 4 Ring counts and projected radiocarbon ages for *A. nilotica* samples that were radiocarbon dated.

Ring count age for HAN 01 was 31 years and its radiocarbon age 49 years. Ring count for HAN 02 was 32 and radiocarbon age was 45.5 years. For the *A. nigrescens* samples the accuracy of both rings was averaged and projected. For UNG 01 ring count was 74.5 and radiocarbon age 73.5. For UNG 03 ring count age was 57 and radiocarbon age 78.

Ring count: stem diameter relationships

Mean diameter in *A. nilotica* varied from 109mm (29 rings counted) to 132mm (34 rings counted) and for *A. nigrescens* diameters varied from 220mm (46 rings counted) to 359mm (74.5 rings counted; radiocarbon age 73.5 years). Mean diameter was compared to ring count. The relationship between ring count and average stem diameter for the six *A. nilotica* specimens (Fig 5) was weak and not significant ($p > 0.05$, $r^2 = 0.32$). For the *A. nigrescens* discs (Fig 6) this relationship was slightly weaker and also not significant ($p > 0.05$, $r^2 = 0.29$). When plotted together however (Fig 7), a significant relationship was found for the 12 trees overall ($p < 0.001$, $r^2 = 0.80$).

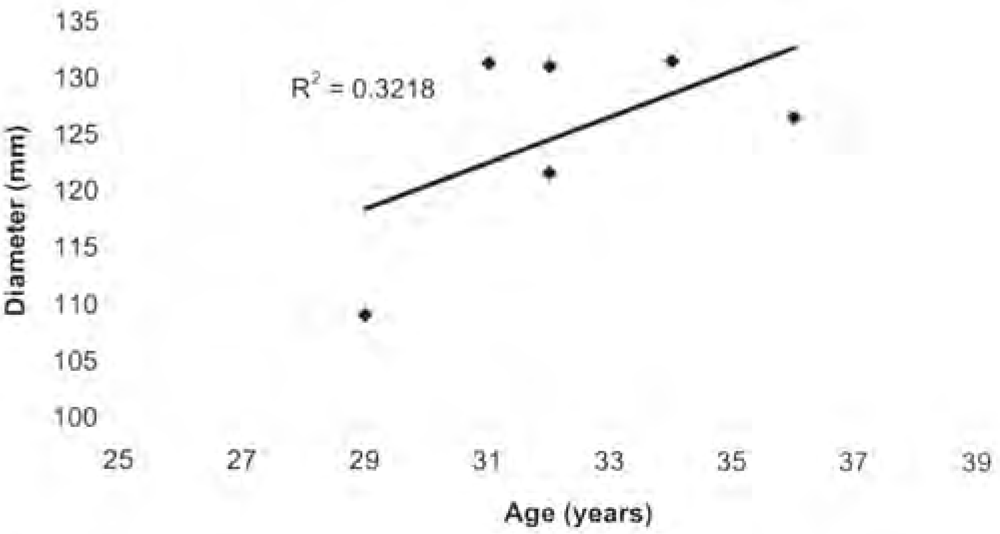

Fig 5 Relationship between ring count and stem diameter in *A. nilotica* samples

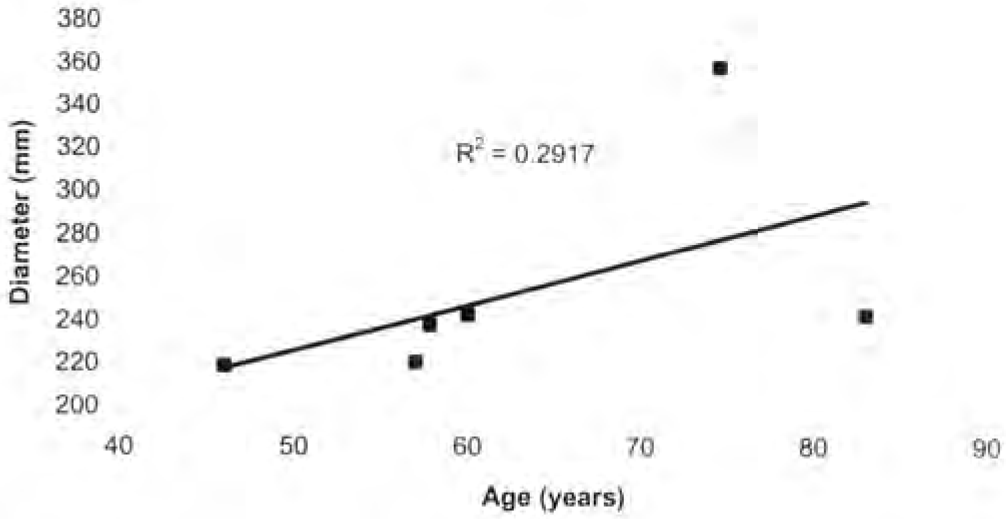

Fig 6 Relationship between ring count and stem diameter in *A. nigrescens* samples

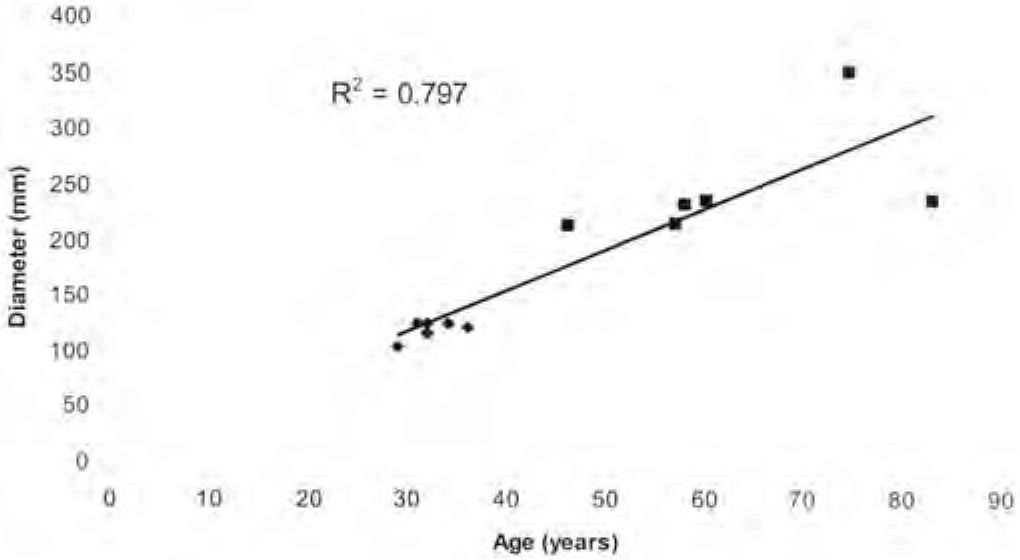

Fig 7 Relationship between ring count and stem diameter in both species combined

A comparison between the two *A. nigrescens* samples with the highest ring counts illustrates the most extreme example of non-correlation: UNG 01 was 378mm in diameter and estimated at 74.5 years old while

UNG 02, measuring only 243mm in diameter, was estimated to be 83 years of age. The latter was the furthest outlier in the combined regression, and when removed the age: diameter relationship for the remaining 11 samples improved further still ($p < 0.001$, $r^2 = 0.95$). Removing the same outlier from the *A. nigrescens* regression, revealed a significant relationship between ring count and diameter ($p < 0.05$, $r^2 = 0.82$). Removing the furthest outlier in the *A. nilotica* regression however, did produce a significant relationship ($p > 0.05$, $r^2 = 0.53$).

For the four discs that were sent for radiocarbon analysis, comparative regressions were performed in order to establish whether ring counts, or diameter measurements, were more accurate estimates of actual tree age. Probably because of the very small sample size, neither set was significantly correlated. However, the correlation for ring count ($p > 0.05$, $r^2 = 0.803$) was stronger than that for diameter ($p > 0.05$, $r^2 = 0.639$).

Growth rate

Ring counts determined the growth rate of *A. nilotica* samples to range from 1.8 (HAN 04) to 2.1mm (HAN 01 and HAN 06) per year. The older radiocarbon dates of the two specimens radiocarbon dated, however, suggest the lower range of ring width increment for this species to be as little as 1.3mm (both HAN 01 and HAN 02) per year. For *A. nigrescens*, ring counts produced a ring widths ranging from 1.5 (UNG 02) to 2.4mm (UNG 01 and UNG 06). Radiocarbon ages for UNG 03 suggest that the lower limit may be slightly less, at 1.4mm.

Ring width: rainfall relationships

Individual and combined chronologies of all *A. nilotica* discs were plotted against rainfall, but none were found to be significant at the 95% interval. The growth reaction of a tree to water can, however, be delayed (Frits 1962). For this reason the above-mentioned set of chronologies was also plotted against rainfall of the previous year, but again no significant correlations emerged. Upon observation the curves seemed in some cases to visually correlate for the first few years, and therefore the set of chronologies was plotted again for the first five years. Again, however, no significant relationships emerged.

An identical full set of chronologies was plotted for *A. nigrescens*. No significant correlations were found between any chronologies and rainfall of the same year. When compared to rainfall of the previous year, however, the sample with the highest ring count (UNG 02) showed a negative relationship between ring width and rainfall for the first five years ($p < 0.05$, $r^2 = 0.79$). Such a negative relationship, nevertheless, is unlikely to exist, and this result is therefore likely to be co-incidental. Another sample (UNG 06), exhibited a weak, but significant positive relationship ($p < 0.05$, $r^2 = 0.13$) for its entire chronology (Fig 8). UNG 06 was also the disc (of either species) whose transects correlated best, and therefore may be the disc with the most accurately counted rings.

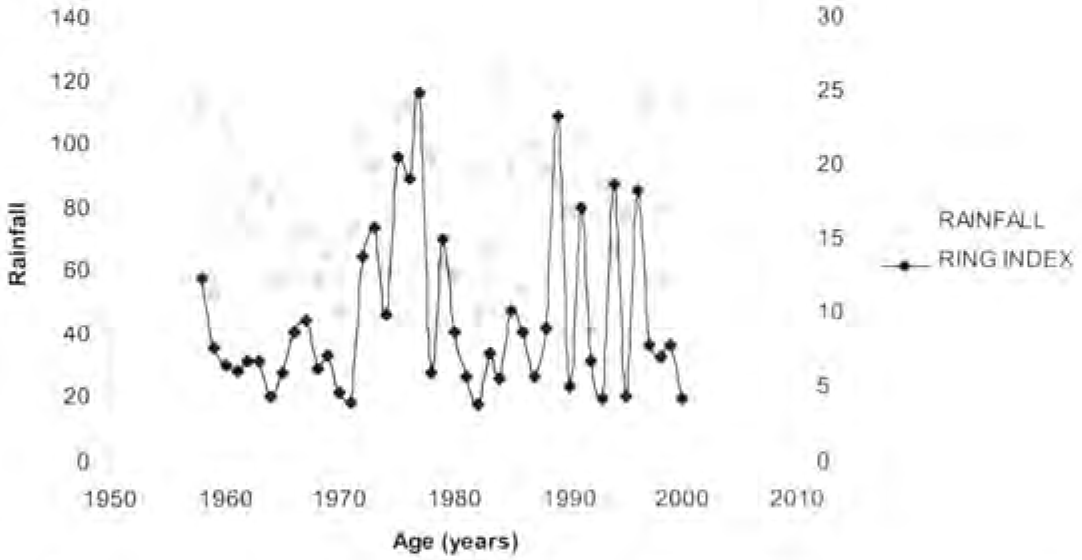

Fig 8 Relationship between ring width and rainfall of the previous year for *A. nigrescens* sample UNG 06

Discussion and conclusions

The aim of radiocarbon cross-referencing for this study was not to directly age the trees (which would have required a single, very large ring from the absolute centre of a stem younger than 50 years of age). Instead the technique was employed to age rings of dendrochronologically estimated age, in order to cross-check the accuracy of the dendrochronological analysis. The stronger the correlation between radiocarbon dating and dendrochronological dating of the samples, the more viable the overall ring counts of the samples, and the more promising dendrochronological analysis of African *Acacia* in general. While other studies have compared ring counts known tree ages, this study used trees of initially unknown age that were calibrated through the reliably accurate method of radiocarbon dating.

It was noted by Gourlay (1995) that *Acacia karroo* specimens were found to succumb to physical or structural damage at an age of 30 to 40 years. It seems that longevity can vary between *Acacia* species, but this study supports the observation of Gourlay's *A. karroo* example and his impression that, generally speaking, *Acacia* are relatively short-lived trees. Structural damage such as woodborer tunnels and pith rot may be limitations to the lifespan of these trees, aside from the rather more evident effect of elephants. The largest, and second oldest of the *A. nigrescens* discs (UNG 01) had the most extensive pith rot, and the widest growth rings (and therefore the fastest growth). This tree may have reached a reliable source of groundwater, permitting rainfall-independent growth. At an advanced age however, this speed of growth may have been to the detriment of the tree, allowing pith rot to occur.

Based on the four *A. nigrescens* sample rings sent for radiocarbon analysis, it appears as though ring count accuracy improves as growing conditions of these trees improve. Rings of marginal parenchyma are more easily distinguished if they are further separated, as with a tree that has a higher growth rate. Due to the narrowness of the rings of the sample with the highest ring count (UNG 02) it is believed that this sample may have been in the region of 100 years old. This disc was also not noticeably damaged and, had it not been toppled by an elephant, would probably have continued growing for some time. However, few *A. nigrescens* observed in the study area exceeded the girth of this sample, and the ring counts of the other samples (two of which already had pith rot and one of which was thicker than UNG 02) suggest that UNG 02 was a particularly long-lived specimen. It is thus estimated that the average life span of the species on the Reserve is between 60 and 80 years of age.

Radiocarbon ages for *A. nilotica* sample rings were considerably older than expected. However, the projected ages of these two samples were probably over-estimates of actual age. The reason for this is that the error in ring count for this species is likely to have occurred by and large in the outermost rings, where a mass of dense banded parenchyma cells made marginal parenchyma distinction extremely difficult. The fact that both *A. nilotica* rings dated, were estimated younger by almost the same number of years supports this assumption. It is therefore probably more accurate to add the missing years to the ring count age rather than to project the accuracy of ring counts. Based on these considerations it is estimated that on the Reserve, these trees usually live for between 30 and 50 years.

It has been suggested that stands of *Acacia*, although of fairly uniform size, are of varying age (Walker *et al.* 1986). However the six *A. nilotica* sampled from one stand appear to be of fairly even age despite considerably variable diameters. Aside from the slightly varying heights at which the discs were cut, it is quite conceivable that these and the other adults in this population are all from the same cohort. Cohort stands imply that either recruitment, or release from the fire trap, occurred simultaneously for all individuals in the stand.

The fact that the combined species' age: diameter relationship was so strong and individual species so weak, suggests either that the individual species' sample sizes were simply too small to indicate a trend, or that this relationship exists only across species of the genus, and not individuals of either species. Wyant and Reid (1992) found a strong correlation ($p < 0.01$, $r^2 = 0.90$) between stem diameter and known age in *Acacia tortilis*. They noted, however, that this correlation weakens as the age of trees increases, and therefore may be useful only in predicting the age of young trees. Most of the trees in their study were less than ten years of age. Their sample size of 83 was, however, also considerably larger than the six of each species in this study.

The comparison between ring counts and diameter measurements, and actual age determined by radiocarbon dating showed that ring counts are a better indicator of tree age. This concurs with Wyant and Reid (1992) in their dendrochronological study of *A. tortilis*, which concluded that despite their inaccuracy, dendrochronology techniques provide an improvement over size measurements for determining tree ages.

Far slower growth rates were measured for trees in this study than for others of the same two species in other studies (Gourlay 1995). Gourlay's *A. nilotica* from Kenya (n=3) had an average radial increment of 7.7mm per year, and those from Somalia (n=2) 5.4mm per year. Rings from the single *A.* nigrescens in that study, from Zimbabwe, had increased by 3.85mm per year. *A. nilotica* in this study had a radial increment of 1.94mm or less per year, and the *A. nigrescens* 2.05mm or less. This may be partly a result of the climatic conditions that influence the respective sites. However, as Gourlay (1995) suggested, the fact that the faster growing trees from Kenya, Somalia and Zimbabwe, had grown outside of game reserves, where they were less likely to be damaged by herbivory and fire, indicates that such pressures may have a severely limiting effect on the growth rate of *Acacia*. Moreover, some of Gourlay's trees established in livestock kraals, where there was likely to be an abundance of nutrients. The presence of livestock is not necessarily detrimental to the growth of African Acacia species (Oba 1998). The *A. nigrescens*, from Harare Botanical Gardens in Zimbabwe may also have tapped into the irrigation lines of the Gardens (Gourlay 1995).

Pith rot in the largest *A.* nigrescens sample suggests that a faster growth rate may have a negative effect on *Acacia* longevity. Trees free of the environmental pressures discussed above, may therefore ironically be shorter-lived than those subject to these pressures.

Although the relationship between a plant and its environment is complex, there is a consensus that, in relatively arid regions, it is rainfall that is most important in determining growth (Fahn *et al.* 1963). Specific site conditions may determine variation in growth within species (Martin & Moss 1997, Midgley & Bond 2001), and the influence of the form of rooting profile and the interaction between climate and geology of sites may account for much of this variation (Gourlay 1995).

Poor, negative, or non-existent correlations between ring width variation and rainfall variation in this study may be attributed to various factors. As confirmed by radiocarbon dating of the samples, dendrochronological analysis was not completely accurate. There are good reasons why dendrochronologists seldom operate in the tropics, and it was not expected, based on previous studies (Lilly 1977, Jacoby 1989), that these analyses would be completely accurate. Slight inaccuracies in ring counts would be enough to throw out an entire chronology. Missing or locally absent rings also occur, frequently due to very dry years or drought (Stokes & Smiley 1968 in Wyant & Reid 1992). The closest correlation between ring width and rainfall among the 12 samples was, as mentioned, for the disc with most closely-matching transects, which may suggest that lack of accuracy was responsible for lack of correlation between ring width and rainfall.

Radiocarbon dating results suggest that ring counts were too inaccurate for dendroclimatological inferences to be made from these specimens. Trees that grew outside game parks like those in Gourlay's (1995) study, and those that grew more easily were more easily aged than wild-growing trees.

It is possible that these trees managed to reach belowground reservoirs of water, making them independent of rainfall fluctuations and drought, as has been recorded for African *Acacia* (Gourlay 1995). This is not surprising in view of the fact that *A. tortilis* roots may reach as deep as 35m (Fagg 1991 in Martin & Moss 1997). It should be noted also, that cambial activity might respond to factors with little or no periodicity, such as browsing and defoliation (Amobi 1974).

More extensive sampling will help to account for missing and false rings. Although African *Acacia* species are not considered to be among the most promising indigenous trees for dendrochronology or dendroclimatology (Lilly 1977), they do display marginal parenchyma rings and they have been shown to be ageable by this study and others, if not with great accuracy. This study has shown the usefulness of radiocarbon dating as a confirmation of ring counts for the species examined as well as the limited accuracy of ring counts. It is hoped that the reasonable success gained through this investigation, and its review of existing literature, will help to spark further studies of a similar nature so that we can determine how wood physiological characteristics vary between species and between areas for this important and extensive group of trees.

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Appendix 1

Table 1 Ring counts and radiocarbon ages for sample rings of *A. nilotica* and *A. nigrescens*

	UNG 01 OUT.	UNG 01 INN.	UNG 03 OUT.	UNG 03 INN.	HAN 01	HAN 02
RING COUNT	19	39	18.5	34	12	19
R.CARBON AGE	20.5	35	26	45	19	27
DIFFERENCE	1.5	4	7.5	11	7	8
ACCURACY	92.68%	89.57%	71.15%	75.56%	63.16%	70.37%

Table 2 Total ring counts and projected radiocarbon ages for *A. nilotica* samples

	HAN 01	HAN 02	HAN 03	HAN 04	HAN 05	HAN 06
RING COUNT	31	32	34	36	29	33
R.CARBON AGE	49.073	45.472				
DIFFERENCE	18.073	13.472				
ACCURACY	63.17%	70.37%				

Table 3 Total ring counts and projected radiocarbon ages for *A. nigrescens* samples

	UNG 01	UNG 02	UNG 03	UNG 04	UNG 05	UNG 06
RING COUNT	74.5	83	57	57.82	60	46
R.CARBON AGE	73.606		77.805			
DIFFERENCE	0.8984		20.805			
ACCURACY	98.99%		73.26%			