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Depicting plant behaviour through human imprints: wild cereals' cultivation in the Holocene Sahara

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Abstract

The human selection of food plants cannot always have been aimed exclusively at isolating the traits typical of domesticated species today. Each phase of global change must have obliged plants and humans to cope with and develop innovative adaptive strategies. Hundreds of thousands of wild cereal seeds from the Holocene “green Sahara” tell a story of cultural trajectories and environmental instability revealing that a complex suite of weediness traits were preferred by both hunter-gatherers and pastoralists. The archaeobotanical record of Takarkori rockshelter in SW Libya covering four millennia of human occupation in the central Sahara gives us a unique insight into long-term plant manipulation and cultivation without domestication. The success of a number of millets was rooted in their invasive-

opportunistic behaviour, rewarded during their coexistence with people in Africa. These wild plants were selected for features that were precious in the past but pernicious for agriculture today. Reconnecting past practices with modern farming strategies can help us to seek out the best resources for the future.

Understanding the long-lasting relationship between plants and humans is of crucial importance to sustainable development, and food is a key determinant of this multifaceted ‘alliance’. Food plants are a central focus for various disciplines which often postulate a marked dichotomy between wild and domesticated species as playing different roles in cultural evolution. From this perspective, plant diversity decreases along an ideal, unilinear, human-controlled axis from resource exploitation to agricultural management^{1 2}. The culmination of this process is the farming of the small number of domesticated species on which people largely rely for food today³. Such crops developed through human selection of desirable traits; by contrast, most wild plants are thought to have grown independently of human aims. Nevertheless, food plants include some minor wild cereals that, interestingly, present what is known as high ‘weediness’: the ability to thrive in human environments due to their preference for disturbed soils⁴. Weedy plants are often prolific and their high rates of phenotypic plasticity and adaptation to agricultural systems, alongside the capacity to act as invaders in natural habitats, often lead to these plants being relegated to the undesirable ‘weed’ category (but for the definition in this paper see below, the Methods)^{5 6}. Here, based on combined archaeological and archaeobotanical data from Saharan Africa, we present the first evidence that non-agricultural societies selected plants for traits that overlap a considerable degree with traits that are characteristic of plants now considered as weeds.

Examination of historical agricultural tradition suggests that several wild plants, defined as ‘weeds’, possess key adaptive characteristics that were successful during past environmental changes. The sharp distinction between ‘unusefulness and usefulness’, typically made on modern-day ‘crop and non-crop’ organisms by agri-food actors, has no analogy in long-term archaeological/environmental records. We suggest that these modern concepts are no longer able to explain complex or intermediate conditions of cultural history such as the *middle ground*⁷ between foraging and farming. Yet understanding plant management in foraging societies, prior to the development of agriculture in their regions, and when links between climate, environment and resources were deeply

embedded in socio-cultural systems, is crucial to our knowledge of what happened when cultivation did not lead to domestication. Here, we present archaeobotanical data which provides direct evidence of long-lasting plant management, with wild cereals persistently adapting to both human desires and environmental changes. The setting is the Holocene “green” Sahara and the period the four millennia from approximately 7500 to 3500 calBC.

Numerous plant species have been gathered and manipulated but this has not always resulted in domestication^{8 9}, a fact often explained as a consequence of the environment being sufficiently starch-protein productive¹⁰ or of plant genetics impeding the isolation of ‘domestic’ traits³. Many partial or abandoned trajectories of trait selections have shown that domestication did not have a single cause or pattern but was a process with different pathways and species¹¹. We can now add that, even when involuntary, selection was not ‘only and always’ directed at isolating the features now considered typical of domesticated species. In the case of cereals, two main phenotypic changes occurring with domestication are usually modifications in seed morphology: the large seed size and the non-shattering rachis^{12 13 14}. The harvesting for these characters is known to have had effects on loss of seed dormancy, reduced vegetative dispersal by rhizomes and changes in reproductive shoot architecture¹⁵. However, these morpho-physiological traits are not detectable in the archaeological record. We present, therefore, the first diachronic archaeobotanical evidence showing that, before clear changes in plants, the primary quality that attracted hunter-gatherers in Africa seeking the benefits of cultivation – implying a shift of labour investment to just a few food plant species¹⁶ – must have been the invasive and opportunistic behaviour of some wild grasses.

The plant remains discovered at various archaeological sites worldwide testify to millennia of systematic gathering, whereas previously the early non-domestication cultivation of wild cereals for food and fodder had only been suggested in the Near East^{17 18}. In this paper, we provide evidence for the systematic gathering, processing and cultivation of wild cereals at a time when the Sahara hosted extensive wet habitats and was covered by a savanna-like vegetation. Highly sophisticated relationships with the environment are apparent in many sites of the mountainous central Saharan regions¹⁹, and especially in the Takarkori rockshelter. This site lies on the first terrace of the Wadi

Takarkori in the southern Tadrart Acacus (Libya), about 100m above the wadi bed (**Figure 1a**). Hence, wild cereal stands were not available in the immediate vicinity of the site but were found closeby in the river plain, along with other plant foods, wild game and fish. The first occupation of Takarkori by Late Acacus hunter-gatherers started at c. 8200 calBC lasting until 6400 calBC. Later, Saharan Pastoral Neolithic groups, exploiting domesticate animals, used the site until c. 3000 calBC^{20 21}. The archaeological deposit comprises an impressive quantity of mainly dried plant remains with excellent preservation, indicative of limited microbial degradation activity. This exceptional feature also characterizes other sites in the area²² and in the Sahara more generally. Human groups at Takarkori had sophisticated subsistence strategies, corralling Barbary sheep²³, exploiting dairy products and cooking vegetables and the site also provides astounding evidence of the human ability to make art and weave fibres^{24 25 26 27}. We now report the unique evidence of plant accumulations from the site, where loose wild cereals were clearly visible on the archaeological surfaces. These accumulations consist of thousands of grass florets/spikelets concentrated on top of the organic sand layers, and distributed around a few different sectors of the site (**Figure 1b,c,d**). The accumulations are evidence of different episodes of plant processing and food plant storage during the period c. 7500-3500 calBC (**Figure 2**). They demonstrate the broad diversity of wild cereals available during the ‘green’ Sahara, though most of these species are now locally extinct in the central Sahara^{28 29}.

Results

Wild cereals accumulated in the site - We identified 30 accumulations of dried seeds clearly visible on the organic sand layers uncovered during fieldwork (**Table 1**). As this record consists largely of wild cereals, the Takarkori seed accumulations are consistent with direct evidence of food at the site, though their use for fodder, and possibly bedding, cannot be discounted.

Based on their morphological features, these plant remains are attributed to *Brachiaria* (including *B. cf. leersioides*-Blue signal grass), *Bromus* cf., *Cenchrus* (including *C. biflorus*-Kram kram, and *C. ciliaris*-African foxtail grass), *Dactyloctenium* (*D. aegyptium*-Crowfoot grass), *Digitaria*,

Echinochloa, *Panicum*, *Pennisetum* (*P. cf. purpureum*-Elephant grass), *Setaria*, *Sorghum*, *Tragus* cf., *Urochloa* (*U. cf. panicoides*-Liverseed), and to undifferentiated Andropogoneae. Combined morphological analysis and ancient DNA extraction made it possible to identify *Panicum laetum* (Wild fonio, or Desert panic), *Echinochloa colona* (Awnless barnyard grass, or Jungle rice) and *Sorghum bicolor* subsp. *verticilliflorum* (Wild Sudan grass) (for identification see Methods, and **Supplementary Information 1**).

The 'spot' vs 'mix' wild cereal accumulations - The ratio of whole to fragmented plant remains allowed us to statistically distinguish between 'spot' (>5; mainly whole spikelets; **Figure 1c**) and 'mix' (<2; mainly spikelet fragments; **Figure 1d**) accumulations (see Methods, and **Table 1**). In total, the 'spots' contained ~150,000 seeds, almost all attributable to the MP1 pastoralists and LA3 hunter-gatherers (71% and 16% of the total seeds in the 'spots', respectively), while the 'mix' accumulations with ~80,000 seeds belonged to the MP2-MP2/LP1 pastoralists (85% of the total seeds in the 'mix') and to the LA2 hunter-gatherers (5%) (**Table 1**).

'Spot' accumulations prevalently consist of whole spikelets (of the millets listed above) without external glumes. This may result from threshing and winnowing, which removed a number of by-products after millet harvesting³⁰. By-products such as unripe grains, de-grained ears, plant stalks and rachis, leaves, spike parts and isolated glumes are fairly insignificant in 'spot' accumulations. Winnowing by shaking, possibly with the help of baskets²⁵, is the most plausible method given the limited space of the rockshelter terrace. The spikelets are unusually uniform in size (*Panicum* and *Echinochloa*: ~2.1±0.1 mm length; *Sorghum*: ~6.4±0.4 mm; see plots in **Supplementary Information 2**), probably as an effect of sieving, a common procedure in the processing of millets³¹. Slight modifications in the seed morphology of millets were observed (see below, and Methods). The cleaned spikelets were stored for consumption. Overall, this evidence is insufficient to tell us whether these seeds were eaten directly in the form of porridge²⁷, stored without further processing for later consumption or kept until the next season for seeding. 'Spots' were found both in a Late Acacus stone hut dated to approximately 7000 calBC (ID 8 and 10, respectively *Sorghum*/Cyperaceae and *Urochloa*/*Brachiaria*) and in a cluster of the Middle

Pastoral period (ID 13-18 and 20-22). Spatial analysis (**Figure 1b**) and study of the radiocarbon dates of these specimens suggest that almost all the MP spots may belong to a single storage facility dated to c. 4500 calBC (4546 <95.4%> 4463 calBC; **Figure 2**). Furthermore, the absence among the spot materials of remains of ants, which are capable of moving seeds, allows us to rule out the idea that these insects were responsible for these seed accumulations. Considering all the data, this archaeobotanical evidence can be interpreted as a residual form of *low-level storage*. This term was used for purpose-built granaries in an early Holocene pre-domestication context of the Jordan Valley, which was interpreted as possible cultivation of wild cereals³². In our case, probably, storage was made possible by the fact that most of these wild cereals exhibit strong seed dormancy, and would thus not have germinated until the following season (late spring and summer in the case of Liverseed and Jungle rice).

The ‘mix’ accumulations consist mainly of plant fragments and glumes, and their function is more ambiguous: depending on the archaeology and chronology, they may be *food-processing waste* or *fodder residues* (as in the case of stable floors). Focusing specifically on the ‘mix’ with food processing residues, as the hulled cereals need dehusking, we found numerous split spikelets with opened external and inner glumes, a number of glumes representing plant processing by-products³⁰³¹, and some charred seeds as refuse from burning activities at the site (**Figure 3**).

In summary, ‘spot’ accumulations suggest the excess from a prevalent gathering activity while the ‘mix’ type seems to originate from the mixed refuse produced by plant processing and animal breeding.

Late Acacus vs Pastoral wild cereal accumulations - In a diachronic perspective (**Figure 4**), the data indicates a major botanical change in the passage from the Late Acacus hunting-gathering phases (12 seed accumulations from c. 7300 to c. 6400 calBC) to the Middle and Late Pastoral phases (11 seed accumulations from c. 4850 to c. 3970 calBC; 7 seed accumulations from c. 3970 to c. 3500 calBC). No accumulation of seeds is recorded from the Early Pastoral phase, probably for taphonomic reasons since these layers suffered heavy erosion in the site¹⁹.

Within the Late Acacus, ~ 800-1600 cereal seeds, with some remains of woody fruit plants such as *Ficus* and *Ziziphus* cf., and one ‘spot’ of ~ 17,000 *Setaria* seeds were found in the earliest five LA2 accumulations, dated c. 7500-7100 calBC. Concentrations generally increase (up to ~10,000 cereal seeds) in the seven LA3 accumulations, dated c. 7100-6400 calBC. At this point, the focus of hunter-gatherers seems to have shifted from the earlier group of cereals (*Pennisetum*, *Sorghum* and other Andropogoneae, and to a lesser extent *Panicum* and *Cenchrus*) towards the tufted annual *Urochloa*-Liverseed, perhaps for a combination of cultural and ecological reasons (see below).

Within the Pastoral Neolithic, relatively higher seed concentrations (~1500-45,000 seeds) are evident in the ‘spots’ of the earliest ten MP1 accumulations, dated c. 4800-4300 calBC. A new cereal, *Echinochloa*, appears and immediately becomes abundant and recurrent in the record. Meanwhile, *Urochloa* continues to be common and sometimes prevalent (65-85% in 4 spots; **Table 1**); *Panicum* and *Setaria* also seem to have been intensively exploited at this time. Although about two thousand years of cultural and environmental changes^{33 34} separate these MP1 samples from those of the LA3 phase, the long-term continuity of the botanical discoveries made by previous hunting-gathering inhabitants is apparent. This can only be explained by the synergy between the adaptive behaviour of some wild cereals and perhaps by cultural transmission from generation to generation. Jungle rice, which probably did not grow in the area before, is a new arrival among the previous cereals. The archaeobotanical diagram (**Figure 4**) suggests that pastoralists brought Jungle rice with them and managed this plant alongside other millets already present in the area. This plant began to dominate whereas the importance of Liverseed decreased and almost disappeared from the MP2 and MP2/LP1 records.

Discussion

Plant processing at the site

The whole spikelets and variable amounts of by-products in ‘spot’ and ‘mix’ accumulations reflect the different plant management and processing activities taking place at the site. Consistency

between the botanical evidence and the archaeological contexts – mostly spatial and chronological data – supports the idea that this type of archaeobotanical record is a strong cultural marker for Saharan societies.

According to ethnographic information^{18 31}, dispersed fruits fallen from wild plants such as *Pennisetum*, *Cenchrus* and *Echinochloa* may have been collected from the ground. Open baskets might have been used to gather seeds, as suggested by the basketry fragments, including some that preserve trapped grains (*Pennisetum*, *Brachiaria*, *Dactyloctenium*), unearthed at Takarkori²⁵ and other sites in the region^{35 36}. These plant accumulations show that cereals were processed at the site, and that selected seeds were probably stored after threshing, winnowing and sieving. The preferential location of ‘spot’ accumulations in stone huts as can be seen in the northern sector of the site (**Figure 1b**), indicates a long occupation by the last Late Acacus hunter-gatherers focusing on abundant and predictable - albeit seasonal - plant resources. Our data show that they particularly harvested and transported Andropogoneae to be processed at the site for about 500 years.

A *low-level storage* phase is evidenced by the spots accumulated after c. 7200-6700 calBC (from ID 7, Panicoideae 57% with predominance of whole spikelets). This early storage seems to have taken place before the ‘change’ from Andropogoneae (*Pennisetum*, *Sorghum*) to Paniceae (*Urochloa*), with a transition dating to c. 7000-6600 calBC (from ID 8 to 9). The *Sorghum bicolor* species are known to have among the longest history of plant management in Saharan Africa^{37 38}. Based on our record, we argue that sorghum was present but not widespread in the area, or alternatively that it grew far from the site, probably in mixed plots (e.g. with fonios³⁹), and that the species was vulnerable to environmental instability. The spot of sorghum (72%, ID 8) also contains a significant amount of small-seed Cyperaceae (11%), perhaps an unwanted weed collected with the food plant when the stem was cut. This special spot suggests that gatherers not only stored sorghum seeds for consumption but also for possible seeding in the subsequent season. If this was for cultivation it appears to have failed, because sorghum did not spread enough to be recorded in other subsequent spots (**Figure 4**). Today, *S. bicolor* (subsp. *bicolor*) is considered a competitive crop but the species is actually less invasive than weeds like Johnson grass (*Sorghum halepense* (L.) Pers.) and several millets. The presence of the prolific weed *Urochloa panicoides*, for example, was found to reduce sorghum yields by 25-40% in modern uncontrolled farms⁴⁰. In the early Holocene Sahara,

although sorghum produced larger seeds than other wild cereals, the weedy Liverseed, with its high seed productivity, offered greater advantages to people. Humans therefore shifted from exploiting cereals with larger seeds (sorghum, **Figure 3**) to the more prolific species (Liverseed), which in turn benefitted from anthropochory, or human dissemination.

The adaptive behaviour of Jungle rice

Archaeobotany suggests that a new influx of useful plants arrived at the site with Neolithic Pastoralists at around 4800 calBC (**Figure 4**). Less drought-tolerant than the sorghum of the Late Acacus phases, *Echinochloa* expanded in the area, likely also favoured by a middle Holocene wet and warm phase. At this time, the Sahara saw the development of wadi vegetation and semi-arid seasonal savanna with fragmented habitats and high lake levels in this area^{20 29}. After a Neolithic MP1 phase of coexistence with *Urochloa* (*U.panicoides*), Jungle rice prevailed over the resident Liverseed during the MP2 (c. 4200-3900 calBC) and MP2/LP1 transition (c. 3970-3760 calBC), a time of great environmental instability in the central Sahara⁴¹.

Echinochloa colona adapts easily to changing habitats in terms of soil water status⁴² and competitiveness. Its monotypic stands cause a decrease of plant species diversity with the increase of river distance and grazing intensity⁴³. The abundance of *Dactyloctenium* during the Pastoral phases may represent an early phase of overgrazing already suggested by pollen²⁰. Specifically, the intensive removal of plant biomass and trampling by small livestock – mostly ovicaprines – led to the establishment of fast-growing opportunistic species that expanded rapidly into native plant communities and vulnerable wetlands⁴⁴. In this sense, these wild plants reacted as the *dump-heap* weeds associated with human-disturbed habitats that are thought to have thrived close to pre-agricultural dwellings⁴⁵ (but the weedy origin of the domesticated major crops in the Near East is debated⁴⁶). In our record, where we have weeds without domesticate species, the behaviour of Jungle rice may be only partly explained by its opportunistic-invasive nature. Our data suggest that in the competition between two weedy and very similar plants (*Echinochloa* vs. *Urochloa*), Jungle rice was also favoured by human selection.

Cultivation without domestication in the central Sahara

Despite differences in the subsistence basis of peoples, our archaeobotanical record is evidence that some wild cereals (*Urochloa*, but also *Panicum* and *Cenchrus*) were continuously managed for four millennia, with systematic gathering and processing, possibly shifting towards some forms of cultivation more than once.

Cultivation *before* domestication has been inferred from the presence of species outside their current natural habitats, the distance of natural plots from sites, overexploitation, the import of seeds and climate changes (see ⁹, e.g., the Middle Euphrates). Many of these features correspond with the long-term management of wild cereals in the Sahara. However, the Takarkori record is more analogous with a *cultivation without domestication* with anthropic pressure forcing slight modifications in the seed morphology of *Panicum*, which became plumper, and *Echinochloa*, which became more elongate (**Figure 5**).

In eastern China, c. 4000 calBC, plumper and longer grains were found which reflect significant morphological shifts likely due “towards harvesting of mature panicles as opposed to immature panicles”³⁸. In Syria, minimal changes in seed size suggested the use of plump-grained wild cereals (e.g. wild einkorn), favoured by cultivation without domestication⁹. Such changes are thought to precede the increase in seed size during the domestication process^{47 48}. However, the Saharan pathway seems to have been quite different from that taken by the ancestors of major crops in the Near East, and the shape changes in our record can be regarded as “a directional change under selection by early cultivation practices”¹⁵. In Africa, the domesticated species of pearl millet⁴⁷, t’ef⁴⁸ and African rice⁴⁹ have smaller grains than the wild progenitors, and one major trait isolated in the domestication of pearl millet and t’ef seems to have been the selection for higher grain numbers (a feature common in wild species having more seeds in individual spikes).

From the archaeobotanical diagram of Takarkori (**Figure 4**), we infer some selection of ‘special traits’ in African plants. First, it may have been the weediness of the wild grasses growing in the area (the ID1 to 12 accumulated by the LA2 and LA3), and then the increasing attention towards the collection of mature seeds (*Panicum laetum*) and panicles richer of seeds (*Echinochloa colona*). In this area of central Sahara, the long process from gathering to cultivation resulted in a pre-domesticate state for the two species, but the route seems to have continued (or was paralleled) elsewhere only for *E. colona*. Despite four millennia of human management of Saharan wild

grasses, domestication did not occur. Indeed, the species we identified are still largely reported as non-crop and weedy plants today (see **Supplementary Information 3** for a list of citations in the scientific literature).

The dual nature of wild cereals

With few exceptions, the grasses we found in the Takarkori record are often described as aggressive colonizers, invaders, segetal, ruderal, sometimes mimic, weeds, and generalists growing wild in a broad range of habitats from swamps to open grasslands to semi-desert habitats. Many are annual species producing more seeds than perennials, and summer crops. Since they are drought-tolerant and withstand heavy grazing, they are currently widely cultivated as food or forage grasses in tropical areas (e.g. *Brachiaria* and *Urochloa*⁵⁰). Our plant accumulations demonstrate that some Panicoideae (first *Pennisetum*, *Setaria* and *Sorghum*, then *Brachiaria/Urochloa* with *Panicum*, and *Echinochloa*) were continuously managed, and even actively propagated by seeding, so many of them survived environmental changes and lived in the area until desertification and water loss definitively limited their growth starting from c. 3500 calBC²².

Interestingly, in Eastern China, wild *Echinochloa* was processed with grinding stones but this became an agricultural weed once cultivated Asian rice became dominant in cultivation⁵¹. In the absence of any domesticated crop, our African records show that *Echinochloa colona* was cultivated in association with *Panicum laetum* among the others. The early cultivation practices may have comprised a mixture of small-grained millets. High-value Panicoideae played an important role in human dietary starch-protein intake, and seem to have spread easily by moving into newly-created human environments¹⁴. Abundance and predictability were important factors in their evolutionary success, as the weedy traits were selected and appreciated first by early Holocene foragers for their food security and culinary practices, and later by Neolithic herders²⁷.

The selection of weediness

The Late Acacus hunter-gatherers settled near large stands of wild cereals to harvest huge amounts of seeds; the pastoralists continued this tradition, harvesting larger quantities of mature grains, likely not simply selecting only for 'large and non-shattering' seeds. Humans selected invasive and opportunistic plant behaviour before morphological traits of some grasses.

The archaeobotanical record that shows, with overlapping, the trend from gathering under prevalently natural selection to the cultivation under both human and natural selections⁵² (from ID 1-12 to ID 13-30, respectively; **Figure 4**). People selected weediness because it was an easier way to grow plants. By this process, we argue that humans elicited biological responses by these weeds, and the selected plants were rewarded as they improved their own fitness.

Considering these human actions like parts of a 'long process'¹⁵, our data show that the selection of weediness has continued during the transition from gathering to farming (**Figure 4**). The use of resilient plants (mainly *Urochloa* in our record) seems to have been a more conscious early action than the subsequent involuntary selection for the richest panicles searching for abundant grains (that likely caused the elongation of our *Echinochloa* spikelets).

Efficient dispersal mechanisms, seed dormancy, and phenotypically plastic genotypes are common traits in the weed syndrome rooted in their capacity for rapid adaptation to environmental changes⁵³. Interestingly, some wild cereals such as fonios are considered semi-domesticated species that have lost their efficient natural seed dispersal, a step towards domestication in many Poaceae. These plants present advantageous adaptations for cultivation, as they are able to grow with other crops and also highly competitive with weeds³⁹ in subsistence agro-ecosystems. Although each weed species may have a diverse and unique history, our data suggest the revision of some commonly held opinions on these invasive field weeds. Specifically, we argue that: a) the selection of large natural stands was not a form of low-skilled pre-cultivation but a genuine human strategy based on the presence of opportunistic-invasive behaviour of some grasses; b) these plant species were the direct object of long-term human manipulation and not ancillary plants that spread *after* crops; and c) weedy millets had sometimes behaviours that, according to our data, make them pre-adapted to spread with domestic crops (including the aptitude to mimicry). This may have been effect of long-time human pressure on wild species. From a co-evolutionary perspective¹, people selected for weediness - including abundance and predictability - thus ensuring that both plants and humans adapted successfully to environmental crises. The cultivation system, often regarded as beneficial only to humans, also proved highly advantageous to some 'special' wild plants.

Reconnecting past and future

Wild cereals present both wild (weed) and cultivated (crop) behaviours and characteristics. The genera of millets found at Takarkori rockshelter include species that have been domesticated in

parallel numerous times. We argue that their tendency to evolve as crops is probably rooted in the very long history of manipulation and management the record of Takarkori shows for the African route to domestication. We agree with Viguera et alii⁵³ that our weeds “*compose a unique evolutionary state, neither wild nor domesticated, that has developed in parallel to crop domestication*”. Signs of selection for lost-value traits are hard to be recognized today but it is probable that these were not ‘aborted trajectories’ as millennia of sophisticated plant management should have affected plant traits as well as human culture. The opportunistic behaviour of these wild cereals favoured their development in unstable environments while the human pressure did not cause severe limits¹¹ on the chances of their autonomous survival. Today, based on their ecology⁵⁴, we should change our view of such weeds. The same behaviour that allowed these plants to survive in a changing environment in a remote past makes them some of the most likely possible candidates as staple resources in a coming future of global warming. They continue to be successfully exploited and cultivated in Africa today and are attracting the interest of scientists searching for new food resources. Our research suggests that, like modern gatherers, we should pay renewed attention to these plants in the hope of finding innovative responses to tackle desertification and biodiversity loss.

Methods

Definition of the term ‘weediness’ and the main traits of our weeds

The term “weed” has been variously defined, depending on the different perspectives of ecologists, agronomists, archaeobotanists and the public, and we do not know a definition that has met a universal agreement⁵⁵ (see **Supplementary Information 3**).

The ‘weediness’ described in this research on the Saharan prehistoric, and pre-domestication, landscape requires a definition of the term in an ecological perspective. Weeds possess many adaptive strategies to survive such as the phenotypic plasticity (i.e., the ability of an organism to express different phenotypes depending on the biotic or abiotic environment⁵⁶), abundant seed production, prolonged viability of propagules with dormancy (so as to survive under unfavourable conditions), ability to fast growth of seedlings, spread at a high rate, high tolerance to environmental heterogeneity and to changes in environmental conditions, strong interspecific competition and resilience. Weeds are part of a dynamic ecosystem⁵⁷ and all these traits make these weeds ideal for easy proliferation.

Our weeds include invasive and opportunistic species.

The term ‘invasive’ is often used to indicate these plants (problematic today) as “they can successfully establish and spread following introduction into novel, often non-managed areas”. The authors of the previous definition reported also that “invasives are considered weeds in the broadest sense of the term; some authors (not the case of this paper) prefer to use the designation ‘weed’ only for problematic plants in agriculture, and reserve the term ‘invasive’ to indicate problematic plants growing in non-managed or wild areas”⁵⁵. Moreover, the species we identified in our archaeobotanical record are characterised by ‘opportunistic behaviour’. In ecology, an opportunistic plant can thrive in different conditions, and rapidly takes advantage of environmental changes because the species is behaviourally flexible.

Excavation and sampling

Takarkori was excavated entirely by hand, using small trowels. The plant accumulations were identified by sight, mapped using an Electronic Total Station (ETS) and removed. The samples were then gently dry-sieved with a 0.6 mm screen in the laboratory, and the residue was examined to check for smaller parts (seeds were not found). Direct radiocarbon datings of each plant accumulation placed them in a chronological trend from the hunter-gatherer (Late Acacus: LA2, LA3) to Pastoral Neolithic phases (Middle and Late Pastoral: MP1, MP2, MP2/LP1), known for the stratigraphy of the site and the Tadrart Acacus region^{19 58} (see Table 1, with archaeological phases and calibrated ages⁵⁹; Figure 2). Stereomicroscope examination showed that the plant accumulations consisted largely of dried yellow to brown spikelets of Panicoideae with a few other

plant taxa dispersed in the residual sand. These accumulations are consistent with one or a few plants entering the archaeological deposit contemporaneously.

Entomological analyses demonstrated that insects played no role in transporting plant parts into the site.

Insect search was carried out on 13 samples: seven spots (ID 2, 9, 10, 12, 17, 20, 25), one mix (ID 30), and five samples of soils external to the plant accumulations but belonging to the same stratigraphic unit and used as controls. The search was performed using a stereomicroscope and every arthropod fragment was isolated using micro-paintbrushes and identify at the lowest taxonomic level. In all the samples fragments of spider beetles (Coleoptera, Ptinidae) and of migratory locusts (Orthoptera, Acrididae) were detected. Few fragments (mainly heads) of ants (Hymenoptera, Formicidae) were found only in the control samples, whereas among the plant accumulation material no ant fragments were identified.

Taxa identification and morphometry

The botanical finds were hand-sorted and morphologically identified by observation under an Olympus SZ60 stereomicroscope at 40x-80x magnification, with the help of the specialized literature^{60 61 62 63 64 65 66}.

Whole spikelets (grain enclosed by lemma and palea) of all the species mentioned above dominate in the archaeobotanical record; spikelets consisting of the persistent papery tissues of external glumes (upper and lower glumes) and the smooth to verrucate inner glumes (lemma and palea) are also found in some accumulations. Since *Brachiaria* and *Urochloa* inter-hybridize, the boundary between the two genera is sometimes unclear and a variable number of intermediate phenotypic stages (from *quasi*-awnless to mucronate tip spikelets) were observed, suggesting that large stands hosted mixed populations. In the accumulations studied here, *Pennisetum* mainly takes the form of involucre of soft and plumose sessile bristles, and *Cenchrus* of the spiny involucre fused at the base. Alongside the fertile spikelets we observed sterile or immature spikelets of *Pennisetum* and *Sorghum*, both presenting the typical wild species morphology. The sorghum has hulled spikelets with the shattering wild type of spikelet basis, and its immature florets/spikelets are flattened and sometimes with persistent rachillae, probably reflecting the ripening variability of the panicle (see SEM images in **Supplementary Information 1**).

Variable amounts of non-grass fruits/seeds including *Ficus*, *Ziziphus* cf., Cyperaceae, *Persicaria* and various few others (Asteraceae, Amaranthaceae, Apiaceae, and *Colocynthis*) were also present. Given the nature of the archaeological deposit, comprising mostly organic sands¹⁹, the seed accumulations also include small

amounts of stems (grasses and sedges), leaves and charcoal fragments, a few undetermined flowers and charred plant remains.

From each plant accumulation, whole spikelets of *Panicum laetum* Kunth, *Echinochloa colona* (L.) Link. and *Sorghum bicolor* (L.) Moench subsp. *verticilliflorum* (Steud.) de Wet ex Wiersema & J. Dahlb. - syn. *S. arundinaceum* (Desv.) Stapf - were extracted under the stereomicroscope. The main morphological and morphometrical characters, on fertile, mature and intact spikelets, are:

P. laetum: elliptic shape with pointed ends; bright spikelets, brown to reddish, with nuances of orange; fine longitudinal linear striations on lemma and palea; lemma: concave, lateral edges folded on the palea, 5-7 longitudinal veins are clearer than others; palea: almost flat, with two longitudinal veins more clear. The species is native to tropical Africa, and it has considerable importance in areas of marginal subsistence where it is often consumed as a famine food. Measurements on 690 specimens: 2.01 ± 0.09 mm (length) x 1.23 ± 0.10 mm (width) x 0.90 ± 0.08 mm (thickness).

E. colona: elliptic to oblong shape; notched apex (three points, the central one is thicker and longer than the others), curved downwards; awnless, shiny spikelets, yellow to light brown; fine longitudinal linear striations on lemma and palea; lemma: concave, lateral edges folded on the palea, five longitudinal veins with three veins more evident than the others, and the middle one slightly larger; palea: flat. The species is hexaploid, native to several regions including Africa⁶⁷, and the wild progenitor of *Echinochloa frumentacea* Link (syn. *E. colona* var. *frumentacea* (Link.) Ridl; sawa millet or Indian barnyard millet)^{68 69}. The close DNA affinity between the two species is supported by their cross-compatibility⁷⁰. Although, phylogenetic relationships within *Echinochloa* species are not fully understood, the ploidy differences between wild and crop species suggest that gene flow from cultivars has not a role in the weed's evolution⁵³. Measurements on 750 specimens: 2.11 ± 0.13 mm (length) x 1.32 ± 0.09 mm (width) x 0.88 ± 0.10 mm (thickness).

S. bicolor subsp. *verticilliflorum*: lanceolate shape; pointed apex (often covered with fine hairs, especially on the rachilla attachment point); shiny spikelets, dark brown with reddish hues; lemma: widely convex, without streaks, lateral edges folded on the palea; palea: convex; without streaks. The species is diploid, or tetraploid, native to Africa, and is the wild progenitor of *S. bicolor* subsp. *bicolor* (domesticated grain sorghum)⁷¹. Measurements on 100 specimens: 6.41 ± 0.35 mm (length) x 2.33 ± 0.14 mm (width) x 2.35 ± 0.17 mm (thickness).

Photos of the spikelets in dorsal and lateral view were taken using the Leica MC170 HD camera connected to the stereomicroscope, maintaining constant parameters (default options for white background), and the magnification of the stereoscope (9.0x) (Figure 3). The length, width and thickness of each spikelet were measured using the software package Leica Application Suite - LAS EZ version 3.0.0 (Leica Microsystems). These identifications were supported by molecular analyses. Ancient DNA was successfully recovered from the spikelets of *Panicum*, *Echinochloa* and *Sorghum*, allowing for the Polymerase Chain Reaction (PCR) amplification and sequencing of the barcode regions used for the taxonomic determination. Chloroplast marker *rbcL* provided the identification of the three genera. The DNA barcode sequence obtained from *Echinochloa* matched with maximum identity value (99%) seven samples in GenBank: the five accessions identified as *E. colona*, one accession of *E. frumentacea* [(Roxb.) Link] and one accession of *E. ugandensis* (Snowden & Hubbard). Moreover, the multi-locus approach (*rbcL*, *matK*, *trnH-psbA* and *trnL* markers) allowed for the species identification of *Panicum laetum*^{72 73}.

Spikelet number estimations

All the specimens in the accumulations of ≤ 15 ml were counted (ID 5, 9, 11, 13, 14, 15, 16, 20, 23, 24, 25, 27, and 28). To estimate the total number of macroremains in the other twenty-one accumulations, three separate 2, 4, 10 ml sub-samples were taken from each accumulation. The number of specimens in each sub-sample was used to compute the average number providing estimates according to the total volume. To account for differences in the counts, the weighted average and the absolute error were calculated for the final estimate in the total volume as shown in Table 1. The number of seeds in the 30 plant accumulations was used to calculate the total number of seeds in each cultural phase and in the archaeobotanical record.

The number of broken spikelets was recovered by a visual validation according to the known size and morphology of the whole spikelet⁷⁴. A spikelet was determined by a lemma-palea association, or by 3-8 fragments depending on their size. The amount of spikelets recovered by inspecting the broken parts of *Brachiaria*, *Urochloa*, *Panicum*, *Echinochloa*, *Digitaria*, *Dactyloctenium* and *Setaria* was used to calculate the percentage ratio of whole to fragmented spikelets in each plant accumulation. This ratio was helpful in

describing what was evident on visual examination, i.e. the different status of plant accumulations with prevalent whole spikelets ('spots') and those with prevalent chaff and processing by-products ('mix'). The morphology and fragmentation of the soft parts, and the general archaeological context, provide a better understanding of the nature of 'mix' accumulations. For example, the most recent samples are more abundant in isolated glumes (e.g., of *Dactyloctenium*), accompanied by other cereal chaff and straw, and may be remains of fodder.

Data availability

The data that support the findings of this study are available from the corresponding authors upon request.

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Methods section

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Author contributions

S.d.L. and A.M.M. conceived and planned the project. A.M.M. and S.d.L. wrote the paper. A.M.M. studied the archaeobotanical record and S.d.L. the stratigraphic and archaeological context. R.F.

performed morphometry and data analysis. M.G. made GIS analysis. S.V. made the entomological study. S.d.L. designed and directed the excavations and field sampling. All authors read and approved the final manuscript.

Legends

Table 1 – The 30 plant accumulations from the archaeobotanical record of Takarkori rockshelter: archaeological context and archaeobotanical results.

Cultural phases (*) = LA: Late Acacus; MP: Middle Pastoral; LP: Late Pastoral. From the oldest, they are: LA2: 8500-7900 uncal bp; 7600-6650 calBC; LA3: 7900-7400 uncal bp; 7050-6100 calBC; MP1: 6100-5500 uncal bp; 5200-4250 calBC; MP2: 5500-5000 uncal bp; 4450-3700 calBC; LP1: 5000-4000 uncal bp; 3950-2350 calBC.

Calibrated years BC (**) = date calibration was carried out using OxCal Online v. 4.3 ⁵⁹

Figure 1 – Context of the archaeobotanical record of Takarkori rockshelter. a) The Tadrart Acacus Mountains, SW Libya, and location of the site (red circle); b) GIS map of the excavation and position of plant accumulations by type (mix, spot) and chronology (Late Acacus: yellow; Middle Pastoral: blue; Middle/Late Pastoral: grey); c) ‘spot’ accumulation of the Middle Pastoral = MP1 phase (ID 17 in the map ‘b’); d) ‘mix’ accumulation of the Late Acacus = LA3 phase (ID 6 in the map ‘b’).

Figure 2 – Multiplot of calibrated (calBC) radiocarbon dates of the 30 archaeobotanical samples (Late Acacus: yellow; Middle Pastoral: blue; Middle/Late Pastoral: grey). See Table 1 for details of dates (generated using OxCal Online ver. 4.3 ⁵⁹).

Figure 3 – “Spot” and “mix” plant accumulations.

‘Spot’: a) overview (ID 15); dorsal and ventral view of the spikelets of: b) *Panicum laetum* (ID 15); c) *Echinochloa colona* (ID 15); d) uncharred grain (ID 14); e) *Sorghum bicolor* subsp. *verticilliflorum* (ID 8). ‘Mix’: f) overview (ID 24); g) split spikelets of *E. colona* (ID 24); h) charred grains in dorsal and ventral view (ID 26); i) outer glumes of *E. colona* (ID 23).

Figure 4 – The archaeobotanical record of plant accumulations from Takarkori rockshelter is unique in showing so clearly and gradually the data on the long transitional process from gathering to cultivation. Histograms show the percentages of seeds/fruits identified and counted in the plant accumulations, and their

total concentrations (in 10 ml); samples are plotted in chronological order from the oldest (bottom) to the youngest (top) accumulation.

Figure 5 - Morphometry of ellipticity.

The graphs show changes in the spikelet morphology of Wild fonio and Jungle rice during the occupation of the site. The ellipticity (the degree of deviation from sphericity) of Wild fonio decreases, with the spikelets tending towards an increasing roundness, especially visible when comparing length and thickness. The ellipticity of Jungle rice increases because the spikelets tend to lengthen. This is especially visible when comparing length and width (n = number of measured spikelets).

| ID | Context & Chronology | | | | | Archaeobotanical sample | | | Main features and botanical composition | | | Seed storage vs food |
|----|---------------------------|-----------------|-----------------------------------|------------|--|-------------------------|-------------------|----------------------------------|---|--|---|---|
| | Stratigraphic context | Cultural Phase* | ¹⁴ C age (uncal yr BP) | Lab code | Cal yr BC** | total weight (g) | total volume (ml) | records estimated on tot. volume | cereals on total seed remains (%) | main taxa | type of plant accumulation | estimation of whole / fragmented spikelet records (%) |
| 1 | Organic Sands | LA2 | 8341 ± 55 | LTL16829A | 7533BC (90.6%) 7286BC 7273BC (1.4%) 7255BC 7227BC (3.5%) 7191BC | 63.7 | 100 | 1585 ± 29 | 50 | <i>Brachiaria</i> 26%, cf. <i>Ziziphus</i> 18% | mix of Paniceae with chaff | 25/75 |
| 2 | Organic Sands | LA2 | 8256 ± 45 | LTL15247A | 7460BC (95.4%) 7130BC | 189 | 265 | 16939 ± 34 | 86 | <i>Setaria</i> 71% | spot of <i>Setaria</i> | 85/15 |
| 3 | Organic Sands | LA2 | 8236 ± 55 | LTL16830A | 7452BC (8.9%) 7395BC 7376BC (86.5%) 7081BC | 20.6 | 30 | 644 ± 42 | 80 | <i>Brachiaria</i> 19%, <i>Brachiaria/Urochloa</i> 17% | mix of Paniceae with chaff | 30/70 |
| 4 | Organic Sands | LA2 | 8222 ± 55 | LTL16828A | 7450BC (5.2%) 7406BC 7371BC (90.2%) 7073BC | 11.6 | 25 | 1035 ± 193 | 96 | <i>Urochloa</i> 45%, <i>Andropogoneae</i> 16%, <i>Pennisetum</i> 14% | mix of <i>Urochloa</i> and Panicoideae with chaff | 58/42 |
| 5 | Organic Sands | LA2 | 8209 ± 65 | LTL16836A | 7451BC (5.5%) 7400BC 7372BC (89.9%) 7063BC | 7.4 | 14.5 | 839 | 50 | <i>Pennisetum</i> 11%, <i>Ficus</i> 26%, cf. <i>Ziziphus</i> 20% | mix with <i>Pennisetum</i> and chaff | 23/77 |
| 6 | Organic Sands | LA3 | 8090 ± 55 | LTL16831A | 7296BC (4.6%) 7223BC 7190BC (82.1%) 6899BC 6889BC (8.7%) 6825BC | 113.7 | 175 | 7312 ± 76 | 94 | <i>Pennisetum</i> 25%, <i>Brachiaria - Urochloa - B/U</i> 32% | mix of Panicoideae with chaff | 23/77 |
| 7 | Organic Sands | LA3 | 8056 ± 65 | LTL16532A | 7190BC (94.0%) 6740BC 6730BC (1.4%) 6700BC | 25.6 | 50 | 490 ± 21 | 72 | <i>Andropogoneae</i> 27%, <i>Pennisetum</i> 15%, <i>Sorghum</i> 15% | spot of Panicoideae | 85/15 |
| 8 | Organic Sands | LA3 | 7930 ± 30 | UGAMS#8708 | 7030BC (95%) 6680BC | 76.2 | 160 | 4320 ± 78 | 86 | <i>Sorghum</i> 72%, <i>Cyperaceae</i> 11% | spot of <i>Sorghum</i> | 99/1 |
| 9 | Organic Sands | LA3 | 7880 ± 50 | LTL16529A | 7030BC (10.9%) 6930BC 6920BC (6.3%) 6870BC 6850BC (78.2%) 6600BC | 7.2 | 10 | 1762 | 95 | <i>Urochloa</i> 87% | spot of <i>Urochloa</i> | 97/3 |
| 10 | Ring/Enclosure | LA3 | 7746 ± 60 | LTL15245A | 6680BC (95.4%) 6460BC | 46.6 | 70 | 10170 ± 112 | 97 | <i>Urochloa</i> 75%, <i>Brachiaria</i> 15% | spot of <i>Urochloa - Brachiaria</i> | 99/1 |
| 11 | Organic Sands | LA3 | 7648 ± 100 | LTL16528A | 6690BC (92.0%) 6330BC 6320BC (3.4%) 6250BC | 3.3 | 7 | 1919 | 8 | <i>Polygonum</i> 87%, <i>Pennisetum</i> 2% | spot of <i>Polygonum</i> with Panicoideae | 87/13 |
| 12 | Organic Sands | LA3 | 7629 ± 55 | LTL16091A | 6600BC (95.4%) 6400BC | 22.6 | 30 | 4185 ± 182 | 99 | <i>Urochloa</i> 63%, <i>Panicum</i> 11% | spot of <i>Urochloa</i> | 90/10 |
| 13 | Organic Sands | MP1 | 5887 ± 45 | LTL16834A | 4895BC (2.2%) 4866BC 4850BC (91.4%) 4667BC 4638BC (1.8%) 4617BC | 6.7 | 8.2 | 2304 | 97 | <i>Echinochloa</i> 48%, <i>Panicum</i> 32%, <i>Urochloa</i> 11% | spot of <i>Echinochloa</i> and <i>Panicum</i> | 98/2 |
| 14 | Organic Sands | MP1 | 5851 ± 45 | LTL16832A | 4831BC (95.4%) 4587BC | 7.5 | 9.6 | 3765 | 91 | <i>Echinochloa</i> 52%, <i>Panicum</i> 16%, <i>Urochloa</i> 15%; uncharred grains 7% | spot of <i>Echinochloa</i> and <i>Panicum</i> | 99/1 |
| 15 | Organic Sands | MP1 | 5686 ± 45 | LTL16092A | 4690BC (93.6%) 4440BC 4420BC (1.8%) 4390BC | 15 | 10 | 3406 | 99 | <i>Urochloa</i> 75%, <i>Echinochloa</i> 12% | spot of <i>Urochloa</i> | 99/1 |
| 16 | Organic Sands | MP1 | 5678 ± 45 | LTL16833A | 4669BC (2.7%) 4637BC 4618BC (87.4%) 4443BC 4421BC (5.3%) 4373BC | 8.4 | 8.2 | 1454 | 91 | <i>Urochloa</i> 65%, <i>Echinochloa</i> 12% | spot of <i>Urochloa</i> | 85/15 |
| 17 | Organic Sands | MP1 | 5660 ± 25 | UGAMS#8706 | 4550BC (95%) 4440BC | 63 | 80 | 19022 ± 68 | 99 | <i>Urochloa</i> 83% | spot of <i>Urochloa</i> | 99/1 |
| 18 | Organic Sands | MP1 | 5610 ± 30 | UGAMS#8709 | 4500BC (95%) 4360BC | 39.6 | 40 | 11014 ± 343 | 94 | <i>Echinochloa</i> 59%, <i>Panicum</i> 19%; uncharred grains 4% | spot of <i>Echinochloa</i> and <i>Panicum</i> | 84/16 |
| 19 | Pit | MP1 | 5583 ± 45 | LTL15246A | 4500BC (95.4%) 4340BC | 41.4 | 50 | 6577 ± 122 | 96 | <i>Urochloa</i> 82% | spot of <i>Urochloa</i> | 99/1 |
| 20 | Organic Sands | MP1 | 5572 ± 45 | LTL16531A | 4490BC (95.4%) 4340BC | 13.4 | 15 | 4255 | 84 | <i>Echinochloa</i> 50%, <i>Panicum</i> 17%; uncharred grains 7% | spot of <i>Echinochloa</i> and <i>Panicum</i> | 92/8 |
| 21 | Organic Sands | MP1 | 5543 ± 45 | LTL16095A | 4470BC (95.4%) 4320BC | 221.4 | 250 | 45193 ± 231 | 98 | <i>Urochloa</i> 64%, <i>Echinochloa</i> 18% | spot of <i>Urochloa</i> and <i>Echinochloa</i> | 99/1 |
| 22 | Floor/Trampling | MP1 | 5507 ± 45 | LTL16093A | 4460BC (85.4%) 4310BC 4300BC (10.0%) 4260BC | 52.5 | 65 | 6336 ± 59 | 95 | <i>Echinochloa</i> 48%, <i>Panicum</i> 20% | spot of <i>Echinochloa</i> and <i>Panicum</i> | 98/2 |
| 23 | Organic Sands | MP2 | 5254 ± 45 | LTL16835A | 4230BC (12.9%) 4192BC 4177BC (82.5%) 3972BC | 7.9 | 10 | 1009 | 93 | <i>Echinochloa</i> 50%, <i>Panicum</i> 15% | mix of Paniceae chaff | 2/98 |
| 24 | Organic Sands | MP2/LP1 | 5064 ± 45 | LTL16089A | 3970BC (94.1%) 3760BC 3740BC (1.3%) 3710BC | 26.5 | 15 | 2537 | 95 | <i>Echinochloa</i> 78% | mix with <i>Echinochloa</i> chaff | 5/95 |
| 25 | Straw | MP2/LP1 | 4987 ± 45 | LTL16094A | 3950BC (21.8%) 3850BC 3830BC (73.6%) 3650BC | 9.9 | 10 | 2690 | 94 | <i>Echinochloa</i> 65%, <i>Panicum</i> 18% | spot of <i>Echinochloa</i> and <i>Panicum</i> | 88/12 |
| 26 | Organic Sands | MP2/LP1 | 4970 ± 25 | UGAMS#8707 | 3800BC (95%) 3660BC | 269.4 | 400 | 46573 ± 167 | 94 | <i>Echinochloa</i> 49%, <i>Panicum</i> 34% | mix with <i>Echinochloa-Panicum</i> chaff | 18/82 |
| 27 | Organic Sands | MP2/LP1 | 4939 ± 45 | LTL16090A | 3900BC (1.4%) 3880BC 3800BC (94.0%) 3640BC | 7.3 | 10 | 1350 | 94 | <i>Echinochloa</i> 65%, <i>Panicum</i> 9% | mix with <i>Echinochloa-Panicum</i> chaff | 2/98 |
| 28 | Organic Sands | MP2/LP1 | 4895 ± 45 | LTL16088A | 3780BC (94.3%) 3630BC 3560BC (1.1%) 3540BC | 6.1 | 15 | 1574 | 93 | <i>Echinochloa</i> 79% | mix with <i>Echinochloa</i> chaff | 21/79 |
| 29 | Organic Sands | MP2/LP1 | 4764 ± 45 | LTL16837A | 3645BC (80.2%) 3497BC 3435BC (15.2%) 3377BC | 26.5 | 30 | 1091 ± 76 | 81 | <i>Echinochloa</i> 37%, <i>Dactyloctenium</i> 20% | mix with <i>Echinochloa-Dactyloctenium</i> chaff | 4/96 |
| 30 | Multiple Ash Accumulation | MP2/LP1 | 4732 ± 45 | LTL16530A | 3640BC (63.2%) 3490BC 3460BC (32.2%) 3370BC | 13.4 | 25 | 11014 ± 102 | 99 | <i>Echinochloa</i> 77%, <i>Urochloa</i> 16% | mix with <i>Echinochloa-Urochloa</i> chaff | 3/97 |