Evidence of Selection for Rapid Growth in Traditional agroecosystems: Comparative reproductive ecology of wild and domesticated cassava

EVOLUTIONARY SCENE

PS2-13

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SUSPECT

***Manihot esculenta* Crantz ssp. *esculenta* ALIAS**

Domesticated cassava

Environment :

Amerindian slash-and-burn agriculture, the Guianas

● Ecological characteristics

Disturbances are predictable and have predictable traits
Large size (area of the field of cassava)
High intensity (complete removal of vegetation)
Predictable frequency (length of the fallow period)
Predictable timing of disturbance (at the beginning of the rainy season)

Environment is relatively resource-rich

High availability of water	(1) Seedlings germinate at the beginning of the rainy season (2) Slash-and-burn agriculture has enabled cassava to inhabit more humid environments than the wild ancestor
High availability of nutrients	Large amount of ash from the burning
High availability of light	Fields are cleared of most vegetation

Mixed reproductive systems in the fields:

Vegetative propagation by farmers

Traditional landraces are propagated strictly vegetatively by means of stem cuttings.

Spontaneous sexual reproduction

Sexual processes (open pollination of flowers, seed dispersal by ants, dormancy a germination of seeds) escape human control.
Farmers allow volunteer seedlings that appear to grow.

How do these two reproductive systems interact in evolution?

Regular incorporation of products of sexual reproduction in clonally propagated landraces

At the end of the cultivation cycle: Stem cuttings are prepared for the next crop using planted cultivars but also using plants that originated from volunteer seedlings. Only the most vigorous volunteer plants with agronomically interesting traits are incorporated in traditional landraces.

⇨ ***Repeated cycles of recombination and selection can permit accumulation of domesticated traits, as in seed-propagated crops***

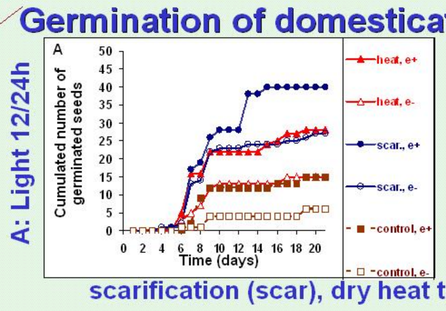
Has natural selection in agricultural ecosystems led not only to evolutionary maintenance of adaptive traits of seeds, seedlings and volunteer plants, but also to evolutionary modification of germination, growth and photosynthesis of domesticated cassava?

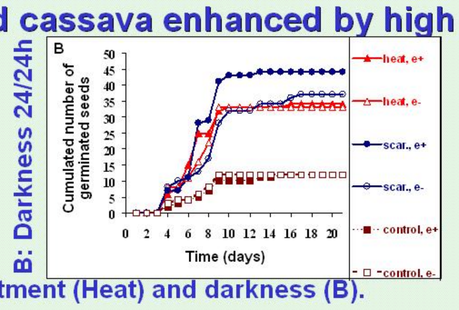
EVIDENCE 1

GERMINATION :

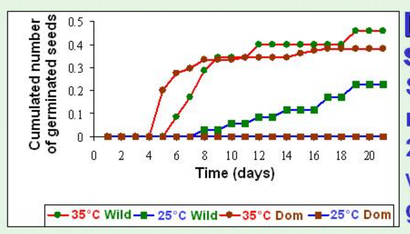
Breaking Physiological Dormancy of Cassava Seeds

Germination of domesticated cassava enhanced by high T°





scarification (scar), dry heat treatment (Heat) and darkness (B).



Domesticated cassava had a more stringent temperature requirement

Seeds of the domesticate germinated more rapidly at 35°C than those of wild cassava. At 25°C (temperature allowing some germination in wild cassava), no domesticated seeds germinated over a period of 21 days.

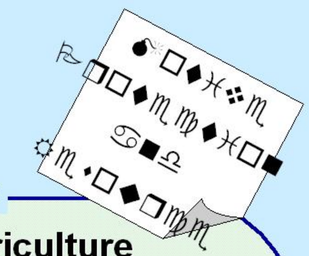
Adaptations to slash-and-burn cultivation?

This pattern suggests adaptation of dormancy to periodically disturbed habitats (predictable human removal and burning of vegetation cover)

WITNESS

Manihot pruinosa

ALIAS *Wild cassava*



CONCLUSION OF THE INVESTIGATION :

Domestication in slash-and-burn agriculture

Contrasting life history traits

Selection pressure acting on these two taxa have been sufficiently strong, and sufficiently divergent, to generate strong contrasts in traits of germination, growth and photosynthesis.

Contrasting ecology of wild and cultivated habitats

The difference in disturbance regime results from the reduction in variability of intensity and frequency of fires in cultivated habitats. In fields, disturbance is human-managed. Pyrophytic adaptations such as seed burial by ants and temperature-dependent physiological dormancy were conserved during domestication. Nevertheless, modification of plant traits appeared to follow the new optimal strategy of growth in traditional cultivation.

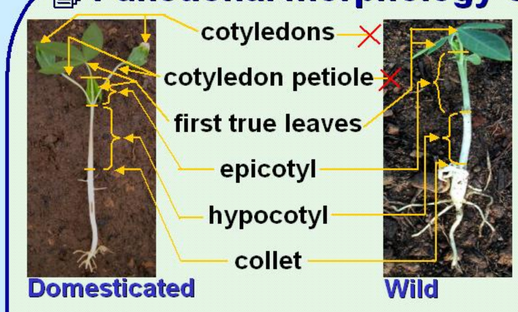
Contrasting life history strategies

Whereas the optimal strategy of wild cassava in savanna habitats is geared for conservation of acquired resources, the strategy of domesticated cassava is geared for rapid growth rate. This strategy is optimal in resource-rich habitats and in habitats where fire and other disturbances are managed by farmers.

EVIDENCE 2

Growth :

Functional morphology of seedlings



Contrasted development

In domesticated cassava, the hypocotyl elongated (epigeal germination) and cotyledons were phanerocotylar (emerged from the testa) and foliaceous whereas in wild cassava, the hypocotyl did not elongate (hypogeal germination) and cotyledons were cryptocotylar (enclosed in the testa) and reserve-type.

Fixed or plastic?

Field observations showed that the difference in hypocotyl length between wild and domesticate, detected in the experimental study, is a fixed trait. However, cotyledons of wild cassava seedlings that germinated from very shallow depth are foliaceous and photosynthetic. Their morphology is plastic, depending on the environment experienced by the germinating seed.

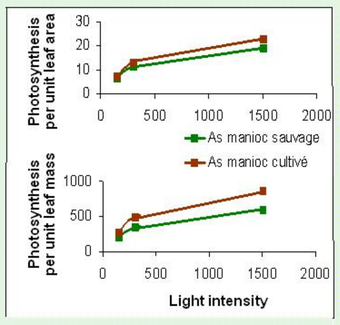
Adaptations to slash-and-burn cultivation

Epigeal germination and photosynthetic cotyledons confer higher growth rates, a pattern favoured by agricultural habitats, whereas wild cassava is adapted to fire- and drought-prone savannas, where hypogeal germination of buried seeds confers greater tolerance to risks facing above-ground parts.

EVIDENCE 3

PHOTOSYNTHESIS :

Leaf structure, gas exchange and nutrient use efficiencies



Differences in photosynthetic traits

CO_2 exchange rate, specific leaf area, nitrogen content and nitrogen use efficiency were greater in domesticated cassava, whereas leaf dry matter content and the ratio of carbon and nitrogen contents in leaves were higher in wild cassava.

Adaptations to slash-and-burn cultivation

Significant divergence in photosynthetic traits, especially in specific leaf area, may have been a key adaptation under domestication, during which selection favoured rapid growth in relatively resource-rich agricultural environments.