Paper 32

THE EVOLUTION OF TEMPERATURE ADAPTATION IN MAIZE AND BEANS: IMPLICATIONS FOR BREEDING IN COOL TEMPERATE ENVIRONMENTS

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ABSTRACT

Maize (*Zea mays* L.) and beans (*Phaseolus vulgaris* L.) are crops of tropical American origin and both have been cultivated for about 7000 years. Both crops reached temperate regions in the modern U.S.A. in pre-Columbian times.

The cultivated species of maize and beans and their close relatives, teosinte and wild beans, grow from under 800 m altitude to above 2500 m altitude in Mexico, and maize, cultivated beans and wild beans grow over a similar, wide altitudinal range in the Andean region. Temperatures differ markedly over these altitudinal ranges and races of cultivated maize and beans from different altitudes differ widely in temperature adaptation. From ecological principles, races of wild species from different altitudes should also differ in temperature adaptation.

The information on temperature adaptation and racial origin is integrated into a hypothesis which states:
- The genetic bases for differences in temperature adaptation in maize and cultivated beans were present in their wild relatives before domestication and were simply preserved after domestication.
- The genes necessary for the highest levels of adaptation to cool, temperate regions may occur at very low frequencies or even be absent in temperate zone races, if temperate zone races were not developed from highland races.

The implications of the hypothesis for maize and bean breeders in cool, temperate environments are discussed.

KEYWORDS

Low temperature adaptation, *Phaseolus*, *Zea*, evolution, plant breeding, teosinte, wild beans, race formation.

INTRODUCTION

Maize (*Zea mays* L.) and beans (*Phaseolus vulgaris* L.) are crops of tropical origin which are important in the economies of many temperate countries. Both these crops are regarded as warm season crops and are grown at temperate latitudes during the frost-free period between spring and autumn. In regions with a continental climate, these crops are usually affected by low temperatures only at the beginning and end of the growing season. In these continental regions, the development of short-season cultivars allows reliable crop production to occur during the period of favourable summer temperatures. · In some maritime, temperate environments, such as those of New Zealand, temperatures are lower throughout the growing season (Eagles, 1979), with considerable variation among seasons (Hardwick 1983, Eagles and Fordyce 1984). Periods of cool weather in maritime environments do not always cause visible injury, but may delay crop development to the extent that grain filling is not completed before the normal occurrence of autumn frosts (Hardwick 1983, Eagles and Fordyce 1984, Stamp 1984).

In this paper, the evolution and temperature adaptation of maize and of beans are reviewed, and a hypothesis is proposed to explain the distribution of low temperature adaptation in races of maize and beans. The implications of the hypothesis are discussed in relation to maize and bean breeding in cool, temperate climates.

CROP ORIGINS

Maize

Controversy still exists about the origin of cultivated maize, however, most botanical and archeological evidence suggests that maize was first domesticated in southern Mexico about 7000 years ago (Mangelsdorf 1974, Galinat 1985a, MacNeish 1985). A cultivated form of maize was grown in Peru about 4000 years ago, suggesting either an independent domestication or early introduction of maize to South America (Grobman and Bonavia 1978).

Although the exact nature of the wild ancestor of maize is still controversial, there is no doubt that the closest wild relative of maize is teosinte. Teosinte grows along the western escarpment of Mexico and Guatemala at altitudes between 800 m and 2500 m above sea level (Wilkes 1977).

Teosinte hybridizes readily with maize, and the hybrid is fully fertile.

Maize was introduced to temperate regions in pre-Columbian times, and became an important food plant for the people of the New England region of the modern United States (Griffin, 1978). The race grown in the New England region was the Northern Flint, which probably arrived about 1000 years ago (Brown and Anderson 1947). The Northern Flint race may have evolved from an eight-rowed race from northwestern Mexico (Mangelsdorf 1974, Galinat 1985b). From northwestern Mexico, it probably spread in a northeasterly direction across the modern United States, eventually reaching the New England region (Galinat and Gunnerson 1963). A second race, or racial complex, the Southern Dent, probably arrived in the southeastern modern United States after 1500 (Galinat 1985b). This race is similar to some races of low to intermediate altitudes of Mexico (Brown and Goodman 1977, Wellhausen *et al.* 1952).

The Corn Belt Dent race was produced in the mid-nineteenth century from crosses between the Northern Flint and Southern Dent races (Anderson and Brown 1952). Subsequently, extensive breeding programmes have produced highly productive hybrid cultivars from within the Corn Belt Dent race, with some use of the Northern Flint race in short-season, high latitude regions of North America and Europe (Goodman 1976).

Beans

The wild form of the common bean (*P. aborigineus*) grows at altitudes between 800 and 3000 m above sea level in Mexico and adjacent Central American countries (Mesoamerica), and at similar altitudes along the eastern slopes of the Andes from Venezuela to northwestern Argentina (Gentry 1969, Berglund-Brucher and Brucher 1976, Kaplan 1981).

Archeological evidence shows that domesticated forms of beans have been grown in both Mesoamerica and South America for at least 7000 years (Kaplan 1981). The actual location of the first domestication is still being debated and it is possible that common beans were domesticated independently in Mesoamerica and South America, and possibly at several locations in both regions (Harlan 1975).

Beans, like maize, were introduced to temperate regions of North America in pre-Columbian times and were grown as far north as the New England region of the modern United States (Griffin 1978). A diverse range of cultivars were grown before the advent of modern plant breeding (Hedrick 1931). Beans were taken to Europe during the sixteenth century and bean cultivation was widespread in Mediterranean countries by the seventeenth century (Evans 1980).

RACE FORMATION

Wild plants

The extensive studies of Clausen and his colleagues in the western United States have produced some definite conclusions about the formation of races in wild plants (Clausen *et al.* 1958). These are:
- To become widespread, a species must develop many ecological races.
- Ecological races develop in response to both biological and climatic factors.
- Relatively small climatic differences may result in statistically detectable differences among races.

Temperature differences between high and low altitude locations in Mesoamerica where both teosinte and wild beans are endemic are large enough to expect the development of very diverse physiological races. For example, at Tlaltizapan at 940 m altitude on the western escarpment of Mexico the mean maximum and minimum temperatures are 31 °C and 17 °C during July and August, the months of the major bean and teosinte growth, while at El Batan, at 2250 m altitude in the Valley of Mexico, the corresponding temperatures are 23 °C and 9 °C (Table 1). Both species have been collected at lower altitudes than Tlaltizapan and at higher altitudes than El Batan. Teosinte has been collected at 2600 m altitude near Amecameca (Wilkes pers. comm.), where temperatures are probably between those of El Batan and Toluca (Table 1).

Based on morphology and geographical isolation, six races of annual teosinte (*Zea mexicana* (Shrader) Kuntze) have been recognised in Mesoamerica (Wilkes 1977). These

Table 1. Mean monthly maximum and minimum temperatures (°C) during the summer growing season at Tlaltizapan (940 m elevation), El Batan (2249 m elevation) and Toluca (2640 m elevation) in Mexico.

Month	Tlaltizapan[1]		El Batan[2]		Toluca[3]	
	Max.	Min.	Max.	Min.	Max.	Min.
May	35	17	26	8	24	3
June	32	18	24	9	23	6
July	31	17	23	9	21	6
Aug.	31	17	23	9	21	6
Sept.	31	16	23	9	21	6
Oct.	31	14	23	6	21	3

[1] 1973-1977 CIMMYT unpublished data.
[2] 1973-1983 CIMMYT unpublished data.
[3] 1975-1983 CIMMYT unpublished data.

are Nobogame, Central Plateau, Chalco, Balsas, Huehuetenango and Guatemala. These races also differ in their chromosome knob and isozyme frequencies (Kato 1984, Doebley *et al*. 1984). Some authors have considered some of these annual teosintes to be separate species (Doebley and Iltis 1980), but this has been disputed (Kato 1984).

From Table 1 of Smith *et al*. (1984), each race occupies a limited altitudinal range, with the exception of the Balsas race, which grows from 800 m to 1600 m (Table 2). Probably, each of these races is physiologically adapted to differing climatic conditions, especially rainfall and temperature (Doebley 1984). Possibly, variation also occurs within these teosinte races for climatic adaptation, especially within Balsas, which is highly heterogeneous for isozymes (Smith *et al*. 1984).

Table 2. Altitudinal ranges for the six races of teosinte included in experiments of Smith *et al*. (1984).

Race	Number of collections	Altitudinal range (m)
Nobogame	2	1850-1850
Central Plateau	12	1700-2150
Balsas	29	800-1600
Chalco	19	2200-2500
Huehuetenango	6	1000-1510
Guatemala	6	1000-1000

Cultivated plants

Cultivated plants which are widespread develop physiological races in the same way as wild plants. However, in addition to the climatic and biological factors which influence race formation in wild plants, race formation is influenced by the preferences and migratory patterns of the human cultivators.

There is no doubt that a diverse range of cultivars of maize has been developed in Mesoamerica. This diverse range of cultivars has been classified into races (Brown and Goodman 1977). At first, the classification was based on morphological and geographical considerations, but later these were supplemented by studies of enzyme variation and chromosome morphology (Doebley *et al*. 1985, Kato 1984). In common with the races of teosinte, each race of maize occupies a limited altitudinal range, with no race growing in both highland and lowland areas (Wellhausen *et al*. 1952).

From a careful consideration of chromosome knob morphology, Kato (1984) concluded that maize was almost certainly domesticated from teosinte in Mesoamerica and that domestication probably occurred independently at several locations from distinct teosinte populations. This implies that differences in temperature adaptation among races of maize may be due, at least in part, to the particular teosinte population from which the various races were derived. It also implies that teosinte preceded maize in Mesoamerica, a conclusion supported by the ecological studies of Deobley (1984).

The classification of beans into races lags behind the work on maize, but there is no doubt that cultivated beans are morphologically diverse and that landraces differ in their adaptation to climatic conditions (Gentry 1969, Kaplan 1981, Laing *et al*. 1984).

Temperature adaptation

Substantial evidence exists in both maize and beans for highly specific temperature adaptation.

For beans, Laing *et al*. (1984) grew cultivars collected at a range of altitudes at high, mid and low altitude sites in Colombia. The crops were grown with irrigation, fertilizer and crop protection to minimize environmental differences among sites other than temperature. Cultivars collected at high altitudes produced high seed yields at the high altitude site but low seed yields at the low altitude site, while cultivars collected at low altitudes produced high seed yields at the low altitude site but negligible seed yields at the high altitude site.

Experiments in Mexico with maize have produced similar results (CIMMYT 1974). Lowland races grew very slowly, if at all, and were chlorotic when grown at the highland Toluca station, while highland races produced very low grain yields at the lowland Poza Rica station (G.O. Edmeades, CIMMYT, personal communication).

Limited controlled environment studies have been conducted to compare the temperature responses of highland tropical, lowland tropical and temperate zone races. Most of these have been conducted at the early vegetative growth stage, especially with maize, because of the high cost of growing large plants in controlled environment facilities. This means that important traits associated with floral fertility and grain filling have rarely been studied.

Controlled environment studies with maize at the vegetative growth stage have consistently shown that races from high altitudes of Mesoamerica and the Andes are better adapted to cool conditions than races from low altitudes of the tropics (Duncan and Hesketh 1968) or from the temperate zone (Hardacre and Eagles 1980, Eagles and Brooking 1981, Eagles *et al*. 1983, Hetherington *et al*. 1983, Stamp 1984).

Origins of temperature adaptation

The information presented in the previous sections on crop origins, races and temperature adaptation will now be integrated into a hypothesis, in two parts, and each part of the hypothesis discussed separately.
1. The genetic bases for differences in temperature adaptation of cultivated maize and beans were present in their wild relatives before domestication and were simply preserved after domestication.
2. The genes necessary for the highest levels of adaptation to cool, temperate regions may occur at low frequencies or even be absent from temperate zone races if temperate zone races were not developed from highland races.

The evidence presented for Part 1 of this hypothesis is

circumstantial and is based on the known distribution of wild populations of teosinte and beans in Mesoamerica. This part of the hypothesis has been developed from the hypothesis of multiple domestication (Harlan 1975, Kato 1984) but it is compatible with the hypothesis of a single, unique domestication followed by the introgression of genes from wild populations to provide adaptive divergence.

Part 1 implies that genes determining adaptation to temperature are conservative; and that new alleles, conferring improved adaptation to specific temperature conditions are not likely to evolve rapidly within the cultivated species.

Individual gene loci determining temperature adaptation have not been identified, but studies comparing isozymes in maize and teosinte have shown that few new isozymes have been found in maize which are not present in existing populations of teosinte (Doebley et al. 1984, Smith et al. 1985), supporting the hypothesis of a conservative rate of evolution at enzyme loci with important biochemical functions. Assuming that wild beans and teosinte are ancient species, then natural selection for allele frequencies producing maximum fitness under prevailing temperature conditions must have occurred for long periods of time, much longer than the 7000 years since domestication.

Part 1 implies that cultivated maize and beans are unlikely to be important crops outside the range of temperature adaptation of their wild ancestors. Because of the reduction in competition from other species for a cultivated annual compared to a wild annual, some expansion of temperature range is expected. However, an examination of the worldwide production and adaptation data of Shaw (1977) for maize and the Latin American production and adaptation data of Laing et al. (1984) for beans, indicates that neither crop has become important in environments much warmer or cooler than those present within the range of teosinte and wild beans in Mexico.

More substantial evidence for Part 1 could be obtained by growing collections of teosinte and wild beans from different altitudes at a range of temperatures in controlled environment facilities and at different altitudes in Mexico or an Andean country. Genetic evidence could be obtained by crossing populations of wild and cultivated species and then observing segregating patterns for temperature adaptation in F_2 and other segregating generations. This proposal could be criticised on the basis that parallel variation in adaptation in wild and cultivated species simply reflects a high level of reciprocal introgression, or introgression predominantly from cultivated to wild populations. This criticism cannot be completely discounted; however, Kato (1984) has shown that some chromosome knobs occur in teosinte which do not occur in maize growing in the same location. Because these chromosome knobs are not always present in teosinte, and therefore are unlikely to be closely linked to gene complexes controlling the essential traits differentiating maize from teosinte, Kato (1984) concluded that introgression of genes from maize to teosinte must be absent or at least occur at a very low frequency. Doebley (1984) supported the conclusion of Kato (1984) and showed that the morphological and adaptive diversity present in teosinte could be explained by ecological principles.

The basic premise for Part 2 of the hypothesis is that alleles conferring maximum fitness under cool conditions are different from those conferring maximum fitness under warm conditions. The circumstantial evidence from racial adaptation studies support this hypothesis, but there is no direct evidence because the gene loci important for determining temperature adaptation have not been identified. Genetic differences for low temperature adaptation in maize appear to be polygenically inherited (Eagles, unpublished), in common with other chilling sensitive species (Paull et al. 1979), suggesting that individual loci may be difficult to locate with existing genetic technology.

There is little doubt that the wild ancestors of maize and beans did not grow in temperate regions of North America and that maize and beans were introduced as cultivated species from Mesoamerica. The genetic changes which produced races capable of successful cultivation in the New England region is unclear, but for maize, archaeological data suggest that it may have involved introgression of genes from teosinte into the Chapalote race (Galinat and Gunnerson 1963). Chapalote is an ancient race predominantly from low altitudes (Wellhausen et al. 1952), but the genetic nature of the teosinte is unknown. From geographical considerations, the teosinte may have come from northwestern Mexico, and may still be represented by the teosinte population at Nobogame. Further isozyme and chromosome knob studies may help to clarify this situation.

Practical implications

For the applied plant breeder, the hypothesis developed in the previous section implies that high altitude races should be the best sources of genes for improving the adaptation of maize and beans to cool, temperate environments. The hypothesis also implies that teosinte and wild beans may contain desirable alleles not transferred to the cultivated species. However, races adapted to high altitude tropical regions have not been improved to the same extent as modern temperate zone cultivars for important agronomic traits such as lodging resistance.

As an alternative to using high altitude races, the applied breeder could improve the low temperature adaptation of elite, temperate zone populations by recurrent selection. This method assumes that the alleles required for improving temperature adaptation are present in temperate races, although possibly at low frequency, or are generated by mutation during plant breeding time scales. For maize, there is definitely genetic variability present in Corn Belt Dent populations for tolerances to low temperatures during the early stages of growth (Mock and Eberhart 1972) and this responds to recurrent selection procedures (Mock and Bakri 1976). However, it is not yet known whether the populations produced by recurrent selection are as tolerant to low temperature as highland

tropical material.

Some recent field studies with beans in England and maize in New Zealand have shown that the use of maize and beans from tropical regions may not be as difficult as photoperiod and seasonal temperature patterns may suggest. In England, cultivars of beans identified in controlled environment studies as cold tolerant and of Central and South American origin produced higher and more stable seed yields than cultivars from North America (Andrews *et al.* 1983). In New Zealand, a maize hybrid produced using an inbred line from highland Mexican germplasm as one parent produced grain yields and grain moisture levels comparable to those of elite hybrids in most seasons and was superior in a particularly cool season where grain filling was not completed by many hybrids during the normal growing season (Eagles and Fordyce 1984, Eagles and Hardacre 1985).

At this stage, it is impossible to determine whether an applied plant breeder should work entirely within highland tropical races, entirely within temperate races, or within populations synthesized from both types of germplasm. The situation is further complicated because Mesoamerican and Andean races may be genetically distinct, and for maize, where hybrids are possible, heterotic combinations may extend the range of temperature adaptation beyond the levels possible in random mating populations. Some of these questions are currently being investigated with maize in our research programme at Palmerston North.

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SYMPOSIUM DISCUSSION

Dr A.D.H. Brown, CSIRO, Canberra

What are you going to do with the teosinte races you have.

Eagles

I would like to find out if they really are adapted to specific temperature environments, by growing them in controlled environment facilities under different temperatures — a similar cross-over experiment to the one Laing did in Columbia with beans. I would also like to cross them with material of our own, both of highland tropical origin and temperate origin, and look at the distribution patterns which occur in the F2. But I am not sure if we have the resources to do it, or if it is worthwhile.

Dr R.L. Cuany, Colorado State University

Do you not think there is a lot of evidence that some of the European non-temperate races may have come from highland tropical material brought by the Spaniards, probably to a greater extent than any highland origin might have come into the Canadian flints?

Eagles

I have never seen any temperate zone material that looks like highland tropical material.

Cuany

It seems that Spaniards did a lot of collecting from the mountains, and they probably took seed of many races back to Europe. Do you think the European plants have no relationship to the highland races?

Eagles

I do not think it has been studied extensively enough to know. It seems to me that most temperate zone cultivars are from cornbelt dent which came from a cross between northern flint and southern dent races, or it is cornbelt dent back to northern flint. Most of the European material that I have brought into my programme looks like northern flint — 8 row with the same kernel shape and the same plant shape. Races from the highlands of Mexico look quite different.