nature plants

SUPPLEMENTARY INFORMATION
https://doi.org/10.1038/s41477-019-0470-4

In the format provided by the authors and unedited.

Grazing animals drove domestication of grain crops

Robert N. Spengler III[1]* and Natalie G. Mueller[2,3]

[1]Archaeology Department, Max Planck Institute for the Science of Human History, Jena, Germany. [2]Horticulture Section, School of Integrative Plant Sciences, Cornell University, Ithaca, NY, USA. [3]Department of Anthropology, Washington University in St. Louis, St. Louis, MO, USA.
*e-mail: Spengler@shh.mpg.de

Crop	Binomial	Earliest Domest. Evidence	Trait of Domest.	Region/Center	Refs
Flax	*Linum usitatissimum* L.	7500 BC	I	Southwest Asia	(1, 2)
Little Millet	*Panicum sumatrense* Roth	2500 BC	I	Savannahs of West India	(3, 4)
Sesame	*Sesamum indicum* L.	2700 BC	I, T	South India	(4)
Browntop Millet	*Brachiaria ramosa* (L.) Stapf	1500 BC	I	South India	(4)
Broomcorn Millet	*Panicum miliaceum* L.	6000 BC	I	Northeast China	(5-9)
Foxtail Millet	*Setaria italica* (L.) P. Beauv.	6000 BC	I	Northeast China	(5-9)
Hemp	*Cannabis sativa* L.	3000 BC	I, M	East and likely west China	(10)
Buckwheat	*Fagopyrum esculentum* Moench	1000 BC	I, T	Southern Himalaya	(11, 12)
Buckwheat	*Fagopyrum tataricum* (L.) Gaertn.	1 AD	I, T	Southern Himalaya	(11, 12)
Japanese Millet	*Echinochloa esculenta (A.Braun) H.Scholz.*	1000 BC	I	Japan	(13, 14)
Sunflower	*Helianthus annuus* L.	2500 BC	I	Eastern North America	(15)
Goosefoot	*Chenopodium berlandieri* Moq.	1500 BC	D, I, T	Eastern North America	(16)
Marshelder	*Iva annua* L.	2500 BC	I	Eastern North America	(17)
Knotweed	*Polygonum erectum* L.	1 AD	D, I, T	Eastern North America	(18)
Little Barley	*Hordeum pusillum* Nutt.	500 BC	I, T	Eastern North America	(19)
Maize	*Zea mays* L.	6500 BC	I, T, M	Mesoamerica	(20, 21)
Quinoa	*Chenopodium quinoa* Willd.	3500 BC	D, I, T	Andes	(22)
Amaranth	*Amaranthus caudatus* L.	1 AD	I, T	Andes	(23)
Pearl millet	*Pennisetum glaucum* (L.) R. Br.	1500 BC	I, T	West Africa Sahel	(24-27)
Sorghum	*Sorghum bicolor* (L.) Moench	2000 BC	I, S, T	Eastern Africa Savannah	(27, 28)
Fonio/krebs	*Digitaria exilis* (Kippist) Stapf	N/A	N/A	West Africa Sahel	(29)
Guinea millet	*Brachiaria deflexa* Schumach.	N/A	N/A	West Africa Sahel	(29)
Finger millet	*Eleusine coracana* (L.) Gaertn.	1000 BC	I, S, T	Eastern African Highlands	(30-32)
Teff	*Eragrostis tef* (Zuccagni) Trotter	1 AD	D, I	Ethiopian Plateau	(27, 33)

*D-loss of dormancy; T-thinning of testa or pericarp, or loss of adhering palea,lemma, or glumes; S-loss of shattering rachis or dehiscent pod; A-loss of bristles or awns; I-increased seed/fruit size; M-other morphological changes, such as shape of the embryo scar or dimorphism. Refs. Provide documentation of morphological changes.

Table SI-1. This table displays most of the early examples of small-seeded crops, domesticated in each center or region of domestication globally. These early grain crops all show traits of domestication that are characteristic of a switch from an endozoochoric dispersal mechanism to anthropogenic dispersal. While teosinte is not particularly small-seeded, it shares many characteristics with the plants discussed here, and further investigation of endozoochory in maize domestication may be warranted.

References

1. Asouti E & Fuller DQ (2013) A Contextual Approach to the Emergence of Agriculture in Southwest Asia. *Current Anthropology* 54(3):299-345.
2. Fuller DQ, Willcox G, & Allaby RG (2011) Cultivation and Domestication had Multiple Origins: Arguments Against the Core Area Hypothesis for the Origins of Agriculture in the Near East. *World Archaeology* 43(4):628-652.
3. Fuller DQ (2006) Agricultural origins and frontiers in South Asia: a working synthesis. *Journal of World Prehistory* 20(1):1-86.
4. Fuller DQ (2011) Finding plant domestication in the Indian subcontinent. *Current Anthropology* 52(S4):S347-S362.

5. Bettinger RL, Barton L, & Morgan C (2010) The origins of food production in north China: A different kind of agricultural revolution. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews* 19(1):9-21.
6. Cohen DJ (2011) The beginnings of agriculture in China: A multiregional view. *Current Anthropology* 52(S4):S273-S293.
7. Miller NF, Spengler RN, & Frachetti M (2016) Millet cultivation across Eurasia: origins, spread, and the influence of seasonal climate. *The Holocene* 26(10):1566-1575.
8. Zhao Z (2011) New archaeobotanic data for the study of the origins of agriculture in China. *Current Anthropology* 52(S4):S295-S306.
9. Fuller DQ (2011) Pathways to Asian civilizations: Tracing the origins and spread of rice and rice cultures. *Rice* 4(3-4):78-92.
10. Clarke RC & Merlin MD (2013) *Cannabis: Evolution and ethnobotany* (University of California Press, Berkeley).
11. Hunt HV, Shang X, & Jones MK (2018) Buckwheat: a crop from outside the major Chinese domestication centres? A review of the archaeobotanical, palynological and genetic evidence. *Vegetation History and Archaeobotany* 27(3):493-506.
12. Ohnishi O & Konishi T (2001) Cultivated and wild buckwheat species in eastern Tibet. *Fagopyrum* 18:3-8.
13. Crawford GW (2011) Advances in understanding early agriculture in Japan. *Current Anthropology* 52(S4):S331-S345.
14. Matsui A & Kanehara M (2006) The question of prehistoric plant husbandry during the Jomon period in Japan. *World Archaeology* 38(2):259-273.
15. Smith BD (2014) The domestication of *Helianthus annuus* L. (sunflower). *Vegetation History and Archaeobotany* 23(1):57-74.
16. Smith BD (1984) Chenopodium as a Prehistoric Domesticate in Eastern North America: Evidence from Russell Cave, Alabama. *Science* 226(4671):165-167.
17. Yarnell RA (1972) *Iva annua* var. *macrocarpa*: Extinct American Cultigen? *American Anthropologist* 74:335-341.
18. Mueller NG (2017) An Extinct Domesticated Subspecies of Erect Knotweed in Eastern North America: *Polygonum erectum* L. ssp. *watsoniae* (POLYGONACEAE). *Novon* 25(2).
19. Adams KR (2014) Little Barley Grass (*Hordeum pusillum* Nutt.): A Prehispanic New World Domesticate Lost to History. *New Lives for Ancient and Extinct Crops*, ed Minnis PE (The University of Arizona Press, Tuscon), pp 139-179.
20. Dorweiler JE & Doebley J (1997) Developmental analysis of teosinte glume architecture1: a key locus in the evolution of maize (Poaceae). *American Journal of Botany* 84(10):1313-1322.
21. Piperno DR, Ranere AJ, Holst I, Iriarte J, & Dickau R (2009) Starch grain and phytolith evidence for early ninth millennium BP maize from the Central Balsas River Valley, Mexico. *Proceedings of the National Academy of Sciences* 106(13):5019-5024.
22. Bruno MC (2006) A Morphological Approach to Documenting the Domestication of *Chenopodium* in the Andes. *Documenting Domestication: New Genetic and Archaeological Paradigms*, eds Zeder MA, Bradley DG, Emshwiller E, & Smith BD (University of California Press, Berkeley), pp 32-45.
23. Pearsall DM (2008) Plant Domestication and the Shift to Agriculture in the Andes. *Handbook fo South American Archaeology*, eds Silverman H & Isbell W (Springer, New York), pp 105-120.
24. Brunken J, de Wet J, & Harlan J (1977) The morphology and domestication of pearl millet. *Economic Botany* 31(2):163-174.
25. Manning K, Pelling R, Higham T, Schwenniger J-L, & Fuller DQ (2011) 4500-year old domesticated pearl millet (Pennisetum glaucum) from the Tilemsi Valley, Mali: new insights into an alternative cereal domestication pathway. *Journal of Archaeological Science* 38(2):312-322.
26. Zach B & Klee M (2003) Four thousand years of plant exploitation in the Chad Basin of NE Nigeria II: discussion on the morphology of caryopses of domesticated Pennisetum and complete

catalogue of the fruits and seeds of Kursakata. *Vegetation History and Archaeobotany* 12(3):187-204.
27. Fuller DQ & Hildebrand E (2013) Domesticating plants in Africa. *The Oxford Handbook of African Archaeology*, ed Lane PMaP (Oxford University Press, Oxford).
28. Harlan JR & De Wet JMJ (1972) A Simplified Classification of Cultivated Sorghum. *Crop science* 12(2):172-176.
29. Harlan JR (1989) Wild-grass seed harvesting in the Sahara and Sub-Sahara of Africa. *Foraging and Farming: The Evolution of Plant Exploitation*, ed Hillman DRHaGC (One World Archaeology, London).
30. Fuller DQ (2014) Finger Millet: origins and development. *Encyclopedia of Global Archaeology*, (Springer), pp 2783-2785.
31. Hilu K, De Wet J, & Harlan J (1979) Archaeobotanical studies of Eleusine coracana ssp. coracana (finger millet). *American Journal of Botany*:330-333.
32. Hilu KW & de Wet JM (1976) Domestication of Eleusine coracana. *Economic Botany* 30(3):199-208.
33. D'Andrea AC (2008) T'ef (Eragrostis tef) in ancient agricultural systems of highland Ethiopia. *Economic Botany* 62(4):547-566.

Date	**Animal**	**Location**	**Poaceae**	**Cyperaceae**	**Polygonaceae**	**Amaranthaceae**	**Boragenaceae**	**Caryophyllacea**	**Asteraceae**	**Fabaceae**	**Malvaceae**	**Other**	**Ref**
ca 40,000BC	Mammoth	Yamal	X	X								X	1
ca 32,000BC	Mammoth	Oyogos Yar	X	X				X	X			X	2
ca 16,500BC	Mammoth	Yakutia	X	X	X	X		X	X			X	3
ca 7500BC	Bison	Chukotka	X	X								X	4
ca 7000BC	Bison	Yakutia	X	X								X	5
ca 8500BC	Bison	Yakutia	X	X								X	6
ca 3400BC	Horse	Yakutia	X	X									7
3500-1200 BC	S, G, C*	Jordan	X			X	X		X	X	X	X	8
ca 2500BC	S, G, C	Maylan	X	X	X	X	X	X	X	X	X	X	9
ca 2000BC	S, G, C	Semirech'ye	X	X	X	X	X	X	X	X	X	X	10
ca 2000BC	S, G, C	Semirech'ye	X	X	X	X	X	X	X	X	X	X	11
ca 2000BC	S, G	Volga	X	X	X	X		X		X		X	12
ca 400-1BC	S, G, C, H	Semirech'ye	X	X	X	X	X	X	X	X	X	X	13
1984	S, G	Black Mesa	X	X		X							9
1984	S, G	Maylan	X	X	X	X		X	X	X	X	X	9
1998	Camalids	Andes	X	X	X	X				X	X	X	14
2011	S, G, C	Semirech'ye	X		X	X	X				X	X	8
2013	Red Deer	NE Poland	X	X	X	X	X	X	X	X		X	15
2013	Moose	NE Poland	X	X	X	X		X	X			X	15
2013	Bison	NE Poland	X	X	X	X		X	X	X		X	15
2015	C	Drenthe	X	X	X	X		X				X	16

*S-sheep; G-goat; C-cow; H-horse

Table SI-2: This table reports the results of paleofeces studies of extant and extinct megafauna. Grasslands, with their attendant diversity of forb communities, coevolved with megafaunal herbivores [17,18]. Further attesting to the time depth of this evolutionary link, fossilized seeds of *Berriochloa* grass were reported from the stomach contents of an extinct Miocene rhinoceros (*Teloceras major*) in Nebraska [19]. Ridley [20] reported preserved seeds from grasses and forbs in the frozen stomach contents of a mammoth. The analysis of the stomach contents of a frozen steppe bison from the early Holocene recovered along the Rauchua River in Chukotka revealed small herbaceous seeds from cold-tolerant grasses and sedges [4]. Many other frozen megafaunal mammals have provided similar seed-rich stomach contents, such as a horse from the region of Ust-Yana, Yakutia, Russia, which also contained tundra seeds of sedges and grasses [7]. The Yuka mammoth (ca. 32,000BC) contained seed from tundra vegetation, including Poaceae, Cyperaceae, Rosaceae, Ranunculaceae, Caryophyllaceae, among other familial clades [2]. Other studies of mammoth stomach contents have found similar results.

References

1 van Geel, B. *et al.* Palaeo-environmental and dietary analysis of intestinal contents of a mammoth calf (Yamal Peninsula, northwest Siberia). *Quaternary Science Reviews* **30**, 3935-3946 (2011).

2 Rudaya, N., Protopopov, A., Trofimova, S., Plotnikov, V. & Zhilich, S. Landscapes of the 'Yuka'mammoth habitat: A palaeobotanical approach. *Review of Palaeobotany and Palynology* **214**, 1-8 (2015).

3 van Geel, B. *et al.* The ecological implications of a Yakutian mammoth's last meal. *Quaternary Research* **69**, 361-376 (2008).

4 Kirillova, I. V. *et al.* An ancient bison from the mouth of the Rauchua River (Chukotka, Russia). *Quaternary Research* **84**, 232-245 (2015).

5 Boeskorov, G. *et al.* in *Doklady Biological Sciences.* 291-295 (Springer).

6 Van Geel, B. *et al.* Multiproxy diet analysis of the last meal of an early Holocene Yakutian bison. *Journal of Quaternary Science* **29**, 261-268 (2014).

7 Gravendeel, B. *et al.* Multiproxy study of the last meal of a mid-Holocene Oyogos Yar horse, Sakha Republic, Russia. *The Holocene* **24**, 1288-1296 (2014).

8 Fall, P. L., Falconer, S. E. & Klinge, J. Bronze age fuel use and its implications for agrarian landscapes in the eastern Mediterranean. *Journal of Archaeological Science: Reports* **4**, 182-191 (2015).

9 Miller, N. F. & Smart, T. L. Intentional Burning of Dung as Fuel: A Mechanism for the Incorporstion of Charred Seeds Into the Archaeological Record. *Journal of Ethnobiology* **4**, 15 (1984).

10 Spengler, R. *et al.* Early agriculture and crop transmission among Bronze Age mobile pastoralists of Central Eurasia. *Proceedings of the Royal Society of London B: Biological Sciences* **281**, 20133382 (2014).

11 Spengler III, R. N., Frachetti, M. D. & Fritz, G. J. Ecotopes and herd foraging practices in the steppe/mountain ecotone of Central Asia during the Bronze and Iron Ages. *Journal of Ethnobiology* **33**, 125-147 (2013).

12 Anthony, D. W. *et al.* The Samara valley project: Late Bronze Age economy and ritual in the Russian steppes. *Eurasia Antiqua* **11**, 395-417 (2005).

13 Spengler, R. N., Chang, C. & Tourtellotte, P. A. Agricultural production in the Central Asian mountains: Tuzusai, Kazakhstan (410–150 bc). *Journal of Field Archaeology* **38**, 68-85 (2013).

14 Hastorf, C. A. & Wright, M. F. Interpreting wild seeds from archaeological sites: a dung charring experiment from the Andes. *Journal of Ethnobiology* **18**, 211-211 (1998).

15 Schepers, M. & Van Haaster, H. Dung matters: An experimental study into the effectiveness of using dung from hay-fed livestock to reconstruct local vegetation. *Environmental Archaeology* **20**, 66-81 (2015).

16 Jaroszewicz, B., Pirożnikow, E. & Sagehorn, R. Endozoochory by European bison (Bison bonasus) in Białowieża Primeval Forest across a management gradient. *Forest ecology and management* **258**, 11-17 (2009).
17 Janzen, D. H. Differential seed survival and passage rates in cows and horses, surrogate Pleistocene dispersal agents. *Oikos* **38**, 150-156 (1982).
18 Janzen, D. H. Dispersal of small seeds by big herbivores: foliage is the fruit. *The American Naturalist* **123**, 338-353 (1984).
19 Voorhies, M. R. & Thomasson, J. R. Fossil grass anthoecia within Miocene rhinoceros skeletons: diet in an extinct species. *Science* **206**, 331-333 (1979).
20 Ridley, H. N. *The dispersal of plants throughout the world*. (Reeve, Ashton, Kent, 1930).

Table SI-3: Crop progenitor germinability post-digestion				
		Feeding studies*	Dung studies^	
Family	Crop progenitor/ relative+	% germinated post-ingestion (%viable) /%germinated control (viable)	# germinated or abundance	Ruminant
Amaranthaceae	*Amaranthus* sp.		Present[1]	*Ovies aries*
	Amaranthus albus	27(45)/83(93)[2]	6[3]	*Antilocapra americana*
	A. graecizans		Present[4]	Wild African ungulates
	A. retroflexus		2[3]	*Bos taurus* *A. americana*
Chenopodiaceae	*Chenopodium mucronatum*		Present[7]	*Ovies + Capra*
	C. album	40(52)/(76(87)[2]	2[3] 2627[5]	*B. taurus* *A. americana* Four deer species
	C. glaucum	10/7[6] 14/7[6]		*Bos grunniens* *O. aries*
	C. leptophyllum		2[3]	*A. americana*
Poaceae	*Avena fatua*	86(88)/85(93)[2]		*B. taurus*
	Brachiaria glomerate		Present[1]	*O. aries*
	Digitaria spp.		Present[4]	Wild African ungulates

	Elymus nutans	24/73[6] 15/73[6]		*B. grunniens* *O. aries*
	Eragrostis sp.		Present[1]	*O. aries*
	E. spp.		Present[4]	Wild African ungulates
	Hordeum bogdanii	~15/95[7]		*O. avies*
	H. jubatum	0(0)/58(87)[2]		*B. taurus*
	Panicum coloratum		Present[4]	Wild African ungulates
	Poa spp.	2-15/?[8]	Relatively abundant[9] Relatively abundant[10]	Various
	Pennisetum clandestinum	3.45/?[11]		*B. taurus*[8]
	Setaria viridis	14(17)/88(96)[2]		*B. taurus*
Polygonaceae	*Polygonum* sp.		Present[1]	*O. aries*
	P. aviculare		4[3]	*A. americana*
	P. convolvulus	15(63)/56(96) [2]		*B. taurus*
	P. viviparum	14/0[6] 0/0[6]		*B. grunniens* *O. aries*
	Rumex crispus	46/61[6] 29/61[6]		*B. grunniens* *O. aries*

*Feeding studies, see "Evidence for Endozoochoric Dispersal of Crop Progenitors" Some studies did not have a control sample of un- ingested seeds.

^Dung studies: *Relatively abundant* indicates that a greater number of seeds germinated from these species than would be expected given their abundance on the landscape, but an exact number was not reported. *Present* indicates that an unknown number of seedlings of this species or genus emerged from dung, usually because data was presented in pooled groups such as "grasses" or "forbs" in the publication.

Table SI-3: Feeding and dung studies where the progenitors or close relatives of small-seeded annual grain crops were found to be viable after endozoochoric dispersal by grazing megafauna. For a full review of studies on the effects of endozoochory on seed viability, see Jaganathan et al. 2016 in main references.

References

1 Milton, S. J. & Dean, W. Seeds dispersed in dung of insectivores and herbivores in semi-arid southern Africa. *Journal of Arid Environments* **47**, 465-483 (2001).

2 Blackshaw, R. E. & Rode, L. M. Effect of ensiling and rumen digestion by cattle on weed seed viability. *Weed Science* **39**, 104-108 (1991).

3 Wicklow, D. & Zak, J. Viable grass seeds in herbivore dung from a semi-arid grassland. *Grass and Forage Science* **38**, 25-26 (1983).

4 Anderson, T. M., Schütz, M. & Risch, A. C. Endozoochorous seed dispersal and germination strategies of Serengeti plants. *Journal of Vegetation Science* **25**, 636-647 (2013).

5 Eycott, A., Watkinson, A., Hemami, M.-R. & Dolman, P. The dispersal of vascular plants in a forest mosaic by a guild of mammalian herbivores. *Oecologia* **154**, 107-118 (2007).

6 Yu, X., Xu, C., Wang, F., Shang, Z. & Long, R. Recovery and germinability of seeds ingested by yaks and Tibetan sheep could have important effects on the population dynamics of alpine meadow plants on the Qinghai-Tibetan Plateau. *The Rangeland Journal* **34**, 249-255 (2012).
7 Wang, S. *et al.* Recovery and germination of seeds after passage through the gut of Kazakh sheep on the north slope of the Tianshan Mountains. *Seed Science Research* **27**, 43-49 (2017).
8 Cosyns, E., Delporte, A., Lens, L. & Hoffmann, M. Germination success of temperate grassland species after passage through ungulate and rabbit guts. *Journal of Ecology* **93**, 353-361 (2005).
9 Pakeman, R. J. Plant migration rates and seed dispersal mechanisms. *Journal of Biogeography* **28**, 795-800 (2001).
10 Jaroszewicz, B., Pirożnikow, E. & Sagehorn, R. Endozoochory by European bison (Bison bonasus) in Białowieża Primeval Forest across a management gradient. *Forest ecology and management* **258**, 11-17 (2009).
11 Wilson, G. & Hennessy, D. The germination of excreted kikuyu grass seed in cattle dung pats. *The Journal of Agricultural Science* **88**, 247-249 (1977).